NORTH AMERICAN FRESHWATER MUSSELS

Natural History, Ecology, and Conservation

WENDELL R. HAAG

CAMBRIDGE

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Interest in freshwater mussels is growing for two important reasons. First, freshwater mussels are among the most endangered organisms on Earth, and many species are already extinct or face imminent extinction. Their desperate conservation plight has gained intense interest from natural resource agencies, nongovernmental conservation organizations, academia, and industry, and mussels are now the centerpiece of conservation initiatives ranging from local watershed groups to global programs. Second, recent research on mussel ecology, spurred in large part by the needs of the conservation community, has revealed much about the remarkable life history of these animals.

This well-illustrated book highlights freshwater mussels' fabulous diversity, amazing array of often bizarre ecological adaptations, and the history and causes of their decline. Summarizing and synthesizing historical and contemporary information as well as original research and analysis, the book builds a cohesive narrative culminating in the development of explicit frameworks to explain pervasive patterns in mussel ecology. The book dispels the notion that all mussel species are ecologically equivalent and shows how their diverse life history strategies influence assemblage structure, vulnerability to human impacts, and probability of extinction.

The fascinating and colorful role of mussels in human society is also described in detail, including the little-known pearl button industry of the early 1900s and the wild and often violent shell harvests of the 1990s. The final chapter details humans' efforts to save these fascinating animals and gives a prognosis for the future of the North American fauna.

The book provides the first comprehensive review of a wide variety of topics in mussel ecology and conservation for scientists and natural resource professionals in aquatic ecology, conservation biology, fisheries management, and evolutionary biology as well as for freshwater biology students and natural history enthusiasts.

WENDELL R. HAAG is a research fishery biologist with the U.S. Forest Service in Oxford, Mississippi. His research on freshwater mussels has spanned 25 years and has explored an array of topics, including life histories, fish-host relationships, age and growth, biogeography, sampling methods, population dynamics, and conservation issues. In 2008, he was recipient of the Presidential Early Career Award for Scientists and Engineers, presented at the White House. He has published more than 50 peer-reviewed papers, book chapters, and technical reports as well as a number of popular articles.

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This book is dedicated to the small but growing group of people worldwide who have devoted themselves to the study and protection of freshwater mussels. These people come from diverse backgrounds but are united in their abiding affection for the unsung bivalved treasures of our rivers and lakes.

As a rule . . . we have to take nature as we find her, and for those who expect always to find a raison d'être for each creature, this nursing of the yellow sand shell by the voracious gar will satisfy the belief that things are as they should be.

Arthur D. Howard, 1914:44

After people have destroyed all people everywhere, I see heaping mounds of money strewn over the earth, floating on and sinking into the sea. The animals and fish, who have no use for money, are kicking it out of the way and splattering it with dung. Money and stink, the stink of dung, the stink of money, so foul that in order for the flowers to get a breath of fresh air, the winds will come together and whip the sea into a rage, and blow across the land. Then the green leaves of trees, and grass, will give up their chlorophyll, so that the sea, the wind, the beasts, and the birds will play and sing Nature's old, sweet melody and rhythm.

Duke Ellington,
Music Is My Mistress, 1973

Contents

The color plate section follows page 214.

Preface

"Why do you want to study mussels? They don't do anything."

This question was posed to me as an undergraduate student by one of my great natural history mentors, who was interested in salamanders, orchids, and other more flashy creatures and who thought mussels were little more than living rocks. Granted, at first glance, mussels are not the most dynamic animals. But his question deflated me only briefly because by that time, I had come firmly under the spell of freshwater mussels. I'm not the only one; mussels have fascinated people for thousands of years. Prehistoric people used mussel shells and pearls to adorn themselves and their dead, and they ate prodigious quantities of mussels. During the natural history craze of the 1800s, mussels were a particular obsession of many Victorian naturalists, who amassed great collections of shells. In recent times, interest in mussels has burgeoned along with the growth of environmental and conservation professions. Lots of people just seem to like mussels, and they often get dangerously hooked.

Why are mussels so fascinating? As odd as it may sound, I think mussels have a certain aura of mystery. The idea of a great but unsung fauna hidden in the gravel of rivers in our very backyards is compelling to many people. When I was about 10 years old, my family was camping along the Red River not far from our home in Lexington, Kentucky. While wading in the river, I stumbled onto a bed of freshwater mussels. I was stunned. I thought shells could only be found at the faraway ocean and had no idea such exotic gems lived in my own neighborhood. I took some shells home and set them on my desk alongside my seashells from the beach. Like me, many people are intrigued first by mussel shells: "the most careless observer could not but be struck with their beauty, and led to admire their rich pearly luster, and variegated surface. But the more carefully they are inspected, the more beauties he will find to attract his attention and call forth his wonder" (Hildreth 1828, 276).

Although we may be drawn initially to the beauty of their shells, the more we learn about mussels, the more surprises they reveal. First, one discovers the staggering diversity of mussels in North America, home to more than 300 species – the most diverse mussel fauna on Earth. Second, one learns of the complex life histories of mussels, especially the remarkable host-fish relationship that includes elaborate mimicry and other bizarre strategies to attract the hosts necessary for survival of mussels' parasitic larvae. Living rocks indeed! Finally, one comes to the sad realization that these unique animals that have captivated so many people are disappearing rapidly.

The purpose of this book is to tell the story of freshwater mussels in both an ecological and human context, an endeavor that was not possible until recently. Thirty years ago, we knew virtually nothing about the basic ecology of freshwater mussels. With a few notable exceptions, mussel research prior to that time had focused on the important and necessary tasks of naming and classifying species and determining their geographical distributions. These pursuits usually involved collecting mussels, getting rid of the "meat" as quickly as possible, and whisking the shells away to museum drawers. Students of mussels during this period often tellingly referred to themselves as "conchologists" (those who study shells). This historical focus on shells is at least partially responsible for the long-standing perception of mussels as living rocks or, at best, quaint natural history curios. But during the last 30, and especially in the last 10–15, years, ever-increasing numbers of dedicated biologists have been spending long, cold hours with their faces in the water, studying mussels on their own terms. Only through these efforts has the story of the animals themselves finally begun to emerge.

This is essentially a natural history book. I don't use the term *natural history* in the old-fashioned or derogatory sense, which usually implies a lack of serious ecology or scientific rigor; rather, I use a definition proposed by Herman (2002, 934): "Natural history is the scientific study of plants and animals in their natural environments. It is concerned with levels of organization from the individual organism to the ecosystem, and stresses identification, life history, distribution, abundance, and inter-relationships. It often and appropriately includes an esthetic component." This succinctly describes what I will attempt to cover in this book (with the exception of identification). I agree that an aesthetic component is appropriate in a work such as this, at least in some places. People are drawn to mussels because they are beautiful and interesting. And one of the reasons we seek to conserve these animals is that we've made an aesthetic decision that they're worth having around in the future.

The book begins with an introduction to mussel ecology, followed by a discussion of diversity and biogeography at large scales. Next come several chapters dealing with specific aspects of mussel ecology and life history. This is followed by a discussion of how these factors interact to structure mussel assemblages and determine species' distributions and abundance. The book closes with three chapters on interactions between mussels and humans, including our efforts to exterminate them (wittingly and unwittingly) and our efforts to save them. This section is last because how successful we are in conservation depends, of course, on how well we understand mussel ecology. Furthermore, it is unavoidable that we will be forced to make some painful decisions about conservation in the future. Because conservation is a uniquely human concern (as far as we know), these decisions will be based not only on objective scientific criteria and pragmatic realities but also on subjective, aesthetic values.

There are several purposes this book does not attempt to serve. This book is not a field guide to identification or a manual of field and laboratory methods; a number of excellent resources on these topics exist elsewhere. For the same reason, I do not delve deeply into mussel anatomy, physiology, or toxicology, except where these topics have direct bearing on ecology, natural history, or conservation (e.g., how physiological adaptations for desiccation resistance allow some species to persist in ephemeral habitats or the potential role of agricultural chemicals in mussel declines). I also focus mainly on the North American fauna, although I bring in findings from elsewhere in the world as appropriate. With the exception of the small European mussel fauna, we currently know much less about the ecology of mussels on other continents than we do about those in North America.

I certainly don't think I'll be able to tell the whole story of freshwater mussels or get it all right in this book. The study of freshwater mussel ecology is still in its infancy. My goal in telling this story now is to put disparate pieces of information about mussels into something of a cohesive framework for anyone interested in natural history and to assist future researchers in framing specific hypotheses about mussel ecology. By doing so, I hope this book will foster increased interest and research about freshwater mussels that will help to save these marvelous animals.

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Many people within the freshwater mussel community and beyond have helped with this book directly or indirectly, but the following people deserve special mention. Mel Warren has been a faithful colleague, mentor, and friend for the last 20 years, and he created a work environment in which undertaking a task such as this was not only possible but encouraged. During the writing of the book, he was a patient and enormously helpful sounding board for an endless array of off-the-wall ideas and questions, and he read and provided valuable comments on several key chapters. Bob Butler read the entire manuscript. His meticulousness and insight as an editor are unsurpassed, and he probably knows as much about freshwater mussels as anyone; he improved this book immeasurably. Guenter Schuster was my first great mentor on freshwater mussels and is largely responsible for setting me (as well as countless others) on a deeply fulfilling career path; he also read and commented on much of the book. Amy Commens-Carson was a staunch ally throughout all phases of the work: locating obscure literature, managing the swelling bibliography, reading and providing comments on much of the text, and preparing final versions of all the figures. Carla Atkinson, Tom Augspurger, Dave Berg, Robert Bringolf, Greg Cope, Jeff Garner, Don Hubbs, Paul Johnson, Greg Patton, Bernard Sietman, Caryn Vaughn, and Jim Williams graciously provided insightful comments on selected chapters and helped in other ways. Any errors or unsound reasoning in the book were likely pointed out by these people at some point, and the blame for their retention is solely mine.

For the use of their wonderful mussel photographs and other courtesies, I owe special thanks to David Aldridge, Chris Barnhart, Paul Freeman, Paul Frese, David Herasimtschuk, Paul Johnson, Jess Jones, Jacqueline Madill, Andre Martel, Jeremy Monroe, Ethan Nedeau, Christine O'Brien, Allan Oman, John Ratcliff, Bill Roston, Robert Scholl, Bernard Sietman, Jim Stoeckel, Keith Sutton, and Barry Wicklow. In particular, I thank Dick Bryant for his patience and generosity while working with me on the shell photos; his simple, elegant images are truly works of art that bring out the subtle beauty of freshwater mussels. With regard to the shell photos, I would also like to thank Kevin Cummings and Tom Watters for loaning me mussel specimens from the collections in their care. Thanks also to the following institutions or people for providing the fascinating historical photographs: Alabama Power Company; Augustana College; Robert Baker; Timothy Pearce, Carnegie Museum; the Public Library of Cincinnati and Hamilton County and the Cincinnati Historical Society; Davenport (Iowa) Public Library; Muscatine (Iowa) Arts Center; Musser Public Library (Muscatine, Iowa); University of North Carolina at Chapel Hill; Tennessee Valley Authority; and U.S. Geological Survey Central Region Library (Denver, Colorado). The selfless efforts of Art Bogan, Kevin Cummings, Christine Mayer, and Tom Watters in maintaining the freshwater mollusk bibliography (http://ellipse.inhs.uiuc.edu:591/mollusk/) and mussel–host databases (http://www.biosci.ohio-state.edu/~molluscs/OSUM2/) have made my life and those of many other researchers much easier.

Many other people generously fielded questions and inquiries – often with little context – or provided important information. For this, I thank the following people and apologize to those I've inadvertently omitted: Susie Adams, Steve Ahlstedt, Paul Angermeier, Art Bogan, Sherry Bostick, Michael Buntin, Kevin Cummings, Chris Davidson, Ron Dimock, Ryan Evans, Steve Fraley, John Fridell, Dan Graf, John Grizzle, John Harris, Paul Hartfield, Hill Grove Missionary Baptist Church, Mark Hove, John Jenkinson, Bob Jones, Kody Kuehnl, Bernie Kuhajda, Jim Layzer, Rachel Mair, Bill Matthews, Chris Mayer, Stuart McGregor, Bill Posey, Charles Randklev, Andy Roberts, Kevin Roe, Andrew Rypel, Tim Savidge, Dan Spooner, Michael Stewart, Dave Strayer, Matt Thomas, Mark Vogel, Nathan Whelan, and Greg Zimmerman. I also would like to thank my other coworkers at the U.S. Forest Service for helping and supporting me in many ways on this project: Mickey Bland, Cathy Jenkins, Ted Leininger, Erynn Maynard, Liz McGuire, Gordon McWhirter, Anthony Rietl, and Leann Staton.

Most authors of books ultimately thank their families, and now I understand why. My wonderful wife, Jennie, and spectacular children, Lila Grace and Henry, encouraged and supported me throughout the preparation of this book and – especially in the final throes – patiently endured an often absent or distracted husband and daddy. Finally, my parents, Jim and Katie Haag, and my grandparents instilled – and later tolerated – an obsession with natural history that has resulted in a most satisfying life.

WRH
Oxford, Mississippi

Chapter 1

Introduction to mussels and mussel ecology

Freshwater mussels are a conspicuous and important element of aquatic ecosystems in much of North America and throughout the world. Mussels are bivalve mollusks and, generally speaking, are built much like marine bivalves. Most people today associate bivalves exclusively with marine systems and aren't aware that bivalves live in freshwater at all. Part of the reason for this is that mussels have disappeared from many rivers and lakes in the last 100 years. However, mussels remain abundant in many places and can occur at densities greater than 100 animals per square meter. Freshwater mussels also are a surprisingly diverse group of animals. North America has the richest fauna on Earth, with more than 300 species, but Southeast Asia and Central America also have greater than 100 species (Graf and Cummings 2007).

People in the past had a greater awareness of these animals. Prehistoric Americans made great use of mussels. They ate them, used mussel shells and pearls to make jewelry and implements, and tempered pottery with lime slaked from the shells (Chapter 9). Mussels also were well known to people in historical times. Pearl hunting and the mother-of-pearl button industry employed thousands of people during the first half of the twentieth century, and nearly everyone wore clothing with shell buttons. People have adorned their graves with mussel shells, paved roads with them, and fattened hogs on mussel meat. The Cherokees referred to mussels as *dagvna* and to Muscle (Mussel) Shoals on the Tennessee River as *dagvnahi* or *dagunawelahi*, which means "place of mussels" (Bright 2004). Shell Creek, Nebraska, was named from the Pawnee word *skā pĭr 'ĭ ūs kĭts' ū*, meaning "shell water" (from *skā pĭr rūs*, "clamshell"; Grinnell 1913), and the Rio Concho, Texas, named by early Spanish explorers, means "river of shells." Across North America, the abundance of place-names referring to freshwater mussels (Table 1.1) attests to the indelible impact these animals have had on the cultural landscape and shows how plentiful and conspicuous mussels must have been.

The main reason people today know about mussels is because of the recognition that we are rapidly losing this unique part of our natural and cultural heritage. Within

Table 1.1. *Place-names in North America likely referring to freshwater mussels*

Place	U.S. states and Canadian provinces
Clam Brook	NF (2)
Clam Cove	NV
Clam Creek	AK, MB, MT, ON
Clam Falls	WI
Clam Lake	AK (3), BC, CO, MA, MB, MI (2), MN (3), MT, NS (2), ON (4), SK, WI (2)
Clamshell Lake	MN, ON (2), NS
Clamshell Pond	MA, NH, NY
Clam River	MA, MI (2), NF (2), WI
Mussel	AL
Mussel Bar	AR
Mussel Bayou	LA
Mussel Brook	NF
Mussel Creek	AL, BC, MO, SC
Mussel Fork	MO
Mussel Lake	OR, MS
Mussel Run	NC, TX
Mussel (Muscle) Shoals	AL (2), KY (2), MO, OK, TX
Mussel Slough	CA
Mussel Swamp	VA
Mussel Point	AR
Musselshell River	MT
Musselshell Creek	ID, NC, MN
Pearl Bayou	MS
Pearl Branch	AR, KY, MO (2)
Pearl Brook	MA, NJ
Pearl Creek	AB, AK (3), CO (2), ID (5), LA, MN, MT, NE, NV, NY, ON (2), OR, SD (2), SK (2), WA (2), WI
Pearl River	LA/MS, NF, ON
Pearl Island	ID, IL, IN, KY
Pearl Lake	AB, BC, CO, CA (2), GA, ID, IL, MB (2), MI (3), MN (5), MT (2), ND, NF, NH, NY, ON (8), OR, PA, QE (3), SD, SK, TX, UT, WI (2)
Pearl Pond	KY, ME (3)
Shell Branch	OK, TN
Shell Brook	ON, SK
Shell Creek	AL, BC, GA, ID, TN, MB, MN, NE, OK, WY, YT
Shell Lake	AK, BC, CA, GA, IN, MB (3), MI, MN, MS, NE, ND, OK, ON (2), SK, WI, WY
Shell Lake Slough	AR
Shell Pond Brook	NH
Shell Pond	NF
Shell Run	IN, VA, WV
Shell River	MB, MN

Note: Names from coastal areas are not included because they likely refer to marine bivalves (e.g., Mussel Point, Clam Rock). Numbers in parentheses indicate multiple place-names in a state or province. Data from Geographic Names Information System, U.S. Geological Survey (http://geonames.usgs.gov/), and Geographical Names of Canada, Natural Resources Canada (http://geonames.nrcan.gc.ca/).

the last 100 years, we've already lost forever 30–40 species, and many more are highly vulnerable to extinction in the near future (Chapter 10). Understanding the ecology of freshwater mussels is central in our efforts to save what's left. Highlighting the fascinating ways mussels go about their lives and the vital ecological role they play also will help increase awareness and concern for these animals.

1.1. Terminology

A few notes on terminology are necessary at the outset. When I say *mussels*, I am referring to freshwater bivalves of the order Unionoida, and I will mostly be discussing the North American fauna (north of Mexico), which includes the families Unionidae and Margaritiferidae. The order Unionoida contains about 85 percent of all freshwater bivalve species worldwide, and nearly 70 percent are members of the family Unionidae (Section 1.2).

The name "mussels" is somewhat confusing. When I tell people I study mussels, or when someone asks why I'm lying in a stream with my face in the water, almost invariably, the first question they ask is, "Can you eat 'em?" The answer is, "Yes . . . well, maybe," but we'll talk about that in Chapter 9. If there is a second question, often it is, "What's the difference between a clam and a mussel?" In marine waters, these terms are somewhat distinct and therefore useful: *clam* usually refers to an infaunal bivalve that burrows into the bottom (e.g., hard clam, *Mercenaria mercenaria*), and *mussel* refers to an epibenthic bivalve that attaches itself to hard substrates (e.g., blue mussel, *Mytilus edulis*). This convention is followed for some freshwater bivalves, including fingernail clams (Sphaeriidae) and Asian clams (*Corbicula*), which burrow, and zebra mussels (*Dreissena*), which attach onto hard objects. Unfortunately, and for reasons unknown to me, the Unionoida are usually referred to as mussels even though they burrow into the substrate like marine clams, but the terms *mussel* and *clam* are often used interchangeably. Prior to the 1970s, scientists referred to freshwater mussels as *naiads* or *najades*. In Greek mythology, Naiads were nymphs who inhabited and gave life to fresh waters. A Naiad was intimately connected to a specific body of water, and her existence depended on it; if a stream dried up, its Naiad expired. Clearly "naiad" is a fitting name for freshwater mussels. Unfortunately, naiad is already applied to the larvae of several aquatic insects as well as to aquatic plants of the genus *Najas*.

So what should we call them? The logical thing would be to start calling them *freshwater clams* owing to their burrowing habits, but this would just confuse everyone. In this book, I will follow common and long-standing usage and refer to our subjects as *freshwater mussels* or, simply, *mussels*, even though this terminology is arbitrary. I once asked my grandfather whether the familiar roadside animal should be called a groundhog or a woodchuck. He replied, "It should be called a groundhog because that's what it is." You can't argue with that, so call them what you like.

Table 1.2. *Freshwater representatives in the class Bivalvia worldwide*

Major groups	Families	Number of genera	Number of species	Native distribution
Subclass Protobranchia[1]	–	0	0	–
Subclass Pteriomorpha				
Order Arcoida	Arcidae	1	4	OL
Order Mytiloida	Mytilidae	3	5	AT, OL
Subclass Paleoheterodonta				
Order Unionoida	Etheriidae	4	4	AT[2]
	Hyriidae	17	71	NT, AU
	Iridinidae	6	43	AT
	Margaritiferidae	3	12	PA, NA, OL
	Mycetopodidae	12	36	NT
	Unionidae	142	674	PA, NA, AT, NT, OL, AU
Subclass Heterodonta				
Order Veneroida	Cardiidae	2	5	PA
	Corbiculidae	3	6	PA, AT, OL, AU
	Sphaeriidae	5	196	PA, NA, AT, NT, OL, AU
	Dreissenidae	3	5	PA, AT
	Solenidae	1	1	OL
	Donacidae	2	2	AT
	Navaculidae	1	2	OL
Order Myoida				
	Corbulidae	1	1	PA
	Erodonidae	2	2	AT, NT
	Teridinidae	1	1	NT
Order Anomalodesmata				
	Lyonsiidae	1	1	NT

Note: List includes all subclasses of bivalves but shows only orders and families with freshwater representatives. Abbreviations for distribution refer to major biogeographical regions: PA, Palearctic; NA, Nearctic; NT, Neotropical; AT, Afrotropical; OL, Oriental; AU, Australasian (classification adapted from Giribet 2008; data from Bogan 2008 and Graf and Cummings 2007).

[1] Includes Nuculanoidea

[2] Putative Etheriids also occur in the Neotropical and Oriental regions, but the taxonomic placement of these species is uncertain (Graf and Cummings 2007).

1.2. Freshwater mussels in the context of global bivalve diversity

The class Bivalvia contains approximately 20,000 living species worldwide, the vast majority of which are marine; only about 1,000 species live strictly in fresh waters (Haszprunar et al. 2008). However, freshwater representatives occur in most major bivalve groups and in 19 families (Table 1.2), indicating that there have been multiple, independent bivalve invasions of fresh waters around the world. Most bivalve groups contain few freshwater members; 13 of the 19 families with freshwater representatives

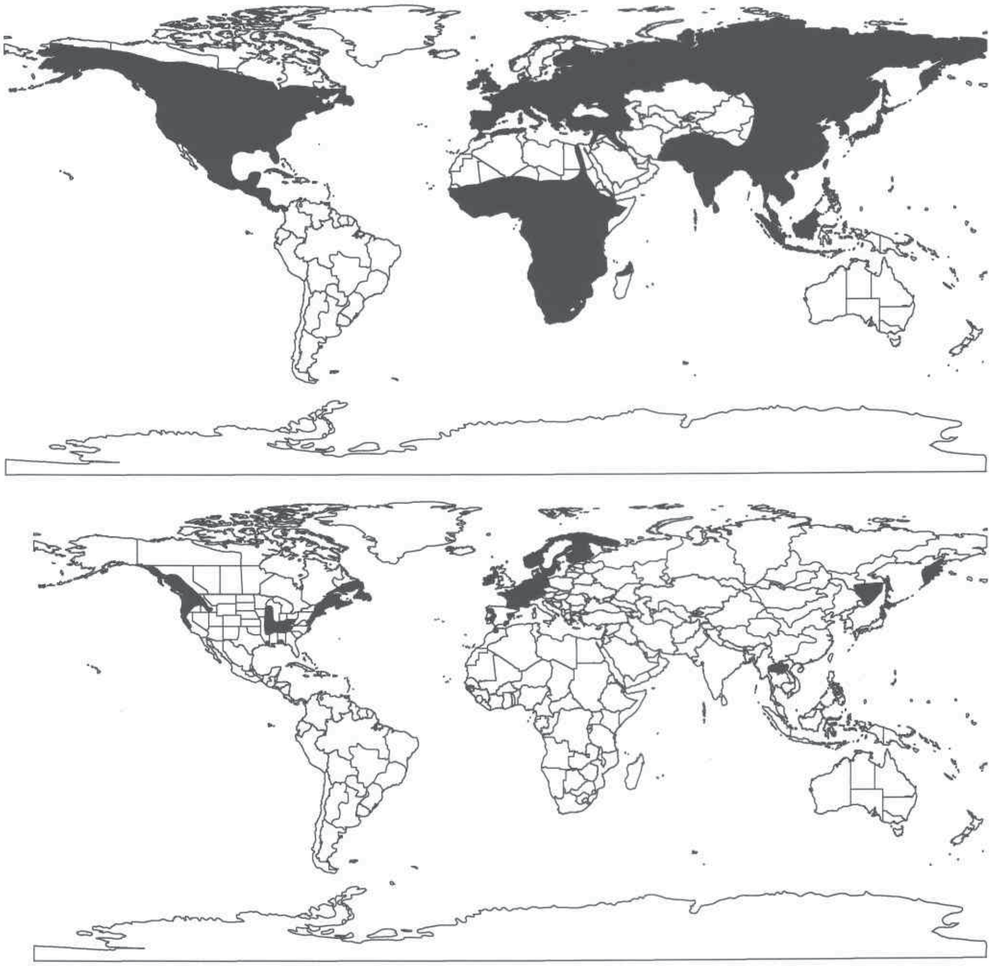

Figure 1.1. Global distribution of the families (top) Unionidae and (bottom) Margaritiferidae (from Bogan 2008).

have six or fewer freshwater species. By far the greatest freshwater radiation has occurred in the order Unionoida, which contains nearly 850 species and encompasses all diverse freshwater bivalve families with the single exception of the Sphaeriidae (order Veneroida). The Unionoida is the only bivalve order that has no marine representatives, although at least one North American species can tolerate brackish water (Section 4.1.B). All other bivalve orders with freshwater representatives have much higher diversity in marine waters, suggesting that their few freshwater species are relatively recent, adventitious colonizers of fresh waters.

The Unionoida is distributed worldwide, with the exception of Antarctica and the Pacific Oceanic Islands (Bogan 2008). The Unionidae is the most cosmopolitan family in the order, occurring widely in North America, Central America, Africa, Europe, and Asia (Figure 1.1). The Margaritiferidae also is wide ranging, but its current distribution is localized and apparently a relic of a previously wider range (Smith 2001; Figure 1.1). The remaining families of Unionoida are restricted to only one or two biogeographical regions, and none of these families occur in North America (Table 1.2).

In addition to being the most widely distributed family, the Unionidae contains about 80 percent of the species in the order (Table 1.2). Diversity of Unionidae is concentrated in eastern North America (about 300 species), southeastern China and Indochina (150 species), and Mesoamerica (90 species); most other regions within the family's range have fewer than 20 species (Graf and Cummings 2007). Although species richness is greatest in North America, higher-level freshwater bivalve diversity is the lowest of any biogeographical region. The Neotropical, Afrotropical, Palearctic, and Oriental regions each have freshwater members of seven to nine families in three to four orders, and the Australasian region has freshwater representatives in four families (Table 1.2). In contrast, North America has freshwater representatives of only three families in two orders: Sphaeriidae (fingernail clams, order Veneroida), Margaritiferidae, and Unionidae (both Unionoida). Representatives of two additional families, Corbiculidae and Dreissenidae (both Veneroida), have been introduced into North America by humans (Chapter 10).

Most North American species are members of the family Unionidae, and five species are in the family Margaritiferidae. Evolutionary relationships within the Unionidae are becoming better known through molecular genetics techniques. Current classifications recognize five tribes (plus an Old World lineage including *Gonidea*), representing distinct evolutionary (monophyletic) lineages, within the family (Graf 2002; Campbell et al. 2005; Figure 1.2), and I use this classification throughout this book. Assignment of genera to these tribes is well supported in most cases, but concepts of the genera themselves are in flux. Many long-used genera, such as *Anodonta, Fusconaia, Lampsilis, Quadrula*, and *Villosa*, are unnatural groupings each containing multiple independent lineages (e.g., Serb et al. 2003; Campbell et al. 2005; Zanatta et al. 2007a). A sixth unionid tribe may be necessary to contain the genus *Reginaia* (including "*Fusconaia*" *ebena* and "*F*". *rotulata*), which is not clearly associated with any currently recognized tribe (Campbell and Lydeard 2012a). These studies show the inadequacy of current classifications, but new generic classifications are only now being formally proposed (e.g., Roe and Hartfield 2005; Campbell and Lydeard 2012a). Numerous genera will need to be resurrected from synonymy or newly named to portray higher-level diversity in the Unionidae, underscoring the remarkable divergence within this family.

According to current concepts, North American species are distributed among approximately 50 genera (Figure 1.2). Estimates of species diversity are about 300, but totals vary slightly among recent accounts (Williams et al. 1993; Turgeon et al. 1998; Graf and Cummings 2007) and will likely increase with additional research (Chapter 3). The vast majority of these species are endemic to North America. Only two are shared with the Palearctic region (eastern pearlshell, *Margaritifera*

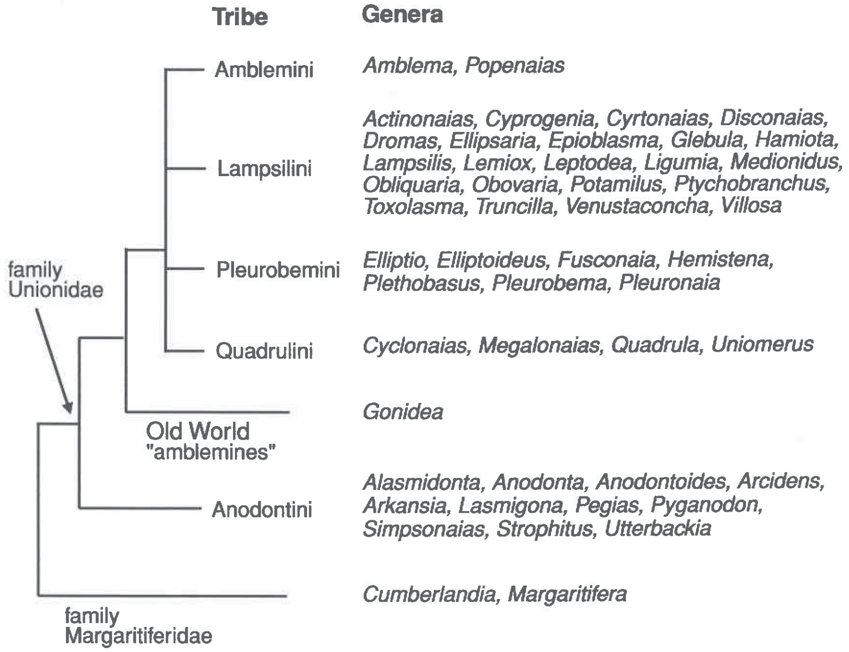

Figure 1.2. Diversity and phylogenetic relationships of North American freshwater mussels; two genera of uncertain phylogenetic affinity (*Plectomerus* and *Reginaia*) are omitted (adapted from Campbell et al. 2005; Graf and Cummings 2007).

margaritifera, and Yukon floater, *Anodonta beringiana*), and at least two are shared with Mexico (Tampico pearlymussel, *Cyrtonaias tampicoensis*, and Texas hornshell, *Popenaias popeii*). Similarly, most genera are unique to North America. In addition to the four genera listed previously, only *Potamilus* and *Megalonaias* potentially have representatives in other regions (Mesoamerica; Graf and Cummings 2007).

The great diversity of the Unionoida, its worldwide distribution, and its lack of marine members suggest that these animals have inhabited fresh waters for a very long time. Indeed, the group's fossil record extends to the Upper Devonian (416–365 million years ago (mya); Giribet 2008). North American unionoids first appeared in the Triassic (250–200 mya), and by the Cretaceous (145–65 mya), the group attained morphological and taxonomic diversity comparable to the Recent fauna (Watters 2001). The antiquity of the Unionoida is further supported by its phylogenetic position within the class Bivalvia. The Unionoida is related most closely to the marine order Trigonioida (Graf and Cummings 2006; Giribet 2008). The Trigonioida is an ancient lineage that was diverse and widespread in the Mesozoic (250–65 mya) but is represented today by only six or seven surviving species restricted to marine waters off Tasmania and Australia (Giribet 2008). Clearly the Unionoida, particularly the Unionidae, is a unique and characteristic component of freshwater ecosystems around the world.

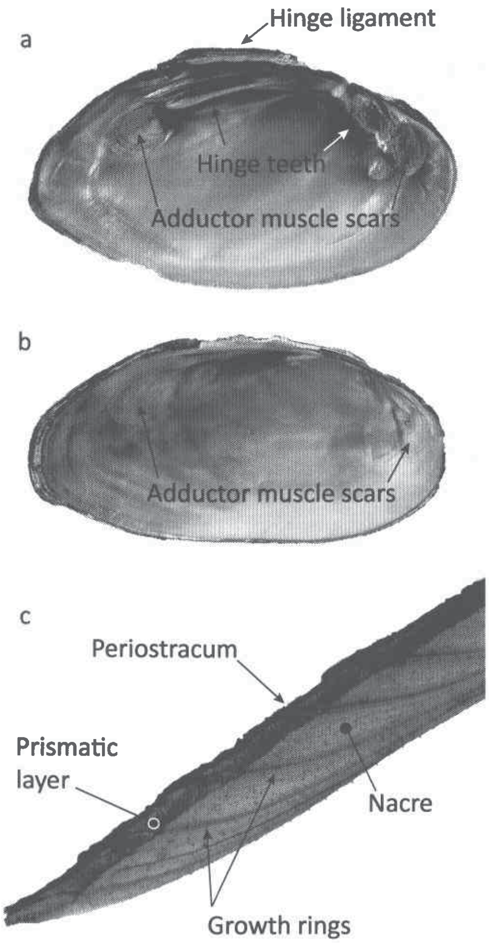

Figure 1.3. Structure of freshwater mussel shells. (a) Interior of the left valve of the Alabama spike, *Elliptio arca*, showing hinge ligament, hinge teeth, and attachment site for adductor muscles (muscle scars). (b) Interior of the alewife floater, *Anodonta implicata*, showing lack of hinge teeth (Richard T. Bryant, photos). (c) Cross section of mussel shell (W. R. Haag, photo).

1.3. Shells

The most conspicuous feature of a mussel is the shell. The shell is the animal's main defense against the world and gives support to the otherwise amorphous body mass. Shell morphology is highly variable and is interesting ecologically because shell features greatly influence how the animals interact with their environment. Furthermore, shells provide a record of growth and other events in the life of an individual. They are also simply gorgeous (see Plates).

The shell consists of two valves, which are held together by a springlike hinge ligament along the dorsal margin and by a pair of adductor muscles within the shell (Figure 1.3). Because muscle tissue can exert force only by contracting, the shell is

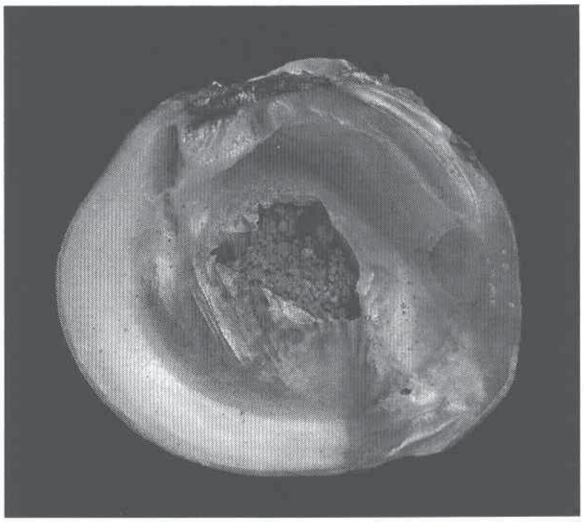

Figure 1.4. Shell of the Alabama orb, *Quadrula asperata*, showing sand grains covered by nacre; nacre has been punctured to show sand (Richard T. Bryant, photo).

opened by relaxing the adductor muscles, allowing the hinge ligament to pull the valves apart slightly; the shell is closed by contracting the adductor muscles. Shells of most species have hinge teeth, which interlock to hold the valves in juxtaposition, but teeth are reduced or absent in the Anodontini (Figure 1.3).

1.3.A. Shell production and growth

The shell is secreted by the mantle, a thin extension of the body wall – unique to mollusks – that underlies the shell. The shell consists of three layers: the periostracum, the prismatic layer, and the nacre (Figure 1.3). Most of the shell is composed of nacre, the lustrous, mother-of-pearl layer visible on the shell interior. The nacre is overlaid by the thin prismatic layer. The nacre and prismatic layer are composed of thin sheets of $CaCO_3$ crystals in an organic matrix including the protein conchiolin. The crystals are oriented parallel to the shell surface in the nacre and perpendicular in the prismatic layer (McMahon and Bogan 2001). Pearls are formed when foreign objects are trapped between the mantle and the shell and encapsulated by nacre; foreign material also is covered by nacre and incorporated into the shell (Rosenberg and Henschen 1986; Neves and Moyer 1988; Figure 1.4). Pearls may be formed particularly around encysted larval trematode parasites, which are common in mussels (Hopkins 1934). The periostracum is a thin, proteinaceous layer that covers the outer shell surface. The periostracum and prismatic layer are secreted only at the mantle edge and are associated with the growing shell margin, but nacre is secreted continuously along the entire inner surface of the shell, thickening and strengthening the shell with age (McMahon and Bogan 2001; Smith 2001). In temperate latitudes, shell secretion

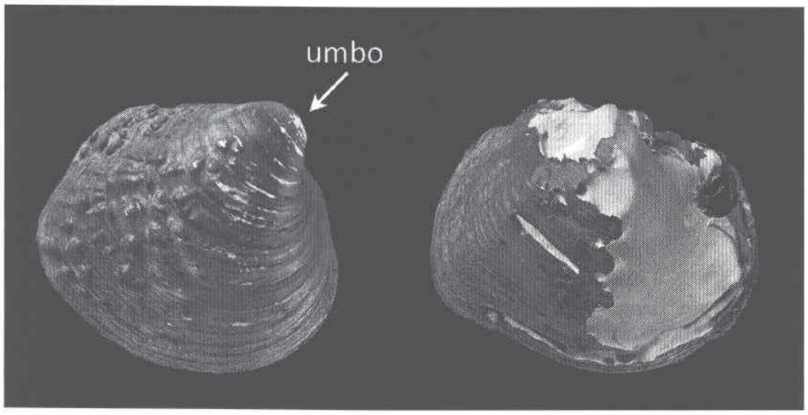

Figure 1.5. (left) Pimpleback, *Quadrula pustulosa*, from a well-buffered stream, showing minimal shell dissolution (Licking River, Kentucky). (right) *Q. pustulosa*, from a poorly buffered stream, showing extensive dissolution (Little Tallahatchie River, Mississippi) (Richard T. Bryant, photos).

occurs primarily in the warm months, beginning in spring at about 12°–15°C and ceasing in fall at about 6°–12°C (Howard 1922; Negus 1966; Dettman et al. 1999).

Because most fresh waters are mildly acidic, shell dissolution represents a major challenge for mussels. The periostracum is relatively impermeable to water, and its proteinaceous structure is resistant to dissolution; therefore this layer is important in protecting the underlying calcareous layers (McMahon and Bogan 2001). Accordingly, the periostracum is generally thicker in freshwater mollusks than in marine species that inhabit well-buffered waters (Watabe 1988). The organic matrix of the nacre also retards shell dissolution (Stanley 1988; Vermeij 1993), and freshwater species that inhabit soft waters have a greater percentage of shell organic material than species inhabiting hard waters (Bauer 2001). Because the periostracum and prismatic layers are secreted only at the shell margin, damage to these structures is not repaired and accumulates over time (Figure 1.5). Adventitious conchiolin layers associated with nacre production are deposited locally by the mantle in response to shell damage (Tevesz and Carter 1980; Day 1984). Nevertheless, mussels often experience shell dissolution at the umbo (the oldest part of the shell; Figure 1.5) or other places where the periostracum has been abraded or damaged. In some cases, dissolution can be extensive, eventually resulting in perforation of the shell and death of the animal (Kat 1982a).

In all bivalves, seasonal variation in shell deposition produces rings, providing a detailed growth record similar to those found in trees; fish spines, otoliths and scales; and permanent, hard structures of many other organisms. Shell deposited during the growing season has a high proportion of $CaCO_3$ relative to the organic matrix. In temperate latitudes, cessation or reduction of growth in winter results in a higher concentration of organic material relative to $CaCO_3$, producing distinct annual rings (Day 1984; Lutz and Clark 1984). Marine bivalve growth rings were noted by Leonardo da Vinci (Jones 1981), and Louis Agassiz concluded in 1862 that rings of freshwater mussels were deposited annually (Watters 1994a). Formation of annual rings in marine bivalves is widely accepted, and they form the basis of our understanding of age and growth (e.g., Rhoads and Pannella 1970; Jones et al. 1990; Jones and Quitmyer 1996). Annual ring formation in freshwater mussels was formerly questioned (Downing et al. 1992; Kesler and Downing 1997; Anthony et al. 2001), but later studies refuted these findings on methodological grounds (Haag and Commens-Carson 2008; Haag 2009a). Like marine bivalves, annual ring formation in freshwater mussels is now widely accepted based on a large number of studies evaluating ring formation throughout North America and Europe (reviewed in Haag 2009a; see also Dettman et al. 1999; Goewert et al. 2007; Black et al. 2010).

In addition to annual rings, mussels deposit other types of shell rings. Marine bivalves produce daily and subdaily rings in response to tidal or lunar rhythms (Richardson 1989). When the shell is closed, dissolution of $CaCO_3$ under reduced pH during anaerobic metabolism leaves an acid-resistant conchiolin residue (Lutz and Rhoads 1977; Gordon and Carriker 1978). Daily rings occur in freshwater mussels but have been examined in few species, and the mechanism of production is poorly known (Day 1984; Dunca and Mutvei 2001; Schöne et al. 2005a; Haag and Commens-Carson 2008). Shell rings potentially associated with spawning were observed in the eastern lampmussel, *Lampsilis radiata*; these rings were composed of a band of nacre crystals thinner than those deposited during the remainder of the growing season and may represent a period of greater energy allocation to gametogenesis (Day 1984). Spawning rings have not been reported in other freshwater species, but they are well known in marine bivalves (Jones 1980; Schöne et al. 2005b). Mussels also deposit disturbance rings during the growing season in response to natural stressors or handling (Isely 1914; Neves and Moyer 1988; Haag and Commens-Carson 2008). Disturbance rings may be caused by shell dissolution during valve closure (Lutz and Rhoads 1977), but they are additionally associated with disruption of the mantle–shell margin connection occurring when the mantle is retracted during shell closure. Reestablishment of the mantle–shell margin connection after disturbance occurs at a slightly different place than the former connection, resulting in misalignment of the prismatic layer and periostracum relative to the original plane of growth (Coker 1921; Haag and Commens-Carson 2008).

1.3.B. Patterns of shell morphology

1.3.B.1. Shell size and mass

Shell size and mass vary widely among North American species. Maximum length varies from about 35 mm in the little-wing pearlymussel, *Pegias fabula*, and the lilliput, *Toxolasma parva*, to more than 250 mm in the washboard, *Megalonaias*

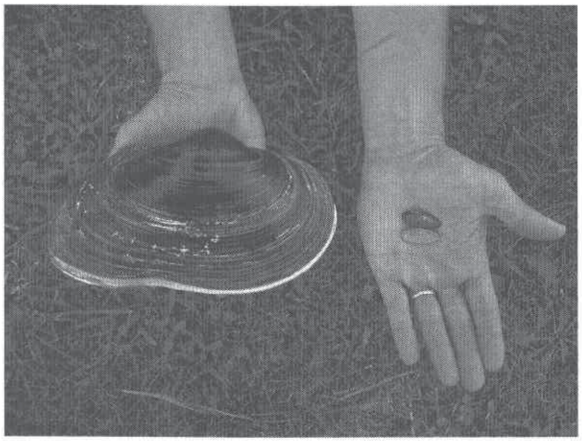

Figure 1.6. Variation in shell size among mussel species showing approximate maximum size for (left) the giant floater, *Pyganodon grandis*, and (right) Alabama moccasinshell, *Medionidus acutissimus* (W. R. Haag, photo).

nervosa, and giant floater, *Pyganodon grandis* (Figure 1.6). Shell thickness varies from thin, fragile shells less than 1 mm thick to heavy, ponderous shells more than 15 mm thick. Within species, shell mass is related closely to length, increasing via a power function, but the mass of thick-shelled species can be more than 10 times greater than the mass of similarly sized thin-shelled species (Figure 1.7). Consequently, across species, shell size explains much less of the variation in shell mass, and this relationship is due primarily to allometric scaling whereby larger species have disproportionately greater shell mass. With allometry removed, the relationship between length and shell mass becomes negative but explains little of the variation in mass (Figure 1.7). This means that larger species do not necessarily have heavier shells per unit size, and the most proportionally massive shells are found in several moderately sized species about 40–70 mm in length. Surprisingly, several species with large, massive shells (e.g., *Amblema plicata*, *Megalonaias nervosa*) have only moderate length-standardized mass (Table 1.3). Other large species have proportionally thin, light shells (e.g., *Cumberlandia monodonta*, *Leptodea fragilis*, *Pyganodon grandis*), and the most massive shells are found in some smaller species (e.g., *Cyprogenia stegaria*, *Obovaria unicolor*, *Quadrula pustulosa*). Other very small species (<50 mm) have massive shells for their size (e.g., *Epioblasma haysiana*, *Lemiox rimosus*, *Villosa fabalis*). Shell size and mass have little phylogenetic basis (Haag and Rypel 2011). Small species (<50 mm) are restricted to the tribes Anodontini and Lampsilini, but otherwise, shell length overlaps widely among groups (Figure 1.8). The Anodontini and Margaritiferidae have characteristically thin shells, but other groups overlap widely in shell mass (Table 1.3). The Lampsilini is often characterized as having thin shells (e.g., Stansbery 1967), but shell mass within this tribe spans the greatest range of any group (Table 1.3).

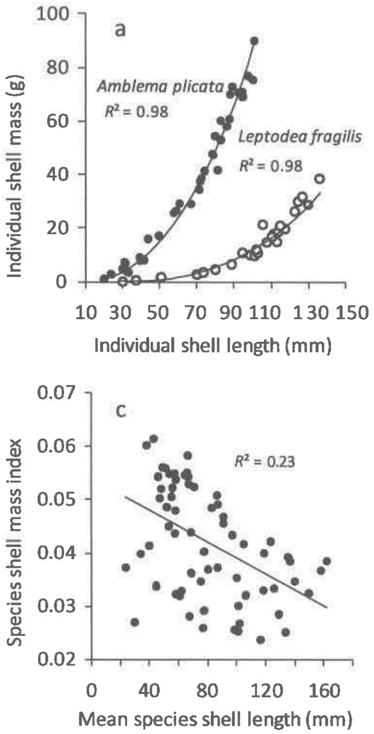

Figure 1.7. Relationships between shell length and shell mass (mass of left valve). (a) Shell length–mass relationships for the threeridge, *Amblema plicata* (Little Tallahatchie River, Mississippi), and fragile papershell, *Leptodea fragilis* (St. Francis River, Arkansas) (W. R. Haag, unpublished data). (b) Relationship between mean shell length and mean shell mass across 47 species (67 populations). (c) Relationship between shell length and shell mass with allometric effects removed (shell mass index = cube root of shell mass/shell length) (data for b and c from Haag and Rypel 2011).

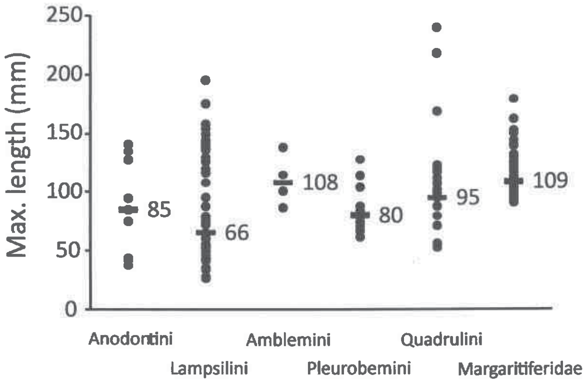

Figure 1.8. Phylogenetic patterns of mussel size. Numbers represent median values for each phylogenetic group (from Haag and Rypel 2011).

Table 1.3. *Shell length and shell mass of representative North American mussel species*

Phylogenetic group	Species	Maximum length (mm)	Maximum shell mass (g)	Length-standardized shell mass (g)
Lampsilini	*Leptodea fragilis*	136.3	38.8	1.0
Anodontini	*Pyganodon grandis*	141.9	76.0	1.1
Margaritiferidae	*Cumberlandia monodonta*	165.0	70.7	1.3
Lampsilini	*Villosa vibex*	77.5	10.3	1.8
Anodontini	*Strophitus subvexus*	80.6	8.9	2.1
Lampsilini	*Medionidus acutissimus*	34.2	0.7	2.8
Lampsilini	*Lampsilis siliquoidea*	104.8	50.9	3.1
Pleurobemini	*Elliptio dilatata*	100.9	44.3	5.4
Quadrulini	*Megalonaias nervosa*	180.0	263.8	7.5
Lampsilini	*Truncilla truncata*	63.8	18.7	10.4
Pleurobemini	*Pleurobema decisum*	56.0	17.3	12.4
Amblemini	*Amblema plicata*	100.9	90.0	15.6
Quadrulini	*Quadrula pustulosa*	79.1	73.0	19.7
Lampsilini	*Obovaria unicolor*	50.0	20.6	20.6
Lampsilini	*Cyprogenia stegaria*	61.1	43.5	26.1

Note: Maximum length and mass are the maximum values observed in samples used to construct length–mass relationships; mass refers to a single valve. Length-standardized shell mass is the predicted mass of a single valve of a 50-mm individual based on length–mass relationships for each species (data from Haag and Rypel 2011).

Within species, shell size and mass can vary nearly 2 times among populations (Haag and Rypel 2011). In some cases, these differences reflect latitudinal gradients, with northern populations reaching larger sizes (Bauer 1992). More frequently, population differences appear related to water chemistry. Mussels often have thinner and smaller shells in waters with low concentrations of calcium and bicarbonate, which are necessary for shell production (Green 1972; Nduku and Harrison 1976; Mackie and Flippance 1983; Hinch et al. 1989; Haag and Rypel 2011). Individuals in enriched rivers may reach larger sizes than those in less productive rivers (Morris and Corkum 1999), and depth, sediment type, variation in streamflow, exposure to wind and current, and perhaps food limitation can also influence shell size and mass (Brown et al. 1938; Harman 1970; Hinch et al. 1986; Bailey and Green 1988; Kesler et al. 2007; Rypel et al. 2009).

1.3.B.2. Shell shape

The striking diversity in mussel shell shape and sculpture can be categorized into several broad themes. These themes recur across phylogenetic groups worldwide, suggesting that considerable evolutionary convergence has occurred. About half of

North American species have generally oval or elliptical shells that are only moderately asymmetrical (Plate 1). These shells occur in all major phylogenetic groups but are most characteristic of the Margaritiferidae, Anodontini, Lampsilini, and *Elliptio* (Pleurobemini). About one-third of the fauna have triangular or quadrate shells that are usually moderately thickened to massive and in which the umbo is often far forward of the shell midpoint, resulting in strong asymmetry (Plate 2); strongly asymmetrical shells of this nature are referred to as *prosogyrous* (Watters 1992). Triangular or quadrate shells are most characteristic of the Pleurobemini, Quadrulini, and *Amblema* (Amblemini) but also occur in the Anodontini (e.g., some *Alasmidonta*, *Arcidens*, *Pegias*) and Lampsilini (e.g., *Ellipsaria*, some *Epioblasma*, *Lemiox*, *Obliquaria*, *Truncilla*). In some species, the angular shape is accentuated by a strong posterior and medial ridge separated by a shallow valley called a *sulcus* (see *Quadrula quadrula* and *Pleurobema cordatum*; Plate 2). Greatly inflated and generally thin shells are found in the Anodontini and Lampsilini (see *Alasmidonta arcula* and *Potamilus capax*; Plate 1). A few species have greatly compressed, lanceloate shells, including *Elliptio shepardiana*, *E. folliculata*, *Hemistena lata* (all Pleurobemini), and *Ligumia nasuta* (Lampsilini) (Plate 3).

About six North American species have flattened, disk-shaped shells with a conspicuous dorsal wing posterior to the umbo (Plate 4). Several are referred to as heelsplitters because the wing protrudes above the substrate, where it could injure a bare foot. *Leptodea fragilis* and *Potamilus* may also have a small, inconspicuous wing anterior to the umbo. The structure of the wing – also referred to as a *claustrum* or an *ala* – differs among phylogenetic lineages, suggesting that it arose independently several times in North America and elsewhere in the world (Savazzi and Peiyi 1992). In the *Leptodea* + *Potamilus* clade (Lampsilini), the shell extends beyond the hinge line, and the two shell valves are fused (termed *symphynote*), creating a cavity that encloses the hinge ligament. The ligament is augmented by a series of septa that fill the space dorsal to the ligament itself (Savazzi and Peiyi 1992). Wings are absent or only weakly expressed in other members of this group (*L. leptodon*, *P. capax*, and *P. purpuratus*). The white heelsplitter, *Lasmigona complanata* (Anodontini), also has a large, conspicuous wing formed by shell fusion and enclosing the hinge ligament. This structure is superficially similar to that of *Leptodea* and *Potamilus* but appears to differ in the location and orientation of the ligament and septa (W. R. Haag, observations). In other *Lasmigona*, shell fusion may be present early in life but later disappears (Ortmann 1919), and shells do not have conspicuous wings. In the winged floater, *Anodonta nuttalliana* (Anodontini), the wing does not extend beyond or enclose the hinge ligament; rather, the wing is created by the unusual orientation of the hinge line at a 45° angle from the ventral shell margin. The flat floater, *Anodonta suborbiculata*, also has a flattened, disk-shaped shell and may have an inconspicuous dorsal wing. Many other North American species have low, winglike projections or ridges posterior to the umbo (e.g., *Amblema plicata*, *Anodonta*, *Cyclonaias tuberculata*, many *Elliptio*

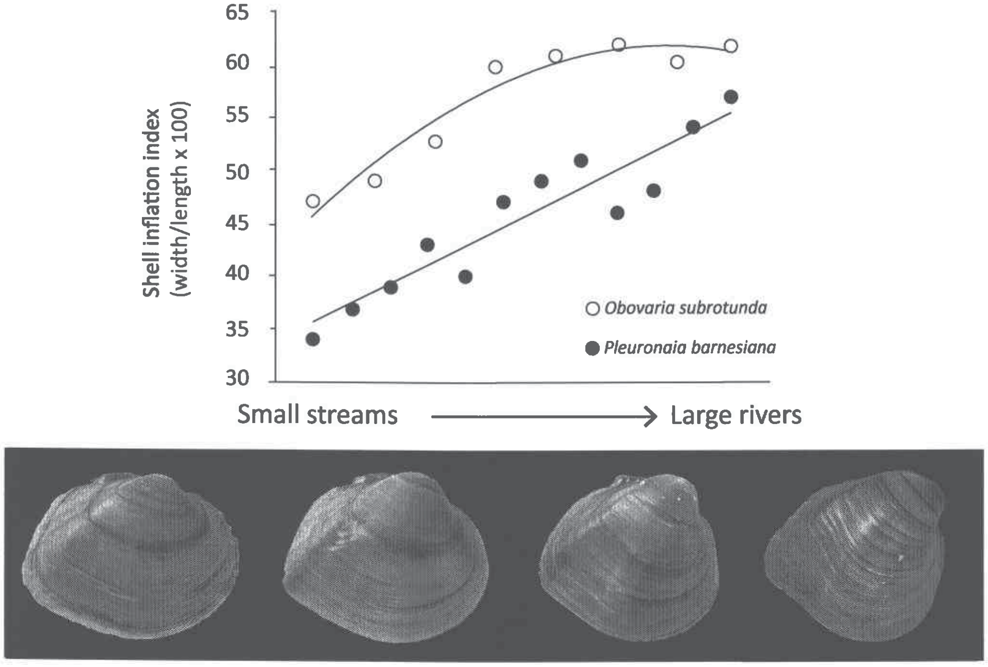

Figure 1.9. Ortmann's law of stream position. (top) Increase in shell inflation with increase in stream size for two mussel species (data from Ortmann 1920). (bottom) Changes in shell shape in the Wabash pigtoe, *Fusconaia flava*, with increasing stream size. From left to right: East Fork Stones River (Tennessee), Stones River, Cumberland River, Ohio River (after Stansbery 1983; Richard T. Bryant, photos).

and *Quadrula*; Plates 1, 2, and 7), but they are generally inconspicuous and variably expressed.

Shell shape often varies across habitats. The most well known pattern is Ortmann's law of stream position, describing clinal variation from compressed shells in small streams to progressively inflated shells in larger streams (Wilson and Clark 1914; Utterback 1916a; Ortmann 1920; Figure 1.9). This phenomenon occurs in several genera in the Pleurobemini (*Fusconaia*, *Pleurobema*, *Pleuronaia*), Quadrulini (*Cyclonaias, Quadrula*), and Lampsilini (*Actinonaias ligamentina*, *Epioblasma torulosa*, *Dromas, Obovaria*) and in *Amblema plicata* (Amblemini) but does not occur in other species in these groups nor in the Margaritiferidae or Anodontini (Ortmann 1920; Ball 1922; Hornbach et al. 2010). The degree of inflation generally increases continuously with stream size but may reach an asymptote in mid-sized streams (Figure 1.9). Shells also tend to be longer, lower (from the umbo to the ventral margin), and more symmetrical in small streams, but in large streams, shells become strongly prosogyrous, with the umbo shifted anteriorly, creating strong asymmetry (Danglade 1914; Ortmann 1920; Stansbery 1983; Hornbach et al. 2010; Figure 1.9). Owing to variation in shell morphology among sites and individuals, these stream-size patterns are expressed only across large scales and often are not evident within smaller river systems (e.g., Mackie and Topping 1988; Brown and Curole 1997).

Other physical factors may influence shell shape. In some species, populations in lentic habitats (e.g., lakes or wetlands) are more inflated than in streams (Ortmann 1919; Clarke 1973). This phenomenon is especially apparent in *Pyganodon grandis*, leading to the previous recognition of the lake form as *P. grandis corpulenta*. The ecophenotypic basis of this variation is demonstrated in a small reservoir in Mississippi, which contains the inflated *corpulenta* form, but in the stream immediately downstream of the dam (about 100 m away), individuals assume the compressed and elongated stream form (W. R. Haag, observations). The inflated form of *P. grandis* also occurs in depositional areas of large rivers. Other patterns of shell shape variation may have an ecophenotypic basis, depending on substrate or flow characteristics (Agrell 1948; Eagar 1978; Hinch et al. 1986; Balla and Walker 1991; Kesler and Bailey 1993) or may be a mixture of genetic and ecophenotypic variation among habitats and geographical regions (Neel 1941; Clarke 1973; Jass and Glenn 1999).

Shell shape varies among sexes in several species, but this trait is distributed unevenly among phylogenetic groups (Plate 5). Sexual dimorphism is widespread in the Lampsilini, occurring to some extent in all genera except *Cyprogenia* and *Dromus*; sexual dimorphism apparently has not been evaluated in *Cyrtonaias*. In lampsilines, the posterior-ventral portion of the female shell is expanded and inflated, presumably to accommodate the gravid gills, which become swollen with glochidia only in their posterior section (Section 1.4.C). Sexual dimorphism is marked in *Ellipsaria, Lampsilis, Lemiox, Leptodea, Ligumia, Medionidus, Obovaria, Potamilus purpuratus, Toxolasma*, and *Villosa*; males are typically larger, and other growth characteristics differ between sexes (Jass and Glenn 2004; Haag and Rypel 2011). Sexual dimorphism is especially conspicuous in *Epioblasma* and *Leptodea leptodon*, in which female shell morphology also is involved in fish host attraction and infection (Plate 5; Chapter 5). Other lampsilines show more subtle and ambiguous sexual dimorphism (Ortmann 1919; Williams et al. 2008). In the Anodontini, strong sexual dimorphism occurs only in *Pegias* (Ortmann 1914), but *Alasmidonta, Anodonta, Arcidens, Pyganodon*, and *Utterbackia* may show subtle but inconsistent dimorphism (Ortmann 1919; Heard 1975; Haggerty et al. 2011; Zieritz and Aldridge 2011). In the Quadrulini, sexual dimorphism occurs only in the pistolgrip, *Quadrula verrucosa*, in which females are greatly elongated relative to males (Plate 5). Qualitative sexual dimorphism is absent in the Amblemini, Pleurobemini, and Margaritiferidae, and there are no sexual differences in size or other growth characteristics (Haag and Rypel 2011). However, in the gulf spike, *Elliptio pullata* (as *E. icterina*, Pleurobemini), sex of 70 percent of individuals was discriminated statistically based on quantitative shell shape variables, indicating that allometric growth may differ subtly between sexes in some species (Kotrla and James 1987).

1.3.B.3. Shell sculpture

Mussel shells are best known for their varied shell sculpture or ornamentation. About 20 percent of North American species have some form of sculpture on the adult shell. A much greater number, including many that lack sculpture as adults, have minute umbo sculpture (also called beak sculpture) that is deposited only within the first few months of life (Coker et al. 1921; Watters et al. 2009). Umbo sculpture is usually obliterated quickly by erosion and is rarely evident on adult shells. Adult shell sculpture can be classified into two broad categories: (1) sculpture only on the dorsal slope with the shell disk smooth (referred to here as dorsal slope sculpture, Watters 1994b; also referred to as posterior slope sculpture, e.g., Williams et al. 2008) and (2) sculpture on the shell disk (often accompanied by dorsal slope sculpture). The western fanshell, *Cyprogenia aberti*, several *Elliptio*, and the birdwing pearlymussel, *Lemiox rimosus*, have weakly developed wrinkles that are not easily classified, but these features are variably expressed. Radial ribs on the shell disk, emanating from the umbonal region to the ventral margin, are common in marine bivalves but absent in freshwater mussels (Watters 1994b). Like shell shape, there has been remarkable convergent evolution of sculpture patterns in freshwater mussels worldwide.

Dorsal slope sculpture (Plate 6) occurs in about 20 species in the Margaritiferidae (*Margaritifera marrianae*, *M. hembeli*), Anodontini (several *Alasmidonta*, *Lasmigona costata*), Lampsilini (*Medionidus*, *Ptychobranchus subtentum*), and Pleurobemini (*Elliptio fraterna*, *E. mcmichaeli*, *Fusconaia burkei*) and is absent only in the Amblemini and Quadrulini. Disk sculpture occurs in about 45 species and in all major groups, except the Margaritiferidae, but it is most prevalent in the Quadrulini, where it occurs in most species, except *Uniomerus*.

Disk sculpture can be further categorized into three main themes: (1) parallel ridges or plications, (2) tubercles or pustules, and (3) spines. Parallel ridges (Plate 7) occur in the Amblemini (*Amblema*), Anodontini (*Arcidens, Arkansia*), Quadrulini (*Megalonaias*), Pleurobemini (*Elliptoideus*), and in one species of uncertain phylogenetic placement (*Plectomerus*). Tubercles (Plate 8) occur mostly in the Quadrulini but also in the Lampsilini (*Cyprogenia stegaria*, *Dromus*, *Epioblasma torulosa*, *Obliquaria*) and Pleurobemini (*Plethobasus*) and are weakly developed in *Pegias* (Anodontini). Spines occur only in three species of *Elliptio* (the spinymussels: *E. collina*, *E. spinosa*, and *E. steinstansana*; Pleurobemini) and are especially well developed in the remarkable Altamaha spinymussel, *E. spinosa* (Plate 9).

Shell sculpture occurs unevenly across biogeographical regions and habitats. Sculpture is largely restricted to the Mississippian and Eastern Gulf regions (Table 1.4). Disk sculpture is most common in the Mississippian region, but dorsal slope sculpture is most prevalent in the Eastern Gulf region. Sculpture is absent in the Pacific region and nearly so in the Atlantic region. In the Atlantic region, dorsal slope sculpture occurs only in *Alasmidonta* and *Lasmigona costata*, species that may be recent colonizers from the Mississippian region (Chapter 3). Spines are unique to the Atlantic

Table 1.4. *Distribution of shell sculpture across biogeographical faunal regions of North America and among stream sizes in the Mississippian region*

		Number of species		
Region or stream size	Total number of species	No sculpture	Dorsal slope sculpture	Disk sculpture
Mississippian	198	150 (76%)	9 (4%)	39 (20%)
Eastern Gulf	58	42 (73%)	10 (17%)	6 (10%)
Atlantic	52	45 (86%)	3 (6%)	4 (8%)
Pacific	6	6 (100%)	0 (0%)	0 (0%)
Mississippian region	–			
Small streams	–	85%	9%	6%
Mid-sized streams	–	68%	10%	22%
Large streams	–	59%	2%	39%

Note: Information about sculpturing distribution among stream sizes is from a dataset of 82 stream sites (see Chapter 8).

region and characterize three of the four species in this region with disk sculpture. Apart from the spinymussels, disk sculpture occurs in the Atlantic region only in the Roanoke slabshell, *Elliptio roanokensis*, but is weakly or variably expressed.

Disk sculpture is generally rare or absent in small streams and becomes increasingly prevalent in larger streams, but species with dorsal slope sculpture or no sculpture predominate in small streams (Hornbach et al. 2010; Table 1.4). Furthermore, several species tend to be heavily sculptured in large streams but lose sculpture in successively smaller streams in a manner similar to the gradual decrease in shell inflation seen along stream-size gradients (e.g., *Epioblasma torulosa*, *Dromus dromas*, *Quadrula* spp.; Ortmann 1920; Ball 1922). However, in *Quadrula*, smooth and heavily sculptured shells often occur together at large stream sites (W. R. Haag, personal observations), and headwater populations of *Amblema plicata* tend to be more highly sculptured than in large rivers (Ortmann 1920; Ball 1922).

In at least one case, sculpturing appears to be expressed locally in response to other habitat factors. In low-gradient, soft-bottomed streams of the Black Prairie region of east central Mississippi and west central Alabama, several species that do not elsewhere have shell sculpture (e.g., *Fusconaia cerina*, *Lampsilis straminea*, *Villosa* spp.) have a profusion of fine, concentric ridges. These ridges do not correspond to annual rings and are similar to the concentric ridges of *Corbicula fluminea* (Williams et al. 2008). These are the only examples of concentric sculpture in North American mussels, and the reason for the occurrence here is unknown.

1.3.B.4. Shell color

North American mussels have an array of color patterns on the external shell surface and in the nacre (see Plates 1–9). External coloration of mollusk shells is due to pigments within the periostracum secreted by cells in the mantle margin (Comfort 1951; Nuttall 1969). Background shell color ranges from light, tawny yellow to shades of green and brown to almost black and may be adorned with striking secondary patterns. The most common secondary pattern is radial rays emanating from the umbonal region to the shell margin. In some species, rays include complex stippling or chevrons. Concentric bands are present in many marine bivalves but appear only rarely in a few freshwater species (e.g., Chipola slabshell, *Elliptio chipolaensis*; southern clubshell, *Pleurobema decisum*; Williams et al. 2008). Shell color patterns are diagnostic for many species but often vary among populations and individuals. For example, rays are distinct in some populations or individuals but absent or reduced in others. Variation in external shell color usually spans a continuous range within a population, but in the three-horned wartyback, *Obliquaria reflexa*, shell color is polymorphic with distinct color phases (Plate 2).

Nacre color is equally beautiful and varied (Plate 10). Nacre color or iridescence is caused by refraction of light by the crystalline shell structure or by pigments within the nacre (Fox 1983; Luttikhuizen and Drent 2008). The nacre may be stained by several elements (e.g., Na, Mg, Al, Si, P, S, Cl, K, and Fe) adsorbed to clay particles that are trapped within the mantle and incorporated into the shell (Rosenberg and Henschen 1986). In many species, nacre color is diagnostic and relatively invariable. Most of these species have uniformly white nacre, occasionally with a faint blush of blue, pink, or orange, but several are characteristically purple or coppery (*Cyclonaias*, *Elliptio*, *Elliptoideus*, *Potamilus purpuratus*, *Quadrula refulgens*, *Toxolasma lividus*), pink or rosy (*Leptodea*, *Potamilus ohiensis*), grayish green or smoky (*Medionidus*, *Pegias*, *Uniomerus*), or two toned (*Amblema plicata*, *Hemistena*, *Obovaria retusa*). Although diagnostic for many species, nacre color often varies within a genus (e.g., *Epioblasma*, *Pleurobema*, *Quadrula*, *Toxolasma*, *Villosa*).

Other species show variation in nacre color within and among populations. Variation usually occurs as a continuous gradation from white to various shades of purple, red, pink, or orange, but the dominant color may vary among populations. Individuals with red or orange nacre may have a corresponding hue in the periostracum and in the soft tissue. A few species show a geographical pattern, with southern populations having a higher proportion of purple or red nacre but with uniformly white nacre in northern populations (e.g., *Obliquaria reflexa*, *Quadrula verrucosa*; Ortmann 1919; Williams et al. 2008). The heritability of nacre color in these species is unknown, but the continuous distribution of color variation and its variability among populations suggests it is due to locally fixed alleles or quantitative genetic traits influenced to a large extent by environment.

In at least three species, nacre color is polymorphic, with individuals having one of three discrete phenotypes: purple, white, or orange (Alabama spike, *Elliptio arca*, and spike, *E. dilatata*; Plate 11) or white, red, or orange (round pigtoe, *Pleurobema sintoxia*). These color phases occur in an approximate 12:3:1 ratio

(W. R. Haag, unpublished data[1]), suggesting that they are determined by epistatic interactions between only a few genes rather than codominance producing an intermediate color phase (i.e., orange) in heterozygotes (see Luttikhuizen and Drent 2008). The relative abundance of color phases can differ among species and populations. For example, orange is the second most abundant color phase in *E. arca* but is less common than white in *E. dilatata*, and orange *E. dilatata* are usually absent in small streams.

1.3.C. Adaptive significance of shell morphology

> The puzzling question often presents itself to the inquirer, why so much elaborateness of construction, and such exquisite ornament as are common to [freshwater mussels], should be bestowed? Destined to pass their lives in and under the mud . . . what purpose can ornament serve in them? . . . We cannot suppose that the individuals have any power of admiring each other . . . [nor can we] form a satisfactory idea of the object the great Author of nature had in view, in thus profusely beautifying creatures occupying so low a place . . .
>
> – *Godman 1842, 298*

The fascinating diversity of mussel shells naturally prompts people to ask the questions, What is the purpose of those knobs? or Why do mussels have those beautiful colors? Although it may be difficult to imagine why such variety is needed by animals that live buried in the bottom, many aspects of shell morphology seem to be adaptive. The high degree of evolutionary convergence in shell characters worldwide and consistent patterns of ecophenotypic variability suggest that these themes are good solutions to common problems faced by mussels. An animal living in the sediment of a river or lake faces three major challenges: (1) maintaining its position in the bottom, (2) burrowing back into the sediment if it becomes dislodged, and (3) avoiding predation. A feature that addresses one of these problems may decrease the shell's effectiveness against other factors; therefore adaptations must be balanced according to the relative importance of these challenges in a specific habitat (Stanley 1981).

Predation is viewed as the least important factor in the evolution of shell morphology in freshwater mussels. In marine ecosystems, there are a multitude of predators specialized for feeding on bivalves; in some populations, more than 80 percent of adult deaths may be caused by predators (Vermeij 1980). Consequently, marine bivalves have an array of antipredator adaptations, including overlapping shell margins and radial sculpture (which increase crushing resistance), denticulated or crenulated inner shell margins (which restrict entrance by crabs or starfish), thickening of the

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[1] *Elliptio arca*, Sipsey River, AL: 163 purple, 31 orange, 9 white; *E. dilatata*, Licking River, KY: 44 purple, 10 white, 2 orange. *Pleurobema sintoxia*, Licking River, KY: 12 white, 3 red, 2 orange; *P. sintoxia*, Spring River, AR: 30 white, 5 red, 2 orange. For all populations, numbers in each color phase did not differ significantly from expectations of a 12:3:1 ratio (goodness-of-fit test).

central portion of the shell (to resist drilling by snails), and adaptations for swimming (e.g., scallops) (Vermeij and Dudley 1985). Freshwater mussels exhibit none of these adaptations, and other shell characteristics or behaviors render them vulnerable to predators. The shells of many species do not close completely and have a small gape at the anterior and posterior ends. The conspicuous mantle lures of *Lampsilis* and other species (Chapter 5) "would be unthinkable in marine bivalves" without auxiliary chemical or other defenses (Vermeij and Dudley 1985). Evidence of nonlethal breakage (caused by thwarted predation attempts) is common in marine bivalves but rare in freshwater mussels (Vermeij and Dudley 1985). Predation on freshwater mussels may be intense for some species or life history stages (Section 7.2.A) but, compared to marine species, seems to have exerted little selective pressure for antipredator shell adaptations.

The ability to burrow into the sediment is vital to bivalves to avoid predation and to reorient themselves after dislodgement, preventing transport by currents to unsuitable habitats. Marine bivalve shells have a variety of adaptations facilitating rapid or deep burrowing. Concentric or divaricate ridges that are asymmetrical in cross section alternately abrade the sediment and serve as anchors during the rocking motion that accompanies burrowing in most species (Stanley 1981; Section 1.4.B). Compressed and elongated shells allow faster burrowing than spherical or inflated shells by reducing drag in the sediment (Stanley 1988; McLachlan et al. 1995) and may reduce the need for repeated rocking during burrowing (Savazzi and Peiyi 1992). Many deep-burrowing species inhabit permanent burrows into which they can retreat rapidly using a greatly elongated and nonretractable foot (Stanley 1988; Savazzi and Peiyi 1992). Similar to antipredator adaptations, North American mussels exhibit few features for rapid or deep burrowing. Concentric sculpture is virtually absent, and only a few species have weak divaricate sculpture (Watters 1994b) or greatly elongated and compressed shells (Section 1.3.B); rather, tubercles and other sculpture are often present at the greatest cross-sectional dimension of the shell, increasing drag during burrowing (Savazzi and Peiyi 1992). Adaptations for burrowing are limited mostly to the absence of sculpture on the anterior portion of the shell and the elongation of tubercles parallel to the axis of burrowing (see subsequent discussion). Consequently, most species are relatively slow and shallow burrowers (Section 1.4.B), although thin-shelled, nonsculptured species may burrow faster than heavy-shelled or sculptured species (Waller et al. 1999).

As Stanley (1981, 384) stated, "a clam's place is in the sediment, and there would seem to be strong selective value for traits tending to keep it there." Most features of freshwater mussel shells appear strongly adapted for maintaining position in the sediment, but the nature of this problem varies among habitats. In lentic habitats or other depositional areas with slow current, the primary challenge may be sinking in anoxic, soft substrates. This problem is dealt with in three ways related to increasing buoyancy in the sediment (Watters 1994b). The most obvious way to increase buoyancy is to decrease shell mass. Species characteristic of soft sediments (e.g., *Anodonta, Leptodea fragilis, Potamilus, Pyganodon, Utterbackia*) have proportionally thin, nonsculptured shells, and mass is reduced further by reduction of hinge teeth. Mass also can be decreased simply by having a diminutive shell (Stanley 1977), as seen in *Simpsonaias* and *Toxolasma*. Buoyancy also can be increased with an inflated shell that increases the amount of shell surface in contact with the substrate (Watters 1994b). Most species with globose shells also have thin shells and occur preferentially in soft substrates (e.g., *Alasmidonta arcula, Potamilus capax*). In *Pyganodon grandis*, the degree of shell inflation increases markedly in soft substrates (Section 1.3.B.2). The most dramatic adaptation for increasing buoyancy is development of dorsal wings and flattened, disk-shaped shells (Section 1.3.B.2). This morphology greatly increases shell surface area with little increase in shell mass or volume and may act in the same way as a snowshoe to prevent sinking into soft substrates (Watters 1994b); accordingly, these species often lie on their sides (W. R. Haag, observation). All species with dorsal wings and disk-shaped shells also are thin shelled and characteristic of soft sediments. Additional or alternate adaptational explanations for the function of wings include stabilization of shells in current, providing a functional replacement for reduced hinge teeth, and supplementing the opening momentum of the hinge ligament (Savazzi and Peiyi 1992; Watters 1994b).

Mussels in streams are faced with dislodgement from the substrate by currents. The major problem for an infaunal organism in flowing water is scour. In moving water, any irregularity in the bottom creates vortex currents that scour sediment from around the object. Dislodgement of a bivalve occurs after scour has been sufficient to expose a large surface area of the shell to the current (Stanley 1981). In experiments with marine and freshwater bivalves, dorsal slope sculpture reduced scour possibly by breaking vortices into a large number of smaller vortices, some producing scour and others deposition but resulting in no net scour (Stanley 1981; Watters 1994b). Dorsal slope sculpture appears most effective in reducing scour when the shell is aligned with the posterior end facing into the current (Stanley 1981); however, freshwater mussels show only a weak or no tendency to be oriented preferentially in this manner (Section 1.4.B.1). Nevertheless, the occurrence of sculpture only on the portion of the shell that is normally exposed to currents (the dorsal slope) or its common occurrence in species with other types of sculpture provide a compelling argument for the antiscouring function of this trait. A more subtle but widespread apparent antiscouring adaptation is a strong posterior ridge, which sets off the angle of the dorsal slope relative to the remainder of the shell (Figure 1.10). This feature occurs in many mussel species, both sculptured and nonsculptured, and may reduce scour by orienting the plane of the dorsal slope nearly flush with the sediment surface, reducing exposure to the current and providing a more streamlined aspect (Watters 1994b).

Other shell features may be adaptations to anchor shells in the substrate. The asymmetrical, prosogyrous shells of many species in large rivers (Section 1.3.B.2)

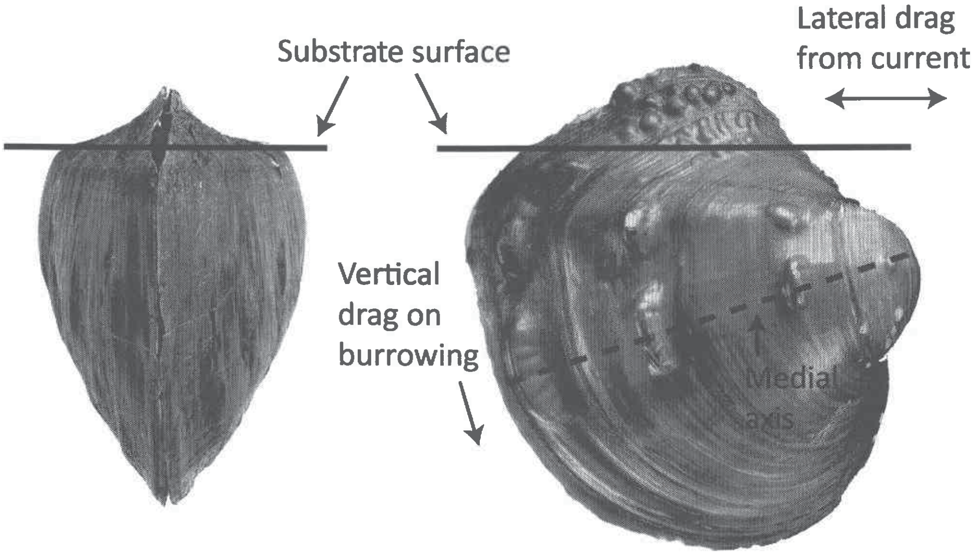

Figure 1.10. Shell adaptations for reducing scour or anchoring shells in the substrate. (left) Posterior view of the pocket-book, *Lampsilis ovata*, showing posterior ridge that reduces shell exposure to the current. (right) Lateral view of the wartyback, *Quadrula nodulata*, showing concentration of tubercles on the medial axis and elongation of tubercules perpendicular to lateral drag created by current but parallel to vertical drag on burrowing (Richard T. Bryant, photos).

shift the center of gravity to the anterior margin (the portion of the shell that is buried most deeply), potentially stabilizing the mussel within the substrate (Savazzi and Peiyi 1992). Similar clinal variation in shell morphology is unknown in marine bivalves, but heavy shells with an anterior center of gravity also are interpreted as having a stabilizing function (Stanley 1977). Spines in infaunal marine bivalves are considered to either thwart predators or to provide stability in sandy substrates (Vermeij 1993). The Altamaha spiny mussel, *Elliptio spinosa*, typically occurs in sand – potentially lending credence to the latter hypothesis – but spines of the two other North American spinymussels are diminutive, and the function of spines in freshwater mussels has not been studied. Other types of disk sculpture are thought to anchor shells by increasing friction against the substrate (Watters 1994b). In many species, tubercles are present primarily along the medial axis of the shell, and tubercles are elongated perpendicular to the axis (Figure 1.10). Concentration of tubercles on this axis presumably maximizes resistance to lateral displacement, but elongated tubercles also reduce drag on burrowing. In laboratory experiments, disk sculpture increased lateral resistance within the substrate relative to specimens in which sculpturing was removed (Watters 1994b). These compelling observations notwithstanding, Stanley (1981) concluded that shell sculpture in marine bivalves functions primarily to reduce scour and not to provide anchorage in the substrate. His reasoning was as follows:

(1) buried bivalves are not exposed to strong, lateral displacement forces and (2) by the time scour is extensive, purported anchoring structures on the shell disk have been exposed and are therefore no longer in contact with the sediment. However, the sculpture patterns studied by Watters (1994b) are rare or absent in marine bivalves, and the function of these features has not been studied further.

Another major question is why anchoring adaptations such as disk sculpture and prosogyrous shells are virtually absent in small streams and in some biogeographical regions. Large and small streams alike can have strong currents capable of dislodging mussels, but small streams tend to have more episodic and turbulent flows (Section 4.1.D.1). This fundamental difference in the nature of small vs. large streams may in part explain consistent patterns of shell morphology among these habitats. In large rivers, disk sculpture and inflated, prosogyrous shells may improve anchoring ability to some extent. However, even well-developed anchoring features may be ineffective in turbulent, small streams, and adaptations that increase the ability to reburrow after dislodgement (e.g., smooth and compressed shells) may be selected for in these environments (Watters 1994b; see also Wilson and Clark 1914). Nonsculptured species also are more prevalent in portions of large rivers exposed to highly turbulent, scouring flows (Bartsch et al. 2010). Likewise, dorsal slope sculpture may be retained in small streams because the lack of sculpture on the shell disk does not impede burrowing. Adaptations for burrowing also may be more important in small streams with coarser, heterogeneous substrates relative to larger streams with finer, more homogeneous substrates.

Historical factors are probably largely responsible for current-day geographical patterns of shell morphology (Watters 1994b). The fauna of the Atlantic region is composed primarily of genera characteristic of small streams in the Mississippian region, which may have colonized the Atlantic region by headwater capture, and the latter region lacks a distinctive large-river guild (Section 4.1.D.4). The virtual absence of shell sculpture in the Atlantic region is best explained not by assuming that sculpture is ineffective or disadvantageous in these streams but by considering that lineages possessing sculpture simply never dispersed into this region.

Potential adaptive benefits of shell color are not readily apparent. In epibenthic marine bivalves, shell coloration may provide camouflage from predators (Seilacher 1972; Stanley 1988). In addition to the apparently minor role of predation in the evolution of freshwater shell morphology, most mussels bury into the sediment, and even the exposed portion of the shell is usually obscured by sediments, mineral deposits, or encrustations of algae and larval insect cases (Plate 12). It is even more difficult to imagine an adaptive role for nacre color, which is never exposed or seen. Internal and external shell color of infaunal mollusks was traditionally considered selectively neutral and simply the result of sequestering metabolic waste products in the shell (Comfort 1951; Cox 1969; Jones and Silver 1978). This view is supported by fossil evidence suggesting that shell color in marine bivalves arose before predators with sophisticated vision (Kobluk and Mapes 1989). Food quality and sediment characteristics also influence shell color (Comfort 1951; Underwood and Creese 1976; Cain 1988). However, recent studies have questioned the nonfunctionality of shell color and suggested that shell pigments have a structural function in the formation of the organic matrix in outer shell layers (Hedegaard et al. 2006). In infaunal marine bivalves, variability in shell color may be under a high degree of genetic control, in some species involving one or two polymorphic genes, and in others involving a polygenic, quantitative trait (Winkler et al. 2001; Evans et al. 2009). The maintenance of these polymorphisms suggests that some sort of balancing selection must prevent fixation of shell color by genetic drift (Luttikhuizen and Drent 2008). The genetic basis of shell color in freshwater mussels and its possible functions remain uninvestigated.

Proposed adaptive functions provide compelling explanations for consistent patterns of variation in mussel shell morphology. However, many shell features also could be historical artifacts of past selection pressures or unavoidable outcomes of physical constraints on shell architecture (Gould 1971; Seilacher 1972; Gould and Lewontin 1979). Unlike marine bivalves, for which shell architecture and function have received much attention, the functional morphology of freshwater mussel shells remains surprisingly understudied. Many concepts from marine bivalves can be extended to freshwaters, but radical differences in the challenges faced by these animals preclude extensive generalization. Because shells interact with the environment to a great extent, further study of their functional significance will provide valuable insight into freshwater mussel ecology.

1.4. The animals inside

Many people appreciate the diversity of mussels and the beauty of their shells, but have the idea that the animals themselves don't do anything very interesting. This idea is understandable. Mussels are primarily filter feeders and therefore don't dramatically pursue and catch their prey. They live most of their lives buried in the bottom of a lake or stream, moving slowly, if at all, and undertake no spectacular migrations. Reproduction occurs by males broadcasting sperm into the water, so there are neither elaborate courtship rituals nor battles between rival males. But there is much more to mussels than this bland portrayal suggests, and research continues to reveal unexpected, complex, and fascinating twists in nearly all aspects of mussel ecology.

1.4.A. Feeding

Mussels are omnivores that feed on a wide variety of microscopic particulate material, primarily less than 20 μm in size, including phytoplankton, small zooplankton, bacteria, fine organic detritus, and potentially fungal spores and dissolved organic matter (reviewed by Strayer 2008; Vaughn et al. 2008). Mussels were traditionally considered

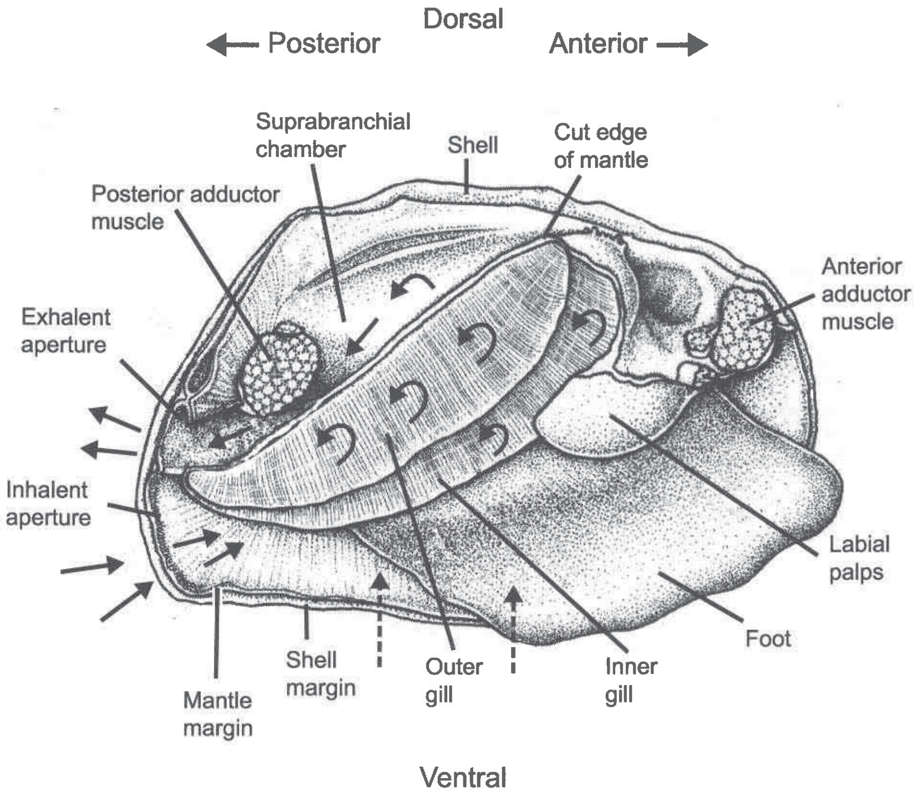

Figure 1.11. Internal anatomy of a freshwater mussel. The right shell is removed and the right portion of the mantle is cut away to show underlying structures. Arrows show the direction of water flow within the animal; arrows with circular stems indicate water flowing through and into the gills, and arrows with dashed stems show interstitial sediment water entering the shell gape. Adapted from Williams et al. (2008).

primarily filter feeders of material suspended in the water column. However, recent research shows that mussels obtain food both by filter feeding and deposit feeding in the sediment (Raikow and Hamilton 2001; Nichols et al. 2005; Vaughn et al. 2008).

1.4.A.1. Mechanics of feeding

Filter feeding is a fundamental process including not only food acquisition but also oxygen uptake, waste excretion, and gamete dispersal and acquisition. Filter feeding occurs via a unidirectional current entering through the inhalant aperture (mussels do not have true siphons like many marine bivalves) and exiting through the exhalent aperture, both located at the posterior shell margin (Figure 1.11). The structure and coloration of apertures differ markedly among many species (Plate 12). The exhalent aperture is dorsal to the inhalant aperture, preventing the uptake of wastes and possibly improving sperm dispersal (Section 1.4.C). The inhalant aperture is ornamented with papillae, which act as a coarse filter; papillae are absent on the exhalent aperture.

The current is established by cilia on the gill surfaces, which draw water through pores (ostia) in the gills, and flow rate can be up to 1 L/hr/individual (see Vaughn et al. 2008). Interstitial water from the sediment also can enter the shell gape along the ventral margin by a current generated by cilia on the foot (Yeager et al. 1994; Nichols et al. 2005; Figure 1.11). In either case, suspended particles are captured on the outer surface of the gills, and oxygen dissolves into the hemolymph carried by vessels in the gills (mussels do not have blood with respiratory pigments such as hemoglobin). Material captured on the gills is moved by ciliary action to the labial palps, two flaps on each side of the mouth that sort food particles from nonedible material. Food particles are transferred to the mouth, and nonedible material is bound in mucus into agglomerations called pseudofeces, which are released into the mantle cavity. Pseudofeces are moved by cilia on the mantle and accumulate at the base of the inhalant aperture and are periodically expelled by rapid valve closure, which forces water out the inhalant aperture counter to the normal direction of flow (McMahon and Bogan 2001); pseudofeces also may be released directly through the shell gape (Nichols et al. 2005).

Deposit feeding occurs in at least two ways: (1) uptake of material through the shell gape by suction via the current generated by cilia on the foot (Nichols et al. 2005) and (2) pedal feeding, in which sediment material is moved into the shell directly by cilia on the foot rather than by a current. Material obtained by pedal feeding accumulates on the ventral surface of the inner gills and is moved to the labial palps similar to material filtered by the gills (McMahon and Bogan 2001). Juvenile mussels pedal feed by sweeping the foot through the sediment while the shell remains stationary or by extending and retracting the foot into the sediment during locomotion (Yeager et al. 1994). Deposit feeding is widespread in marine bivalves, including pedal feeding and use of elongated siphons to vacuum material from the sediment surface (Dame 1996); this latter feeding mode is documented in freshwater fingernail clams (Sphaeriidae; Way 1989) but not in mussels. Fingernail clams and *Corbicula* acquire a large percentage of their energy from deposit feeding, and suspended material may be relatively unimportant (reviewed in McMahon and Bogan 2001). Deposit feeding by freshwater mussels was widely acknowledged only in the 1990s. Juveniles use pedal feeding extensively in addition to suspension feeding (Yeager et al. 1994), but the importance of pedal feeding may decline during the first year as the filtering mechanism becomes better developed (Gatenby et al. 1996). In some situations, adult mussels obtain a substantial portion of their food by deposit feeding, either by suction or pedal feeding (Raikow and Hamilton 2001; Nichols et al. 2005; Brendelberger and Klauke 2009), but the relative importance of deposited versus suspended material remains unknown.

1.4.A.2. Feeding rhythms

The shell must be slightly agape during filter feeding or to extend the foot for deposit feeding (Plate 12). Shell-gaping behavior therefore is indicative of feeding rhythms and other activity patterns. Pumping rate increases linearly with the degree of shell gape (Jørgensen et al. 1988), heart rate is up to 6 times higher when the shell is open than when it is closed (Chen 1998), and respiration rate can be 19 times higher (McCorkle et al. 1979). Active filtering includes frequent, rapid shell closures, as often as 20 per hour and lasting 1–2 sec, followed by gradual reopening requiring 1–3 min (Barnes 1962; Imlay 1968). Rapid shell closures may be associated with locomotion or clearing apertures of sediment (Allen 1923; Barnes 1962; Lewis and Riebel 1984; Section 1.4.B).

Mussels spend much of their time filter feeding, but diurnal or other patterns may exist. In the wild, European *Anodonta anatina* and *Unio tumidus* gaped 65 percent and 93 percent of the time overall, respectively, but nearly 100 percent at night (Englund and Heino 1994a). In the laboratory, the pondmussel, *Ligumia subrostrata*, gaped 40 percent of the time in the day but more than 90 percent at night (McCorkle et al. 1979). In contrast, the pimpleback, *Quadrula pustulosa*, gaped more in the light (62% of individuals) than in darkness (42%), but five other species showed no diurnal rhythm (Chen 1998). Adult western pearlshells, *Margaritifera falcata*, gaped 60 percent of the time, but juveniles gaped almost continuously (Rodland et al. 2009).

The factors regulating filtering activity are poorly known. Light appears to be an important exogenous factor, and there is little evidence of endogenous rhythms governing filtering (McCorkle et al. 1979). Light is thought to be sensed by dermal pigment cells in the mantle margin, and changes in light level can cause either valve closure or opening (Imlay 1968). Food requirements and availability also may be involved. The higher gaping frequency of juvenile *Margaritifera falcata* may be due to higher energetic requirements of rapidly growing juveniles (Rodland et al. 2009). Englund and Heino (1994b) proposed that higher gaping frequency in an oligotrophic lake compared to a eutrophic lake was caused by lower food concentration requiring longer periods of filtering to meet metabolic demands. Similarly, Chen (1998) speculated that nocturnal feeding by a lake species (*Pyganodon grandis*) is related to downward vertical migration of phytoplankton at night, increasing food concentrations near the bottom, but riverine species depending less on phytoplankton feed during the day or have no diurnal rhythm. However, the lack of diurnal pattern in the riverine species as well as constant gaping in juvenile *M. falcata* may be artifacts of their poorer ability to acclimatize to static holding conditions. Shell closure and reduced feeding also are defensive mechanisms in response to stress or disturbance (Aldridge et al. 1987; Pynnönen and Huebner 1995, reviewed in McMahon and Bogan 2001), but valves may gape continuously as temperatures approach lethal levels (Rodland et al. 2009).

1.4.A.3. Diet

Despite more than 100 years of research, a solid understanding of exactly what mussels eat remains elusive (reviewed by Strayer 2008). Isaac Lea (1834:65–66) wrote: "I have in vain attempted to satisfy myself as to the nature of their food . . . it may be pretty safely concluded, that neither animalcula nor food in a more solid state are necessary to the nourishment of Naiades." Determining the diet of mussels is difficult because of the breadth and small sizes of food items ingested and because many ingested items are not assimilated. For example, algal cells may pass through the digestive tract intact and even alive (Coker et al. 1921; Vaughn et al. 2008).

Recent research confirms the long-suspected importance of phytoplankton and detritus in the diet but also shows that mussels feed heavily on bacteria (reviewed in Vaughn et al. 2008). In a stream and lake in Michigan, bacteria were the main source of dietary carbon, but phytoplankton was an important source of vitamins and lipids, and algae-derived carbon represented an important portion of the shell matrix (Nichols and Garling 2000). Therefore, although mussels have cellulolytic enzymes that can digest plant material in detritus, bacteria attached to this material may be a primary food source rather than the detrital particles themselves (Christian et al. 2004). In feeding experiments, the eastern elliptio, *Elliptio complanata*, filtered large numbers of aquatic fungal spores; total energy derived from spores appears low, but they may be rich in micronutrients (Bärlocher and Brendelberger 2004). Mussels also can absorb dissolved organic molecules, such as glucose and NH_3, directly through the gills (Silverman et al. 1997), but such compounds are rarely abundant in solution, and the importance of this food source is unknown (Vaughn et al. 2008). Some freshwater bivalves elsewhere in the world may be partial or complete autotrophs that feed on metabolic by-products of chemosymbiotic bacteria (e.g., *Solenaia* and *Arconaia* (Unionidae) in Indochina; *Mycetopodella* (Mycetopodidae) in South America; *Pleiodon* (Iridinidae) in Africa; Seilacher 1990; Savazzi and Peiyi 1992). The supposition of autotrophy in these species is based on their occurrence primarily in anoxic sediments rich in methane and hydrogen sulfide and on shell and foot morphology similar to autotrophic marine bivalves; this habitat preference and morphology is unknown in North American species.

Diet may vary across habitats and even among species in an assemblage. Mussels in oligotrophic lakes and large rivers appear to feed primarily on phytoplankton and other suspended material, but those in small streams feed across multiple trophic levels, including a heavy reliance on bacteria and benthic sources (Raikow and Hamilton 2001; Griffiths and Cyr 2006, reviewed in Vaughn et al. 2008). It has been proposed that species in an assemblage generally feed similarly on available food resources (Brönmark and Malmqvist 1982; Raikow and Hamilton 2001). However, in stream assemblages, species ingested different algae (Bisbee 1984), and isotopic signatures differed among species, indicating that they selected different components of the available food resource (Nichols and Garling 2000). Furthermore, aspects of gill morphology related to particle capture differ substantially among species, suggesting that they are adapted to using different food resources (Silverman et al. 1997; Galbraith et al. 2009).

1.4.B. Burrowing and movement

1.4.B.1. Burrowing behavior and vertical movement

Mussels live most of their lives burrowed in the bottom of a stream or lake. The anterior end is usually oriented down, with the foot anchored in the sediment (Figure 1.11). The posterior end may protrude into the water but often is flush with the sediment surface such that only the apertures are visible, allowing filtration of the overlying water (Plate 12). In soft sediments, the location of mussels buried just below the surface may be indicated by a shallow depression (Allen 1923; Matteson 1955). Mussels also burrow more deeply, but burrowing depth is modest. Historical reports of mussels buried up to 60 cm deep (Wilson and Danglade 1912) are unsubstantiated and were viewed with skepticism even by contemporaries (Coker et al. 1921). Depending on grain size and other factors, sediments often become anoxic at depths of 10–30 cm (Whitman and Clark 1982). Marine bivalves can burrow more than 1 m deep because their elongated siphons allow access to the sediment surface (Alexander and Dietl 2005). Because freshwater mussels lack true siphons and shell adaptations for deep burrowing (Section 1.3.C), burrowing appears restricted to shallow, well-oxygenated sediments. Adult mussels bury as deeply as 10–20 cm but usually less than 6–10 cm (Balfour and Smock 1995; Shelton 1997; Schwalb and Pusch 2007); in captivity, juveniles buried less than 1 cm (Yeager et al. 1994). The greatest burrowing depth reported in recent literature is 35 cm for European *Unio crassus* in well-oxygenated sediments (Engel 1990, as cited in Schwalb and Pusch 2007).

Anecdotal accounts describe mussels in streams oriented consistently with the posterior end directed into the current (Coker et al. 1921; Baker 1928), presumably to prevent refiltration of waste and to reduce drag on the shell (Di Maio and Corkum 1997). However, existing data show little or no evidence of consistent orientation with the current (Tevesz et al. 1985; Perles et al. 2003). For example, a small majority of individuals (63%) at one site were oriented within 30° of the current, but at another site, only 31 percent were oriented in this manner; at both sites, other individuals were oriented in every possible direction (Di Maio and Corkum 1997).

Burrowing and movement is accomplished by first relaxing the adductor muscles, allowing the hinge ligament to pull the shell valves apart and anchor the shell against the surrounding substrate. Second, the foot is extended into the substrate and the distal end expands, anchoring the foot in its new position. Third, the adductor muscles contract rapidly, releasing the shell's grip on the substrate and forcing a jet of water through the pedal gape, which loosens sediment at the anterior end of the shell. Last, the foot contracts, pulling the shell forward, and the shell opens to anchor the mussel in its new position (McMahon and Bogan 2001; Smith 2001). This burrowing cycle results in a rocking motion within the substrate (Stanley 1988) and is repeated more than 25 times with a pause of about 1 min or more between cycles; the pause may allow sediments to reconsolidate, providing additional anchorage for the next

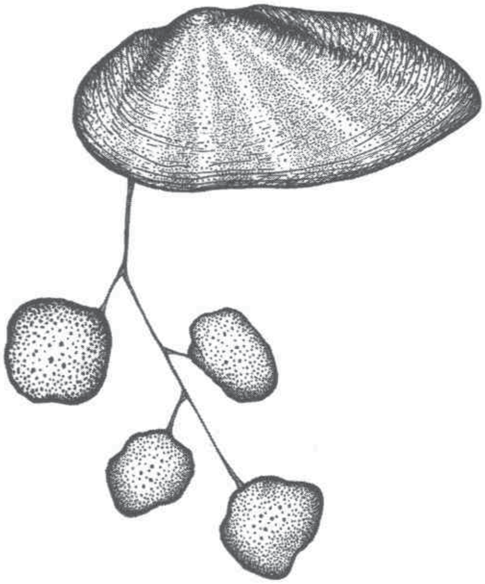

Figure 1.12. Adult *Medionidus acutissimus* (shell length about 30 mm) showing branched byssal thread attached to pebbles (drawn by Stephanie Korschun).

burrowing cycle (Savazzi and Peiyi 1992). Consequently, mussels dislodged from the substrate may require more than 30 min to rebury, but burrowing is more rapid in sand and silt than in gravel (Lewis and Riebel 1984; Savazzi and Peiyi 1992). In most species, the extended foot is about one-third to one-half the length of the shell. Burrowing and anchoring ability is especially well developed in *Hemistena lata*, in which the foot is at least as long as the shell (Ortmann 1915), and it is difficult to extract this species from the substrate (Neel and Allen 1964).

Burrowing is important in reducing dislodgement and transport to unsuitable habitats. In a German river, burrowing depth was correlated positively with discharge and current velocity; although most individuals were at the sediment surface throughout the summer, 60 percent burrowed rapidly but briefly during a flood in July (Schwalb and Pusch 2007). The percentage of *Elliptio complanata* near the sediment surface decreased about 10 percent during summer holiday weekends having heavy boat traffic (Amyot and Downing 1997). Burrowing also can reduce infestation by invasive zebra mussels (*Dreissena* spp.; Nichols and Wilcox 1997; Section 10.4.C). Burrowing has been considered an adaptation for drought survival (Matteson 1955), but this ability appears well developed in few species (Section 4.1.D.1).

Juveniles of some species avoid dislodgment using a byssus, an elastic, proteinaceous thread up to 300 mm long secreted by the byssal gland in the foot (Smith 2000). The byssus may be branched at its distal end and is attached to pebbles, adult mussel shells, sticks, or other objects (Isely 1911; Boepple and Coker 1912; Figure 1.12). Frierson (1903a) speculated that the byssus also might be used for dispersal, similar to the ballooning behavior of hatchling spiders or dispersal in juvenile *Corbicula* (Prezant and Chalermwat 1984). The byssus is present in most Lampsilini but is absent in most Margaritiferidae, Amblemini, Anodontini, Pleurobemini, and Quadrulini (Isely 1911; Coker et al. 1921; Smith 2000). The byssus appears within the first 38 days of life and disappears by the end of the first or, rarely, the second year (Coker et al. 1921; Howard 1922). The byssus is retained in the adult stage only in a few small species, including *Medionidus* spp., the fawnsfoot, *Truncilla donaciformis*, and the rayed bean, *Villosa fabalis* (Howard 1922; Smith 2000; D. Woolnough, personal communication), for which it evidently remains an effective anchor. Adult Alabama moccasinshells, *Medionidus acutissimus*, often lie unburied on the substrate surface and tethered to pebbles even in swift riffles (W. R. Haag, observations; Figure 1.12). Similarly, juvenile mussels appear frequently to lie on or near the sediment surface because they often are collected incidentally when the byssus becomes entangled in fishing or sampling gear (Coker et al. 1921; Havlik 1983), and large numbers of juvenile mussels have been observed tethered to shells of adult mussels (Boepple and Coker 1912). Apart from small species that retain the byssus, adults of few species characteristically remain unburied. The rabbitsfoot, *Quadrula cylindrica*, Cumberland monkeyface, *Q. intermedia*, and pistolgrip, *Q. verrucosa*, often lie completely exposed on the substrate surface, but they typically occur in slack water areas adjacent to the main current, where the danger of dislodgement is lower (Section 4.2.A).

Burrowing appears to have a strong seasonal component. Mussels tend to be near the substrate surface in spring and summer but burrow more deeply in fall and winter. This behavior has been described for nearly two hundred years (Rafinesque 1820, Isely 1914) and is supported by a growing body of evidence (Amyot and Downing 1991, 1997; Watters et al. 2001; Schwalb and Pusch 2007). In a small stream, more than 90 percent of *Elliptio complanata* were buried beneath the substrate surface in December and January, but mussels began to emerge in February; by April, more than 80 percent were near the surface, and this percentage remained over 60 percent into November (Balfour and Smock 1995). Nevertheless, this behavior is variable. Although all studies reported increased burrowing depth in winter, a sizeable proportion of individuals may remain visible at the surface (Watters et al. 2001; Perles et al. 2003), and *Lampsilis siliquoidea* has been seen moving under ice cover in a lake (Evermann and Clark 1918). *Alasmidonta undulata, A. varicosa*, and *Strophitus undulatus* are reported to remain buried in summer but emerge from the substrate in winter (Bogan 2002).

Burrowing behavior also appears to vary among species and populations. In mesocosm experiments, *Actinonaias ligamentina* and *Amblema plicata* buried less deeply and were more active than *Fusconaia flava* and *Obliquaria reflexa* (Allen and Vaughn 2009). Similarly, *Lampsilis cardium* and *Potamilus alatus* reburrowed after disturbance about 3 times faster than *A. plicata* and *F. flava* (Waller et al. 1999). In the wild, the percentage of mussels visible at the sediment surface in summer varied from 8 to 100 percent among several species and from 33 to 83 percent among rivers (all species combined); for *Alasmidonta heterodon*, the percentage near the surface varied from 22 to 64 percent among three sites (Smith et al. 2000).

Burrowing behavior may be influenced by a number of factors. Emergence from the substrate in spring is correlated with day length and water temperature (Amyot and Downing 1997; Perles et al. 2003; Schwalb and Pusch 2007). Proximate cues are unknown, but rapid emergence after ice-out in May, when day length is increasing rapidly but temperatures remain low, suggests that day length is important (Amyot and Downing 1997). *Elliptio complanata* in lakes emerged earlier at sites exposed to winds and wave action than at more protected sites (Cyr 2009). In mesocosm experiments, burrowing activity increased at higher mussel density, suggesting that competition for space causes mussels to adjust their position frequently (Allen and Vaughn 2009).

Emergence from the sediment in spring and summer coincident with spawning and glochidial release suggests that burrowing behavior has a reproductive component (Balfour and Smock 1995; Amyot and Downing 1997; Watters et al. 2001; Schwalb and Pusch 2007). In summer, the percentage of female northern riffleshells, *Epioblasma torulosa rangiana*, at the sediment surface (80%) was nearly twice that of males (45%; Smith et al. 2001), probably because females display mantle lures and release glochidia during this time (Section 1.4.C; Chapter 5). In other *Epioblasma*, mass appearance of females on the sediment surface during periods of lure display is a conspicuous annual event (Jones et al. 2006a; Section 5.3.C.2). Subadult mussels (less than 1 year old) are reported to remain completely buried even during summer (Amyot and Downing 1991; Balfour and Smock 1995; Schwalb and Pusch 2007). This could be an artifact of the difficulty of detecting small individuals at the surface, but such behavior is concordant with a greater risk of fish predation for juveniles (Chapter 7), greater dependence on pedal feeding, and lack of reproductive activity.

1.4.B.2. Horizontal movement

In contrast to their limited vertical movement, mussels can undertake lengthy horizontal movements on the substrate surface. The conspicuous trails left by crawling mussels (Figure 1.13) were noticed by even the earliest observers (e.g., Rafinesque 1820). However, horizontal movement appears limited in most cases, with only occasional individuals undertaking greater movements. Across 37 stream sites involving observations on 2,161 individuals of 22 species, only 2 percent of individuals were associated with trails in the sediment indicating recent movement (Strayer 1981). Similarly, 85 percent of tagged mussels ($n = 164$) were recovered after 1 year at "the very spot where they were planted," and only one recovered individual moved an appreciable distance (about 5 m; Isely 1914). Most *E. complanata* moved less than 6 m (average = 2.9 m) during one year, but a few individuals moved up to 46 m

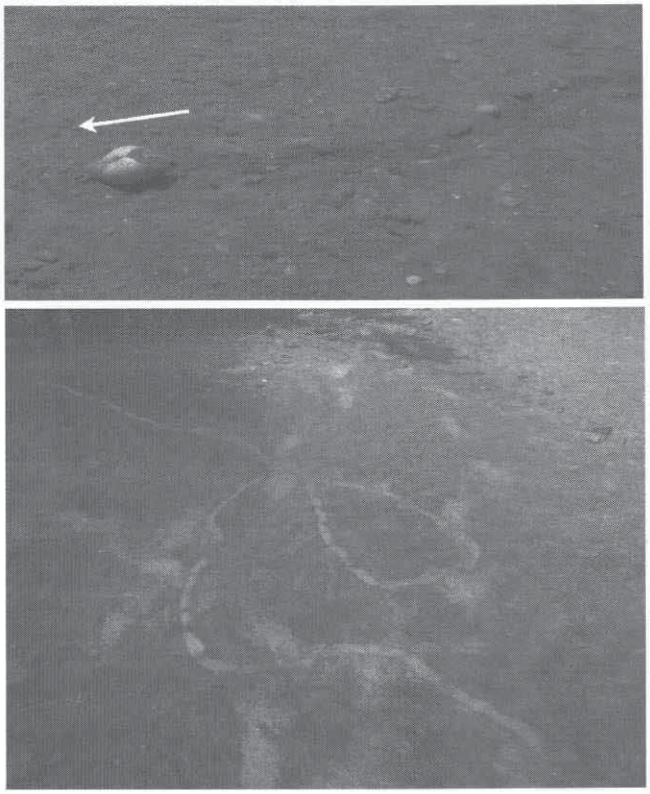

Figure 1.13. Mussel movement. (top) Southern pocketbook, *Lampsilis ornata* (below arrow), moving on the sediment surface in shallow water showing trail behind; arrow indicates direction of movement. (bottom) Long trail crossing back on itself; shoreline is at upper right (James Stoeckel, photos).

(Balfour and Smock 1995). In other studies, weekly movement distances averaged 0–0.1 m, with less than 10 percent of mussels moving 0.3–2.3 m (Amyot and Downing 1997; Schwalb and Pusch 2007).

Anecdotal observations suggest considerable differences in movement among species. Species in the Anodontini and Lampsilini are considered especially active (Call 1900; Isely 1914; Coker et al. 1921). The yellow sandshell, *Lampsilis teres*, was described as "one of the most active of the mussels, responding quickly to changes in [the] environment" (Wilson and Clark 1914, 50), and the fragile papershell, *Leptodea fragilis*, was described as "a lively shell, crawling around frequently, and with a speed unusual in other shells" (Ortmann 1919, 251). The rabbitsfoot, *Quadrula cylindrica* (Quadrulini), also was described as "a rather active species" (Wilson and Clark 1914, 59), but other Quadrulini, as well as the Amblemini, Pleurobemini, and Margaritiferidae, are considered relatively sedentary (e.g., Coker et al. 1921). Movement may be especially limited in dense mussel beds in firmly packed gravel substrates

(Section 4.1.D.4); mussels are extracted from these sediments with difficulty, suggesting that they move rarely, if ever. Mussel beds are dominated by purportedly sedentary Amblemini, Pleurobemini, and Quadrulini but also by a few Lampsilini (e.g., *Actinonaias*, *Ellipsaria, Obliquaria*). Similarly, the spectaclecase, *Cumberlandia monodonta* (Margaritiferidae), often is wedged tightly between boulders (Stansbery 1966), making movement difficult or impossible. In mesocosm experiments, the mucket, *Actinonaias ligamentina*, moved significantly more than three other species (Allen and Vaughn 2009), but few or no other studies have quantified differences in movement among species.

Like vertical movement, the factors that influence horizontal movement are poorly known. Movement was positively correlated with day length in one study (Amyot and Downing 1997) and with temperature in another (Schwalb and Pusch 2007). It is assumed that mussels do not move in winter when they are burrowed in the sediment (Amyot and Downing 1997), but *Lampsilis siliquoidea* under ice cover moved about 0.5 m in a few days (Evermann and Clark 1918).

Water level is widely recognized as a strong cue for movement. Anyone who has visited a stream at low water has seen the trails of mussels retreating to deeper water and those unlucky stranded individuals that didn't make it. Several species appear to track water levels closely, moving shoreward during high water and retreating to deeper water as water levels recede (e.g., Wilson and Clark 1914; Coker et al. 1921; White 1979; Johnson 2001; Gagnon et al. 2004; Allen and Vaughn 2009). For example, a large gravel bar in the Sipsey River, Alabama, was completely exposed and dry throughout summer and fall 1998. By the following April, the bar was submerged and had been colonized by adults of several species (*Lampsilis straminea*, *L. teres*, *Obovaria unicolor*, *Quadrula asperata*, *Pleurobema perovatum*, *Villosa lienosa*), which had moved more than 12 m from the previous low-water shoreline (W. R. Haag, observation). The adaptive value of this behavior is unknown, but the benefits must outweigh the considerable risk of stranding and perhaps predation by terrestrial animals.

In lakes, mussels are reported to move away from shore during periods of high wave action (Headlee and Simonton 1904) and to undertake annual fall migrations to deeper water (Evermann and Clark 1918). In northern climates, offshore movement in fall would reduce the chances of being affected by ice scour along shorelines. However, other studies did not observe fall migration (van der Schalie 1938a; Matteson 1955) and, like movement in relation to water level, this behavior has received little recent study.

Mussel movement also has been suggested to have a reproductive component. A population of *Elliptio complanata* was more aggregated during the spawning season (May–June) compared to the postspawning period (July–October); furthermore, only animals at the sediment surface aggregated in this manner, but the spatial distribution of buried individuals (consisting of a large percentage of immature individuals) did not change during the study (Amyot and Downing 1998). Similarly, 85 percent of Alabama pearlshells, *Margaritifera marrianae*, occurred in purported male–female pairs with individuals located less than 1 m from each other (Shelton 1997). These patterns were interpreted as adaptations for increasing female fertilization (Section 1.4.C). However, sex determination of individuals constituting male–female pairs in *M. marrianae* was based on shell morphology, but reliable sexual dimorphism is not documented in this species (Williams et al. 2008). Moreover, the sensory cues that allow mussels to detect the presence and sex of other individuals are unknown, and increased aggregation during certain times of the year could be related to other movement phenomena. Nevertheless, these findings underscore how little we know about mussel movement and the potential breadth of adaptations that remain undiscovered.

1.4.C. Life history and reproduction

Aristotle thought bivalves arose spontaneously from mud or sand (Heard 1998). This would be remarkable indeed, but as always, the truth is even more interesting. Perhaps more than any other part of their ecology, the fascinating life cycle of freshwater mussels dispels notions that they are bland and uninteresting animals. Many aspects of mussel life history are addressed in detail elsewhere in this book (especially in Chapters 5–7), but I provide here an overview, including topics not addressed later.

The most unique feature of the mussel life cycle – one that distinguishes them from all other bivalves – is the parasitic relationship between mussel larvae and fishes. Freshwater mussels are free living for more than 99 percent of their lives, but in nearly all species, larval development is dependent on a period of a few weeks during which larvae are parasites on fish. In the Margaritiferidae, Unionidae, and Hyriidae, these parasitic larvae are called *glochidia*. An additional parasitic larval form, the *lasidium*, occurs in the African and South American families Etheriidae, Mycetopodidae, and Iridinidae (Wächtler et al. 2001). These host–parasite relationships are complex, sometimes bizarre, and tie the fate of mussels to those of their fish hosts.

1.4.C.1. Sexes and gametes

Most mussel species are gonochoristic, having separate male and female sexes. Occasional hermaphrodites occur but usually compose a small percentage of a population, and hermaphrodites often are functionally gonochoristic (Section 6.2). A few species have a higher incidence of functional hermaphrodites or occur as completely hermaphroditic populations. Parthenogenesis (development of eggs without fertilization) is unknown in bivalves but occurs in a few snails (Dillon 2000). Sex change, including changes in the frequency of hermaphrodites and protandry, may occur in some species but appears to be rare (Section 6.2).

In both sexes, gonads lie within the visceral mass near the base of the foot and are closely intertwined with the digestive system (Mackie 1984). In many species, gametogenesis occurs over much of the year, but developing or fully mature gametes may be held in a suspended state during winter (*Actinonaias, Amblema, Cyclonaias, Elliptio, Medionidus, Lampsilis, Quadrula*, and *Villosa*; Zale and Neves 1982a; Holland-Bartels and Kammer 1989; Jirka and Neves 1992; Haggerty et al. 1995; Garner et al. 1999). In others, gonads are inactive most of the year, and gametogenesis occurs only during 2–4 months prior to spawning (*Arcidens*, *Megalonaias, Potamilus*; Haggerty and Garner 2000; Haggerty et al. 2005; Haggerty et al. 2011). The reasons for these disparate gametogenic cycles are unknown as they appear unrelated to phylogeny or timing of glochidial brooding and release (see subsequent sections). Gametogenic cycles also may differ among populations of the same species (Holland-Bartels and Kammer 1989; Woody and Holland-Bartels 1993; Haggerty and Garner 2000; Haggerty et al. 2005).

1.4.C.2. Spawning and fertilization

Gamete maturation and spawning generally occur from spring to late summer but as late as October in the washboard, *Megalonaias nervosa* (Haggerty et al. 2005). In some species, spawning is highly synchronous, occurring within 1–3 weeks (Zale and Neves 1982a; Haggerty and Garner 2000; Haggerty et al. 2011), but in others, spawning occurs over 2–4 months (Holland-Bartels and Kammer 1989; Jirka and Neves 1992; Garner et al. 1999; Galbraith and Vaughn 2009). Water temperature is considered a primary cue for spawning (Zale and Neves 1982a; Holland-Bartels and Kammer 1989; Hastie and Young 2003; Galbraith and Vaughn 2009). Reproduction was suspended in a population of *Megalonaias nervosa* in a river subjected to chronically low temperature from an upstream hydroelectric dam (maximum temperature less than 20°C), but individuals resumed gametogenesis and glochidial production when moved to a stream with an unaltered temperature regime (Heinricher and Layzer 1999). Other potential factors, such as photoperiod, chemical cues, and food availability, have received little or no study (see Galbraith and Vaughn 2009).

During spawning, sperm are released into the water, where they are taken up by females during filter feeding. Simultaneously, females release eggs from the gonads into the suprabranchial chamber, dorsal to the gills, which is likely the site of fertilization (Yokley 1972; Haggerty et al. 1995; Figure 1.11). Although fertilization occurs within the female's body, this is not strictly considered internal fertilization because it takes place external to the reproductive tract (Mackie 1984). This mode of reproduction is referred to as *spermcasting* or *spermcast mating* to contrast it with *broadcasting spawning*, in which both males and females release gametes and fertilization takes place in the water column (Bishop and Pemberton 2006, Falese et al. 2011).

Mechanisms of sperm uptake and subsequent fertilization of eggs are poorly understood. In hermaphroditic species, some populations show a high rate of self-fertilization (up to 100%), but others are predominantly outcrossing (Johnston et al. 1998). In gonochoristic species, paternity has been investigated in only a single species, the rainbow, *Villosa iris*, in which female broods were fertilized by multiple males (Christian et al. 2007). Females are assumed to obtain sperm haphazardly from the drift, but adaptations may exist to increase the probability of fertilization. Aggregation during spawning is one suggested adaptation (Section 1.4.B.2), but other aspects of sperm release probably represent more widespread mechanisms to increase fertilization. Synchronous, mass spawning, as exhibited by some mussel species, is a common adaptation in marine invertebrates to increase fertilization. In addition, several mussel species release sperm in hollow, spherical aggregates called *spermatozeugmata* or *sperm spheres*. Spermatozeugmata are rare in marine bivalves (Coe 1931; O'Foighil 1989) but appear to be widespread in freshwater mussels.

Spermatozeugmata are composed of a thin spherical membrane about 28–76 µm in diameter into which the sperm heads are embedded with the flagella protruding to the outside. Each spermatozeugmata contains about 3,600–9,000 sperm and may represent the contents of a single primary spermatogonium (Coe 1931; Barnhart and Roberts 1997; Waller and Lasee 1997). Spermatozeugmata may have at least two functions. First, spermatozeugmata swell about 2 times in diameter within a few hours of release, suggesting that the membrane is semipermeable and contains a saline environment that protects sperm from the lower osmotic pressure of freshwater (Ishibashi et al. 2000). The central core of spermatozeugmata also may contain lipids that increase sperm longevity (Falese et al. 2011). Mussel sperm are viable in freshwater for only a few minutes but for more than 48 hours in spermatozeugmata, greatly extending the distance sperm can travel to encounter a female. Second, sperm migrate to one side of the spermatozeugmata shortly after release, and synchronous beating of the flagella imparts directional movement (Barnhart and Roberts 1997; Ishibashi et al. 2000). Dispersal of spermatozeugmata is triggered by exposure to a salt solution, suggesting that sperm are liberated when the structure enters a female, and more significantly, spermatozeugmata could exhibit taxis toward chemical cues such as the presence of a female mussel (Barnhart and Roberts 1997).

Spermatozeugmata are reported in 10 North American species representing all five tribes in the Unionidae (Utterback 1931; Edgar 1965; Lynn 1994; Barnhart and Roberts 1997; Waller and Lasee 1997; Watters et al. 2009; Bringolf et al. 2010) and in two European and six Asian species (Pekkarinen 1991; Ishibashi et al. 2000). The broad phylogenetic and geographic occurrence of spermatozeugmata strongly suggests that they are a general feature of freshwater mussels and an important adaptation for increasing fertilization success (Section 6.2.A).

1.4.C.3. Brooding and glochidia

Fertilized eggs are deposited in the primary water tubes of the gills, where they are brooded by the female (Figure 1.11). The portion of the gills used for brooding varies among phylogenetic groups (Williams et al. 2008). In the Margaritiferidae, Amblemini, most Quadrulini, and two species of uncertain taxonomic placement (ebonyshell, *Reginaia ebena*, and bankclimber, *Plectomerus dombeyanus*), nearly the entire length of all four gills is used for brooding. In *Cyclonaias* and *Uniomerus* (Quadrulini) and in the Anodontini, brooding takes place along the entire length of the outer gills only. Brooding varies within the Pleurobemini. *Elliptoideus, Fusconaia*, and *Hemistena* brood in the entire length of all four gills, but *Elliptio, Pleuronaia, Plethobasus*, and *Pleurobema* brood in the entire outer gills only; *Pleurobema* rarely brood larvae in the inner gills as well. The majority of the Lampsilini brood larvae only in about the posterior half of the outer gills; *Cyprogenia* and *Obliquaria* brood only in less than 10 water tubes in the central portion of the outer gills, and *Dromus* and *Ptychobranchus* brood throughout nearly the entire outer gills. Brood size varies widely among mussel species from several hundred to more than 10 million but is not correlated with the portion of the gills used for brooding (Section 6.2.C).

Eggs are brooded by the female until they develop into mature glochidia. Mussels are considered ovoviviparous, with the developing glochidia nourished by yolk reserves (Tankersley 2000; McMahon and Bogan 2001). However, maternal carbon and calcium are transferred to developing glochidia, the latter representing the primary calcium source for glochidial shell formation (Wood 1974; Silverman et al. 1987), and in some species, brooding females have glycogen deposits in the gills that may be used by developing glochidia (Schwartz and Dimock 2001). Gravid gills become moderately to greatly swollen – up to 30 times their normal thickness – and undergo extensive morphological change (Tankersley and Dimock 1992). In the Anodontini, gravid gills develop secondary water tubes that do not contain glochidia and partially offset reductions in feeding and respiratory efficiency caused by impeded water flow in the gravid primary water tubes; secondary water tubes disappear 1–2 weeks after glochidial release (Richard et al. 1991; Tankersley and Dimock 1993; Tankersley 1996). Secondary water tubes are absent in other mussel groups (Mackie 1984; Richard et al. 1991). In all studied species, gravid water tubes are capped dorsally by septa that isolate the glochidia from ambient water, and ostia in the gill walls are under muscular control, allowing females to constrict these openings (Richard et al. 1991). Isolation of glochidia from ambient water in this manner allows maintenance of a favorable osmotic environment and may protect glochidia from adverse conditions (Richard et al. 1991; Schwartz and Dimock 2001).

The timing and duration of the brooding period varies but can be classified into two broad groups: short-term and long-term brooders. These groups also are referred to by the arcane and cumbersome terms *tachytictic* (short term) and *bradytictic* (long term) (Ortmann 1911). In short-term brooders, eggs are usually fertilized in the spring or summer and brooded until they develop into mature glochidia (requiring 2–6 weeks), and glochidia are released shortly thereafter (Yokley 1972; Weaver et al. 1991; Bruenderman and Neves 1993; Garner et al. 1999). After glochidial release, female gills are empty until spawning in the following spring or summer. In long-term brooders, eggs are fertilized usually in the late summer or fall, and similar to short-term brooders, eggs develop rapidly into mature glochidia in less than 8 weeks (Trdan 1981; Zale and Neves 1982a). However, most long-term brooders then brood mature glochidia over the winter and into the following spring or summer. Glochidial release by long-term brooders may occur somewhat synchronously within a narrow time frame – similar to short-term brooders – but more often occurs over a protracted period sometimes with one or two peaks in spring or summer (Zale and Neves 1982a; Watters and O'Dee 2000; Culp et al. 2011). Gametogenesis accelerates during the end of the brooding period, and fertilization of the next brood usually occurs within less than 2 months of glochidial release; consequently, gills of long-term brooders are gravid much of the year (Trdan 1981; Zale and Neves 1982a; Jirka and Neves 1992). Most species appear to produce only a single brood annually, but multiple broods may occur in some short-term brooders and in the paper pondshell, *Utterbackia imbecillis* (Section 6.2.C).

Considerable variation in timing exists within these brooding strategies. The short-term brooder *Megalonaias nervosa* fertilizes eggs and releases glochidia from September to December, well after most short-term brooders (Howells 2000; Haggerty et al. 2005). Some species in the Anodontini release glochidia mostly in the winter, and the brooding period may therefore be considerably shorter than for other long-term brooders (Barnhart and Roberts 1997; Watters and O'Dee 2000; Haggerty et al. 2011). The reproductive period of *Utterbackia imbecillis* (Anodontini) is not easily classified; some studies have reported multiple, consecutive broods in a season, but others reported only a single gametogenic cycle (Section 6.2.C). Apart from these exceptions, brooding patterns are highly consistent within major phylogenetic groups. Short-term brooding characterizes all species in the Margaritiferidae (Bauer 1987; Baird 2000), Amblemini, Pleurobemini, and Quadrulini. Long-term brooding characterizes all Anodontini (except possibly *U. imbecillis*) and most Lampsilini, within which only the threehorn wartyback, *Obliquaria reflexa*, is a short-term brooder (Ortmann 1919; Williams et al. 2008).

1.4.C.4. Glochidial metamorphosis and the parasitic stage

Glochidia are miniature bivalves having two shells attached by a hinge ligament and a single adductor muscle; otherwise, apart from the mantle, glochidia lack most anatomical features of adult mussels (Wächtler et al. 2001). Glochidia of at least two species in the Anodontini can bypass the parasitic stage and undergo direct development into juvenile mussels while brooded in the female gills; however, these species also can parasitize fishes, and the degree to which direct development is a facultative strategy is unknown (Section 5.2). All other species appear to require the parasitic stage for larval development, and on maturity, glochidia are released from the female to encounter a host. Glochidia can survive about 2–14 days after release, depending on species and temperature; survival is longer at colder temperatures (Fisher and Dimock 2000; Zimmerman and Neves 2002). Because glochidia must encounter a suitable host within a relatively short time, mussels have an array of fascinating strategies to attract host fishes or otherwise increase the chances for host encounters (Chapter 5). Many mussel species use only one or a few closely related fish species as hosts, and host specificity varies widely among mussel species. Consequently, host infection strategies are tailored to increase chances of glochidia encountering only a *particular* fish species or group of species.

When glochidia encounter a fish, stimulation of sensory hairs within the shell causes the valves to clamp onto the fish's gills or fins (Arey 1921). If glochidia attach to a nonsuitable host species, they are rejected by the fish's immune system, usually within 2–3 days. Glochidia that attach to suitable hosts become encapsulated by the fish tissue, forming a cyst in which they undergo an anatomical metamorphosis, including loss of larval structures and development of adult structures such as paired adductor muscles, foot, gills, and the digestive system (Coker et al. 1921; Tucker 1927; Arey 1932a; Waller and Mitchell 1989; Fisher and Dimock 2002a). While encysted, glochidia obtain nutrients from host tissues and blood plasma and potentially from degeneration of glochidial structures (Arey 1932b; Isom and Hudson 1982; Fisher and Dimock 2002b). Glochidia remain encysted on hosts for a variable period usually lasting about 2–4 weeks but ranging from 7 to more than 100 days, and some species may routinely overwinter on hosts (Chapter 5). When metamorphosis is complete, juvenile mussels are liberated from the cyst, perhaps in response to opening of the shell valves and protrusion of the foot (Arey 1932a; Waller and Mitchell 1989); at this time, juveniles fall to the bottom and assume a free-living benthic existence for the remainder of their lives.

1.5. The role of mussels in freshwater ecosystems

Mussels can be abundant and conspicuous components of freshwater ecosystems, and they were even more abundant, if not ubiquitous, in the past. Because of their large size compared to other benthic organisms, mussels often compose more than 50 percent, but sometimes more than 90 percent, of total benthic biomass (Negus 1966; Hanson et al. 1988; Strayer et al. 1994). Even at a low density of $0.03/m^2$, mussels composed about 25 percent of total macrobenthic biomass in a lake (Strayer et al. 1981). In marine waters, bivalves are similarly prominent, and the profound impact of these animals on those ecosystems is widely recognized (e.g., Dame 1996). Like other aspects of their ecology, the functional role of freshwater mussels in a broad context was largely ignored for many years. However, recent research shows that in many cases, mussels are keystone species and ecosystem engineers that have a large impact on other organisms, and they provide tangible benefits to humans as well.

Mussels serve several important functions in aquatic ecosystems (Vaughn and Hakenkamp 2001; Gutiérrez et al. 2003; Zimmerman and de Szalay 2007; Vaughn et al. 2008). Dense mussel assemblages can filter an enormous volume of water that can exceed daily stream discharge. Such heavy filtering can reduce phytoplankton abundance and increase water clarity, and material filtered from the water is later deposited in the sediment as feces and pseudofeces. Biodeposition of filtered material and excretion of dissolved nutrients link pelagic and benthic food webs and increase food availability for other organisms, including other mussels. Burrowing by mussels mixes sediments, increasing sediment oxygen content and releasing nutrients. Filtering and burrowing can stimulate production across multiple trophic levels and play a large role in nutrient cycling. Dense mussel beds can stabilize substrates, and both living and dead shells increase habitat heterogeneity and provide physical habitat for many organisms. Dead shells also may represent an important source of calcium in calcium-poor waters (Green 1980). Finally, mussels serve as food for several fishes, mammals, and birds (Chapter 7).

The ecological role of mussels varies at several levels. Although they may compose a high percentage of biomass, because of the slow growth of many species, production can be low, especially in sparse populations (Strayer et al. 1981). Dense assemblages, especially those consisting of fast-growing species, have much higher production and have greater effects on nutrient cycling and other ecosystem processes (Negus 1966; Vaughn et al. 2004). The magnitude of ecosystem services provided by mussels varies widely according to environmental factors such as temperature and streamflow, which determine metabolic rates and the amount of water processed by filter feeding (Howard and Cuffey 2006a; Spooner and Vaughn 2006; Spooner et al. 2012). The structure and composition of mussel assemblages also have great bearing on ecological function. Because they were considered generalized filter feeders, mussel species were traditionally viewed as functionally equivalent. However, it is increasingly apparent that ecological roles differ greatly among species, and some are particularly important drivers of ecological processes (Vaughn et al. 2007). Furthermore, these roles change along environmental gradients, providing additional complexity in ecological function (Spooner and Vaughn 2008).

The great complexity and variability of all aspects of mussel ecology emphatically dispels the notion that mussels don't do anything interesting. Indeed, the more we learn, the more we realize how many other surprises these animals hold. In addition to their beautiful shells, spectacular diversity, and fascinating life history, the integral ecological role of these animals emphasizes the tragedy of the catastrophic decline of the North American fauna. As mussels are lost from our streams and lakes, the loss of ecosystem services will further hasten mussel declines and have tangible, negative effects on other organisms, including humans. A better understanding of mussel ecology is essential for understanding the evolution of this rich fauna and for developing effective strategies to save it.

Chapter 2

Catching the mussel bug

A history of the study of mussel ecology in North America

2.1. The early naturalists, 1800–1880

Early naturalists in North America marveled at the vast array of previously unknown plants and animals they encountered, especially as they penetrated the interior of the continent west of the Appalachian Mountains. Consequently, they occupied themselves primarily with naming and cataloging new species. In addition to professional scientists, natural history was a popular pastime for laypeople throughout the 1800s in North America and Europe (Porter 1986; Allen 2001). Shell collecting, in particular, became somewhat of a craze during this period (Allen 2001). Many affluent gentlemen amassed large, private collections of freshwater shells and traded specimens widely with other collectors. Little distinction was made between professionals and hobbyists; many professional naturalists lacked formal scientific training, and shell collectors often dabbled in taxonomy. Descriptions of new species referenced the specimens in question as residing in, for example, "my cabinet and the cabinet of Rev. George White" (Clench and Turner 1956, discussing species descriptions of Isaac Lea). Although many of these private collections were lost, some survived and formed the nucleus of current-day research collections (e.g., Stansbery and Stein 1983). For species that went extinct prior to modern scientific study, the majority of, or in some cases, the only, specimens now in existence came from these private collections. It is largely because of the efforts of these early naturalists and collectors that we have some picture of the magnificent mussel fauna of North America when it was relatively intact.

One of the first and most colorful naturalists to see the great diversity of North American mussels was Constantine Samuel (Smaltz) Rafinesque (1783–1840). Rafinesque was a largely self-taught naturalist of French and German descent who immigrated to the United States in 1802 (Boewe 1988). In 1805, he settled in Sicily, where he made a fortune as a merchant, allowing him to retire and devote his full attention to natural history. While returning to the United States in 1815, he was shipwrecked off the coast of Connecticut, losing his natural history library and collections as well as his savings; for the rest of his life, he struggled financially and was often destitute (Boewe 1988). In 1818, he made an extended trip across the Allegheny Mountains and down the Ohio River. This journey focused his passion for natural history discovery. In a letter from the Falls of the Ohio at Louisville, Kentucky, he wrote to a friend in Philadelphia, "My discoveries increasing daily and so fast . . . they have continued to exceed my most sanguine expectations" (Boewe 1988, 53). Shortly after this trip, Rafinesque obtained a position as professor of botany and natural science at Transylvania University in Lexington, Kentucky, which he held from 1819 to 1826. During this period, Rafinesque continued his biological explorations of the frontier and described numerous species of plants and animals, including a monograph on the mollusks of the Ohio River system (Rafinesque 1820, 1831).

Despite his discoveries, many of the species described by Rafinesque are not currently recognizable because of his vague descriptions, crude drawings, and failure to deposit specimens in museum collections (Parmalee and Bogan 1998). In addition to his careless methods, his eccentric and erratic behavior generated considerable enmity from his contemporaries and caused much of his work to be ignored for over a century. His contributions were banned by the *American Journal of Science* and the *Proceedings of the Philadelphia Academy of Natural Sciences*, two of the leading scientific outlets of his day, forcing him to publish his work privately or in obscure outlets (Boewe 1988).

Rafinesque's eccentricity and zeal for describing new species is illustrated by his encounter with John James Audubon during Rafinesque's 1818 trip down the Ohio River. Rafinesque stayed at Audubon's home in Henderson, Kentucky, for 3 weeks, and Audubon recorded the visit in his journals (Audubon 1899). Rafinesque arrived with a letter of introduction stating, "My dear Audubon, I send you an odd fish, which you may prove to be undescribed, and hope you will do so in your next letter." Audubon asked innocently where the odd fish was, whereupon Rafinesque replied, "I am that odd fish I presume, Mr. Audubon." Audubon went on to describe Rafinesque's appearance:

> His attire struck me as exceedingly remarkable. A long loose coat of yellow nankeen, much the worse for the many rubs it had got in its time, and stained all over with the juice of plants, hung loosely about him like a sac. A waistcoat of the same, with enormous pockets, and buttoned up to his chin, reached below over a pair of tight pantaloons, the lower parts of which were buttoned down to the ankles. His beard was as long as I have known my own to be during some of my peregrinations, and his lank black hair hung loosely over his shoulders. His forehead was so broad and prominent that any tyro in phrenology would instantly have pronounced it the residence of a mind of strong powers.
>
> *(Audubon 1899:473-475)*

When Audubon showed Rafinesque a plant with which the latter was unacquainted, "I thought [Rafinesque] had gone mad. He plucked the plants one after another, danced, hugged me in his arms, and exultingly told me that he had got not merely a new species, but a new genus." Rafinesque also "followed the margins of the Ohio, and picked up many shells, which he greatly extolled." Later in his visit, Rafinesque smashed Audubon's prized violin while attempting to capture a bat he thought was a new species. Audubon took revenge by leading Rafinesque on a long, tortuous trip through a large canebrake (a dense stand of river cane, *Arundinaria gigantea*) and later providing him with drawings of several fictitious creatures from the Ohio River, including a fantastical trivalved mollusk with a retractable head that could be protruded through a hinged perforation in the shell. Rafinesque promptly published a description of the animal, which he named *Notrema fissurella*: "I have not seen the living animal myself; but Mr. Audubon of Hendersonville [*sic*], a zealous observer, has drawn it, and it appears to have a head with two eyes . . . jutting out of the perforation" (Rafinesque 1818, 24-25). Whether Rafinesque ever became aware of this prank is unknown, but two years later, he renamed the species *Tremesia patelloides* (Rafinesque 1820).

Thomas Say (1789–1834) was a contemporary of Rafinesque and a rival (at least in Rafinesque's eyes) in the description of new species. Born in Philadelphia, Say was one of the first great American-born naturalists. Although largely self-taught, he came from a strong tradition of natural history study. Philadelphia was the center of science in early America, including Charles Willson Peale's Philadelphia Museum, the first significant natural history museum in the country. Say's great uncle and mentor was William Bartram, famed for his natural history explorations of the southeastern United States, and Say was a close friend and neighbor of the ornithologist Alexander Wilson (Stroud 1995). While in his early twenties, Say became one of the founders and the first curator of the Philadelphia Academy of Natural Sciences. Say described many species of North American mussels and snails, and his *American Conchology*, published in seven parts from 1830 to 1834, was the most comprehensive resource on the fauna at that time. In contrast to Rafinesque's crude drawings, *American Conchology* contained beautiful, expertly rendered color plates of many species. In addition to his contributions on mollusks, Say described many other animal species, including the coyote (*Canis latrans*), and is considered the "father of American entomology." He not only described many new insect species but was one of the first to identify the role of insect pests in agriculture and human health (Stroud 1995).

Say's most important field experience with mussels occurred while living in New Harmony, Indiana, on the Wabash River. Say joined a group of scientists and educators, led and funded by the philanthropists William Maclure and Robert Owen, whose goal was to establish a learned, utopian community on the frontier (Pitzer 1989). The group left Pittsburgh, Pennsylvania, in December 1825 and descended the Ohio River in a keelboat dubbed the *Boatload of Knowledge*, arriving at the New Harmony site early in 1826 (Pitzer 1989). Say lived at New Harmony until his death of typhoid fever in 1834. Although the utopian experiment ultimately failed, Say's most productive years were spent there. During this time, he studied firsthand the magnificent, unspoiled mussel fauna of the Wabash River and other nearby streams and published on a hand press descriptions of new mussel species in the New Harmony newspaper, the *Disseminator of Useful Knowledge*, as well as *American Conchology* (Stroud 1995).

Other early naturalists undertook journeys of similar difficulty to those of Rafinesque and Say with the express purpose of documenting the mussel fauna of poorly known regions. The prominent early American naturalist and paleontologist Timothy Conrad (1803–1877) conducted an extended expedition to the southeastern United States to collect freshwater mollusks. In December 1832, Conrad traveled by schooner from New York to Wilmington, North Carolina, and then by railroad, stagecoach, horseback, and steamboat – collecting along the way – to the plantation of Charles Tait in Claiborne, Alabama, on the Alabama River (Wheeler 1935; Williams et al. 2008). From his base in Claiborne, where he stayed 6 months, he explored many of the rivers in Alabama by steamboat and stage. He collected shells at fords and steamboat landings and collected living mussels "by prodding a sharpened stick between their gaping hinges where they lay in six to eight feet of water" (Goodrich 1931a) and finally departed from Mobile, Alabama, via schooner for New York in February 1834 (Williams et al. 2008). In 1853, John Gould Anthony (1804–1877), a colleague of Louis Agassiz at the Museum of Comparative Zoology at Harvard, walked from Cincinnati, Ohio, through Kentucky, Tennessee, and Georgia "with the double purpose of renovating health, and of collecting the numerous and varied species of fluviatile shells with which our Western streams and rivers abound" (Goodrich 1931a, 46; Turner 1946).

Isaac Lea (1792–1886) was the most prolific early author on North American freshwater mussels. Although he had no formal scientific training, Lea authored over 200 papers on mussels from 1828 to 1876, mostly in the *Proceedings of the Philadelphia Academy of Natural Sciences*, and described over 800 species of freshwater bivalves (Parmalee and Bogan 1998; Williams et al. 2008). This prodigious output is the more remarkable considering that until his retirement in 1851, Lea pursued natural history study in his spare time from his position in a prominent Philadelphia publishing company (Leidy 1887). Unlike Conrad, Rafinesque, and Say, Lea conducted little fieldwork; instead, he corresponded with and solicited shells from a network of people throughout the country, including scientific colleagues and amateur collectors. At least three Union Army officers found time to send shells to Lea during the Civil War, one during Sherman's March to the Sea through Georgia, and other contributors were circuit-riding preachers (Goodrich 1931a). After his death, his collections formed the nucleus of the large freshwater mussel collection at the Smithsonian Institution's U.S. National Museum of Natural History (Williams et al. 2008). Despite his own admonition that "too much stress cannot be laid on the importance of keeping down the [number of] species in all branches of Zoology" (Lea 1870), Lea is now notorious for describing species multiple times based on small variations in shell morphology, often from single specimens. Consequently, only about 28 percent of his described species are recognized today (Graf and Cummings 2008).

Because their primary goal was naming and classifying new species, early naturalists focused almost exclusively on describing the shells. However, these writings include scattered ecological observations relating to the animals themselves. Naturalists in North America and Europe examined mussel gonads and mistakenly concluded that most species are hermaphroditic (reviewed in Say 1830–1838); Kirtland (1834) later showed that the sexes are usually separate and was the first to recognize sexual dimorphism in the shells of some species. Isaac Lea described the anatomy of many species, including mantle flaps and marsupial gills, and illustrated the glochidia of 38 species (Watters 1994a), and he made observations on mussel movement and feeding (Lea 1834). Rafinesque (1820) recorded observations on burrowing behavior and locomotion: "They can when necessary bury themselves in the sand or earth, particularly in winter, and even in summer in the smaller rivers subject to be dried up.... Their progressive motion is very slow, effected by means of their foot, which as slowly furrows the ground" (18); he also alluded to the relationship between shell morphology and predation risk: "its shell [the scaleshell, *Leptodea leptodon*] is so fragile, that it easily becomes the prey of its enemies" (21). In a few other instances, authors made general comments on the habitat and relative abundance of species (e.g., Rafinesque 1820; Say 1830–1838).

Apart from exceptions such as these, the publications of early naturalists are uniformly lacking of ecological information. These naturalists undoubtedly made more detailed observations on mussel ecology in the course of their extensive travels. Rafinesque (1831, 71) criticized Thomas Say: "Mr. Say... knows so little of the animals of these shells, as to have mistaken their mouth for their tail, and their anterior for the posterior part of the shells! If he had seen these animals alive, feeding, moving, and watched their habits as I have done repeatedly, he would not have fallen into such a blunder." Unfortunately, Rafinesque and other early naturalists only rarely recorded such observations.

2.2. The beginnings of mussel ecology, 1880–1933

> The naides have until recently been studied chiefly by amateurs... and from the shells alone.
>
> – *Agassiz 1862*

> During the past twenty years the method of studying animal life, under the stimulating influence of the laws of organic evolution, has greatly changed.... We now have the comparison of thousands of [mussel] specimens from different habitats, studied from the standpoint of the relation of the animal to its environment, the changes of the same species in different environments, and search for the reasons for such changes or adjustments – the Science of Ecology.
>
> – *Baker 1926*

With the development of the university system in the United States and Canada came expanded opportunities in the academic profession, and for the first time, the study of natural history was conducted primarily by formally trained scientists. By the late 1800s, most North American mussel species had been described and, in fact, most had been given multiple names. Taxonomy remained the primary focus of this period, particularly stabilizing the nomenclature and proposing phylogenetic classifications of the fauna (e.g., Simpson 1900a; Ortmann and Walker 1922). However, this period also saw the beginnings of the serious study of mussel ecology.

Improvements in transportation allowed better determination of species' distributions than was possible during the frontier era, leading to the first attempts to examine biogeographical relationships and propose modes and routes of dispersal to explain these patterns (e.g., Call 1878; Frierson 1899; Simpson 1900b; Walker 1900; Adams 1905; White 1907). Distributional surveys intensified further in the early 1900s with the search for raw material for the shell button industry (Section 2.2.B). The rise of comparative and experimental biology led to the first concerted studies of mussel anatomy and physiology (Simpson 1884; Frierson 1903a), reproductive biology (Lillie 1895; Sterki 1898; Conner 1909), parasitology (Kelly 1899), and predation (Lee 1886; Apgar 1887; Adams 1892; Simpson 1899). Perhaps most important, emergence of the sciences of ecology and evolution provided an overarching framework within which to study the biology and natural history of mussels (e.g., Headlee 1906; Baker 1926).

Despite improvements in transportation, travel in much of North America remained difficult at the turn of the twentieth century, making field sampling extremely time consuming. Wilson and Clark (1914, 2) described transportation during their survey of the Cumberland River system in Kentucky and Tennessee: "Investigations [were] conducted by team [horse or mule team and wagon], driving along the banks or visiting convenient fords and shallows.... The party then drove by team to the Cumberland Falls... and thence by rail to Burnside, Kentucky. This is the head of steamboat navigation on the river, and here a small boat was constructed in which to proceed down the main river, thus completing the survey of the entire river." For those unable to invest such time, access to suitable sampling sites was difficult, especially in large rivers. Arnold Ortmann (Section 2.2.A) described his attempts to sample the Tennessee River: "In the Tennessee at Concord, [Tennessee], I got very little; did not find the right place.... I hired a boat but spent the day chiefly in rowing against the current, which I enjoyed, but which did not furnish any Naiades" (van der Schalie and van der Schalie 1950, 448). Even with the advent of the automobile, travel was slow and often difficult. William Clench and Sheldon Remington of the University of Michigan Museum of Zoology made an extended collecting trip in the southeastern United States from July to September 1924: "We bought a 1922 Ford touring car [nicknamed "the good ship 'Asthma'"]... and proceeded to load up the running boards and back seat until it looked like a gypsy outfit" (Remington and Clench 1925, 128). In Kentucky, they changed tires seven times in one day: "Words cannot express the meanness of these roads.... We passed near Lincoln's birthplace and now we know why he left Kentucky" (132–133). They encountered one of their most productive sites, on the

Green River, by accident when they "decided to stop a while and cool the engine" (133) and ended up collecting there for two days. They camped during most of the journey, subsisting mostly on beans, but "country folk are always hospitable and often brought us out cake, pie and other dainties" (130). After collecting throughout Kentucky, Tennessee, and Alabama, they sold the car in Knoxville and took a train back to Michigan.

To overcome these difficulties, scientists in this period followed the methods of the early naturalists by enlisting the aid of local collectors. The most organized and sustained of such arrangements was the "Syndicate," a group of taxonomists led by Bryant Walker and George Clapp who, from 1903 to 1920, funded comprehensive collections of mollusks throughout Alabama and adjoining states by H. H. Smith, the curator of the Alabama Museum of Natural History (van der Schalie 1981; Williams et al. 2008). Smith was among the last biologists to collect at Muscle Shoals, on the Tennessee River (Box 10.1), before construction of Wilson Dam, and was the last person to see many of the large shoals on the Coosa River. In a letter to Walker, he described a final visit to a section of the river that was being flooded by a recently completed dam (Lay Dam, completed 1914): "Several reefs of rock cross the river diagonally, and on them we made our best hauls. . . . We worked until the last possible moment. When we left, Fort William Shoals were entirely covered by the backwater of the power dam" (Goodrich 1922, 8). It is largely because of Smith's efforts and those of local collectors he trained (van der Schalie 1940a) that we know about the incredibly rich original faunas of many rivers in Alabama.

2.2.A. Arnold Ortmann

Foremost among mussel biologists of this time was Arnold E. Ortmann (1863–1927; Figure 2.1), curator of the Section of Mollusks at the Carnegie Museum from 1903 to 1927. Before immigrating to the United States, Ortmann was a favorite student of famed German biologist Ernst Haeckel (Johnson 1977). Ortmann may be considered the father of modern mussel ecology. Although, like most of his contemporaries, Ortmann was primarily a taxonomist, he made invaluable contributions to mussel ecology. Ortmann was the first to systematically and consistently describe the anatomy of a large number of mussel species and to use these characters in a phylogenetic classification, much of which is supported by modern genetic analyses. His analysis of patterns of variation among species in the structure of the marsupial gills, timing of glochidial brooding, and release of glochidia (e.g., Ortmann 1909a, 1910, 1912) anticipated and informed current-day research on mussel life history strategies (e.g., Barnhart et al. 2008). Ortmann conducted extensive research on ecophenotypic variation in shell morphology, leading to the now well-known Ortmann's law of stream position, describing predictable changes in morphology along stream-size gradients (Ortmann 1920; Section 1.3.B.2). He was one of the first to

Figure 2.1. Arnold E. Ortmann (courtesy Carnegie Museum, Pittsburgh, Pennsylvania).

generate and use comprehensive distributional information to develop biogeographical hypotheses about the origin of mussel assemblages (Ortmann 1913), most notably his research on the unique, endemic fauna of the Cumberland and Tennessee river systems (Ortmann 1924a, 1925). His monograph on the mussels of Pennsylvania (Ortmann 1919) became a model for virtually all contemporary mussel field guides with its comprehensive and consistent template for each species, including synonymy, descriptions of the shell and soft anatomy, ecological observations, range maps, and photographs (but see Baker 1898). Finally, Ortmann was one of the first biologists to call attention to the loss of mussel populations and establish this problem as a growing conservation issue (e.g., Ortmann 1909b, but see Simpson 1899). In addition to his extensive work on North American mussels, Ortmann made important contributions to our knowledge of freshwater bivalves in other parts of the world (e.g., Ortmann 1918a, 1921) and was one of the world's leading experts on crayfishes.

On the basis of his published work and the accounts of colleagues, Ortmann was a remarkably perceptive and energetic biologist. On Ortmann's death, Calvin Goodrich, former curator of mollusks at the University of Michigan Museum of Zoology, wrote to a colleague, "I was mighty fond of Ortmann. We had a great trip together in 1913. . . . In going into the upper Tennessee region over the Virginian road [a railroad line], he got wound up on the subject of Unios and presently everyone in the observation car left off gazing at the scenery and opened up their ears in the Doctor's direction. . . . I have never seen another such manifestation of the tremendous power of the mere sound of words. My notion is that he wore himself out at 61, strong as he was. The race is not always to the man with the steam engine innards" (Rosewater 1959, 195). Similarly, H. A. Pilsbry, the eminent American malacologist at the Philadelphia

Academy of Natural Sciences, wrote, "[Ortmann's] enthusiasm for natural history was contagious. . . . In the field he was indefatigable never sparing himself, deterred by neither exposure or fatigue, in the quest of specimens for his researches" (Pilsbry 1927, 111).

2.2.B. The Fairport Biological Station

Simultaneous with the beginnings of the study of mussel ecology as led by taxonomists such as Ortmann was the development of the shell button industry. Harvest of mussels for freshwater pearls was widespread in North America since at least the mid-1800s but increased dramatically and rapidly in the 1890s with the advent of the button industry (Chapter 9). The button industry was centered initially in the upper Mississippi River valley and soon grew to be a dominant economic force in the region, employing thousands of fisherman and factory workers. As early as 1899, declines in harvests and other symptoms of overfishing were apparent in many areas. Concern about the continued supply of raw material for the industry spurred scientific interest in mussel ecology and propagation methods, ultimately leading to the establishment, in 1914, of the U.S. Bureau of Fisheries' Biological Station at Fairport, Iowa, on the Mississippi River. Unlike the research of Ortmann and others, for whom ecological studies were offshoots of their taxonomic work, research associated with the Fairport Biological Station represented the first large-scale efforts focused primarily on freshwater mussel ecology.

The genesis of the Fairport Station can be traced to 1904. Winterton C. Curtis, at the Marine Biological Laboratory at Woods Hole, Massachusetts, began study of the life history and artificial propagation of mussels as early as 1899 (Pritchard 2001). Curtis obtained a faculty position at the University of Missouri in 1901 and continued this work in collaboration with another faculty member there, George Lefevre. In 1904, Lefevre and Curtis obtained funding from the U.S. Bureau of Fisheries (a precursor to the U.S. Fish and Wildlife Service) to expand their studies of mussel life history and propagation, focusing on commercially important species. For the next several years, this research was conducted primarily at the University of Missouri, although much of the focus was related to mussel resources of the upper Mississippi River. In 1908, under the auspices of the Bureau of Fisheries, Lefevre and Curtis spent the summer on the Mississippi River near La Crosse, Wisconsin, working out of temporary laboratory quarters and on the bureau's steamship, the *Curlew* (Pritchard 2001; Figure 2.2).

Also in 1908, encouraged by the results of Lefevre and Curtis, a consortium consisting of the Bureau of Fisheries, button manufacturers, and local congressmen obtained a federal appropriation for the construction of a permanent biological station at Fairport (Pritchard 2001). Construction commenced in 1909, and research began in temporary quarters in 1910 under direction of the newly appointed director,

Figure 2.2. (top) Temporary laboratory near La Crosse, Wisconsin, used by George Lefevre and Winterton Curtis in 1908. (bottom) Steamship *Curlew* (both from Lefevre and Curtis 1912).

Robert E. Coker (Coker 1914a; Figure 2.3). The station opened officially in June 1914 and consisted of a three-storied main laboratory building, staff living quarters, several other dependent structures, and 36 earthen and concrete ponds supplied with river water (Coker 1914a, 1921; Figure 2.4). Interestingly, raw sewage from the station was discharged into the river but "some distance below the intake for the pumps" (Coker 1914a, 392). The station employed a permanent staff of 8–14 people but also included seasonal field crews (Coker 1914a, 1921); in addition, Coker encouraged use of the facility by visiting researchers (Coker 1914b). Although a major focus of the station was on mussel ecology and propagation, a variety of other fisheries research was conducted there, including propagation, culture, and ecology of riverine fishes. The Fairport Station was the first permanent federal facility devoted to freshwater

Figure 2.3. (top) Staff of the Fairport Biological Station at the temporary laboratory building; Robert E. Coker, seated, c. 1910 (courtesy Oscar Grossheim Collection, Musser Public Library, Muscatine, Iowa). (bottom left) Interior of main laboratory building (from Coker 1914a). (bottom right) Robert E. Coker, c. 1930 (courtesy Southern Historical Manuscripts Collection, University of North Carolina).

biology and represented a considerable financial investment and commitment toward research and conservation of freshwater resources (Pritchard 2001).

Aided by the work of Lefevre and Curtis, mussel ecology and propagation research at Fairport began with considerable momentum. In the first few years (even before completion of the main laboratory building), Coker, H. Walton Clark, Arthur D. Howard, Austin F. Shira, Thaddeus Surber, and others completed extensive research on mussel life history and ecology and directed comprehensive surveys of rivers throughout the central United States. The station produced numerous publications in its first years, documenting at least a portion of this groundbreaking research (e.g., Coker and Surber 1911; Clark and Wilson 1912; Surber 1913, 1915;

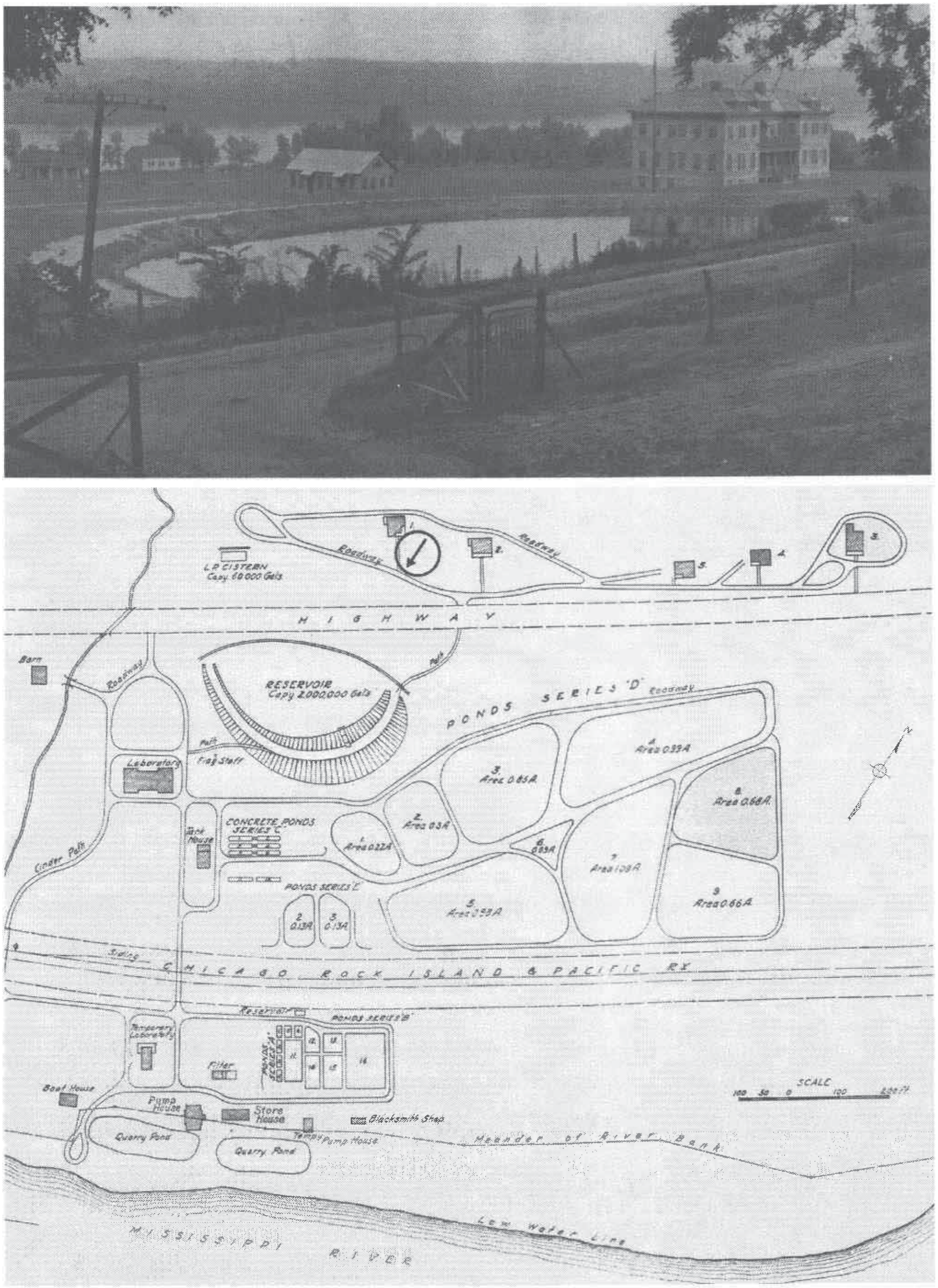

Figure 2.4. The Fairport Biological Station. (top) View of station, c. 1914, showing original main laboratory building at right, water supply storage reservoir in foreground, and temporary laboratory at far left (to left of telephone pole); Mississippi River in background. (bottom) Station plan; circle and arrow show location and direction of top photo (both from Coker 1914a).

Howard 1913, 1914, 1915; Wilson and Clark 1914). However, on December 20, 1917, a fire in the laboratory building destroyed the library and much of the scientific equipment. Most seriously, "records embodying results of tedious investigations" were destroyed in the fire, and much of these data remained unpublished (Coker 1921, 3; see also Howard and Anson 1922).

This serious setback seems to have had little effect on the enthusiasm and productivity of the staff. Work resumed quickly in the small building that had served earlier as temporary quarters during construction of the main laboratory building (Coker 1921). Propagation and life history research continued, resulting in several more landmark publications (e.g., Coker 1919; Coker et al. 1921; Howard 1922), and a new laboratory building was completed in 1920. Despite the great energy of the staff and the tremendously important ecological information they were generating, by the mid-1920s, the value of mussel propagation work at Fairport began to be questioned. Propagation techniques developed at Fairport were successful at producing juvenile mussels, but the quantity that could be cultured and released into rivers was insufficient in the face of intense harvest and general degradation of riverine habitat (Pritchard 2001).

Hope for mussel propagation to sustain commercial harvest rose briefly in the late 1920s. Max M. Ellis, a professor at the University of Missouri working at the Fairport Station, claimed to have developed an artificial culture medium for mussel glochidia that obviated the need for host fish (Ellis and Ellis 1926). This technique was thought to finally make possible large-scale production of juvenile mussels and was promoted by the Bureau of Fisheries and the popular press; in 1931, it was claimed that 60 million mussels would be released into inland waters of the United States (*Time* 1930). However, owing to problems finding sufficient broodstock and suitable release sites, coupled with possible exaggeration about the effectiveness of the technique, these programs were not widely successful (Pritchard 2001). During the early 1930s, mussel research at Fairport was deemphasized and fish culture work took the forefront, but funding for the station as a whole was discontinued in 1933, and the station was closed (Pritchard 2001). Ellis moved his propagation work to Fort Worth, Texas, and continued to receive funding from the Bureau of Fisheries until 1942. The Fairport Biological Station was vacant until 1945, when the main laboratory building briefly housed prisoners from World War II, and it was torn down by 1955 (Pritchard 2001).

The value of the contributions associated with the Fairport Biological Station cannot be underestimated. This research addressed, often for the first time, a wide range of topics in mussel ecology, including habitat requirements, identification of glochidia, determination of host fishes, reproductive timing, age and growth, feeding ecology, and many others. Although these publications are lacking in many methodological details, and study design and data analysis were idiomatic of the time, their level of detail is remarkable. Furthermore, these studies provide data on a broad range of mussel diversity not restricted to commercially harvested species. In addition to work conducted by station staff, most other North American research of the time that focused exclusively on mussel ecology was in some way associated with or sponsored by Fairport (e.g., Isely 1914; Utterback 1916b; Reuling 1919; Arey 1923; Churchill and Lewis 1924; but see Allen 1914, 1921). Coker and others associated with the Fairport Station also were vocal advocates of conservation during an era of intense resource exploitation and river development (Coker 1914c, 1914d, 1916; Shira 1919; Smith 1919; Ellis 1931, 1936). This body of work, along with Ortmann's work, represented the bulk of mussel ecology information available until the 1980s. Many of these publications are now considered classics (e.g., Lefevre and Curtis 1910, 1912; Coker et al. 1921), and all remain essential sources of information.

2.3. Systematic inventory of the North American fauna, 1933–1980

After closure of the Fairport Biological Station, the study of mussel ecology languished for several decades. The decline of the button industry after World War II largely eliminated support for mussel life history and propagation studies. Consequently, most mussel research focused on extending the biogeographical and taxonomic studies of Ortmann and his contemporaries (e.g., van der Schalie 1939a, 1963; Johnson 1970, 1980). The widespread availability of automobiles and better roads made it possible to systematically and comprehensively document the fauna of North America to an extent that was previously impractical. This period also witnessed an acceleration of stream degradation that had only begun in the previous era, and scientists were acutely aware that they were documenting a fauna soon to be lost or greatly diminished (e.g., van der Schalie 1938b; Athearn 1967; Stansbery 1970). Intensive collecting was often conducted immediately prior to dam construction or other impacts (e.g., Clench and Turner 1956; Neel and Allen 1964; Williams and Stansbery 1972). These efforts resulted in a large number of published distributional studies and greatly expanded many research collections. David H. Stansbery, through extensive field sampling from the 1950s to the 1980s, assembled at the Ohio State University the most comprehensive research collection of North American mussels in existence. The intensive inventory of the North American mussel fauna during this period solidified our understanding of mussel biogeographical patterns, provided extensive repositories of comparative material for future studies, and made possible assessments of subsequent declines in mussel populations.

Compared to the prodigious and focused output of the Fairport Biological Station, little ecological research was conducted during this period. From 1933 to 1970, only a handful of papers focused on mussel ecology (e.g., Murphy 1942; Matteson 1948, 1955; van der Schalie and van der Schalie 1963; Imlay 1968; Tedla and Fernando 1969). However, ecology research increased throughout the 1970s with the publication of papers on fish host relationships, reproductive biology, growth, habitat relationships, behavior, and secondary production. This gradual increase in ecological research anticipated the explosion in the field that would occur in the following decades.

2.4. The modern era of mussel ecology, 1981 to present

Similar to the origins of the Fairport Biological Station, the second blossoming of mussel ecology originated with conservation issues. However, rather than concerns about sustaining commercial harvest, the modern study of mussel ecology began in response to growing awareness of an extinction crisis facing the fauna as a whole. During previous decades, scientists documented the ongoing disappearance of mussel species and populations across North America due to habitat destruction, water quality decline, overharvest, and other human impacts (Chapter 10). This crisis was widely acknowledged by 1970 (Stansbery 1970, 1971) but was focused by passage of the U.S. Endangered Species Act of 1973. In 1976, 23 mussel species were listed as endangered under the act, but because of initial priorities on vertebrates and the sheer number of species to be evaluated, no additional mussel species were listed for more than 10 years (Neves et al. 1997). In 1988, the number of endangered and threatened species began to increase rapidly, more than doubling by 1995, and now includes 75 species, with an additional 17 proposed or candidates for listing; together, these species represent nearly one-third of the fauna. Independent assessments painted an even more dire picture, considering more than 70 percent of the fauna of conservation concern (Williams et al. 1993).

Resource managers soon realized that conservation efforts were severely limited by a lack of information about mussel ecology, and available information consisted largely of studies from the early 1900s. This realization, along with increased funding for conservation, spurred a proliferation of mussel ecology research. This period saw establishment of the first sustained research programs on freshwater mussel ecology since closure of the Fairport Biological Station. In 1978, Richard J. Neves initiated a broad research program that ultimately led to establishment of the Freshwater Mollusk Conservation Center at the Virginia State Polytechnic Institute and State University. This program has spanned more than 30 years, produced over 60 peer-reviewed publications on a variety of topics in mussel ecology, and trained numerous graduate students, many of whom now lead their own mussel research programs. Also in the late 1970s, David L. Strayer, at the Carey Institute of Ecosystem Studies in New York, began a long-term research program focused on quantitative investigation of mussel habitat use and development of sampling methods for mussels. In the 1980s and 1990s, mussel ecology research programs were established throughout North America, including numerous government agencies and in academia. The mussel extinction crisis also prompted many state agencies to hire full-time mussel biologists and has engaged private conservation organizations such as the Nature Conservancy and the World Wildlife Fund. As a result of this intense interest, from 1975 to 1995, the annual number of peer-reviewed scientific papers on freshwater mussels increased 10 times, with more than 200 papers appearing between 1995 and 1999 alone (Strayer et al. 2004).

Mussel ecology research and interest in freshwater mussels in general continue to increase rapidly. From 2005 to 2009, an average of 136 scientific papers or reports relating to mussels has appeared annually (Cummings et al. 2010). This growing literature has revealed much about the remarkable ecology of these animals, attracting attention from the scientific community and beyond. Mussel identification guides, written for both lay and technical audiences, are now available for nearly all regions of North America. In the popular press, mussels have received a level of public visibility enjoyed by few invertebrates (e.g., *Smithsonian, Natural History, BBC Wildlife*). Mussels are now used by a wide variety of conservation organizations as a centerpiece to foster interest in conservation initiatives ranging from local watershed groups to global programs. Over the last 30 years, the study of freshwater mussels has been transformed from the realm of a few anachronistic specialists into a vital, diverse field encompassing people from many walks of life. This explosion of interest in freshwater mussels illustrates the curious potency of the mussel bug that has bitten unwitting naturalists for hundreds of years.

Chapter 3

Diversity and biogeography

3.1. North America: The “rainforest” for mussel diversity

North America is blessed with a wonderfully diverse flora and fauna, but biologists in temperate latitudes are accustomed to couching their proclamations to acknowledge that the diversity of the region, however remarkable, is overshadowed by the tropics: “the most diverse *temperate* fish fauna in the world,” and so on. Such qualifications are not needed when discussing the North American freshwater mussel fauna. With about 300 species, North America is home to the most diverse freshwater mussel fauna on Earth, period.

To fully appreciate the staggering diversity of the North American mussel fauna, we must consider the fauna in a global perspective. The Amazon–Orinoco and Congo River basins support the world’s two most diverse freshwater fish faunas, each including 3–5 times as many species as the Mississippi River basin. In contrast, the Mississippi River basin supports 3–4 times as many mussel species as the Amazon–Orinoco and Congo basins (Table 3.1). North American mussel diversity also is exceptionally high at smaller scales. The state of Alabama has more mussel species (about 178; Williams et al. 2008) than any of the world’s major biogeographical regions, except the Indotropical region (Table 3.1). The Tennessee River system alone harbors more mussel species (about 104) than any biogeographical subregion outside of North America (Table 3.2). Alpha diversity, the number of species occurring at a single site, also is inordinately high in some regions (Table 3.3). At an even smaller scale, in mid-sized and large rivers of the eastern United States, it is common to find within a small area of suitable habitat more species than occur on the entire continent of Europe (11 species). For example, in the Saline River, Arkansas, 23 species have been found within 1 square meter of river bottom (C. Davidson, personal communication).

3.2. Assessing the diversity of the North American fauna

Despite more than 200 years of study, an accurate estimate of the number of mussel species in North America remains elusive. Recent estimates range from 281 species

Table 3.1. *Worldwide diversity of freshwater mussels (Order Unionoida)*

Region	Number of taxa
Nearctic	**302**
Mississippi River basin	133
Gulf Coast drainages	147
Atlantic Coast drainages	52
Peninsular Florida	14
Pacific Coast drainages	7
Neotropica	**172**
Mesoamerica	102
Amazon–Orinoco basins	42
Paranà–Paraguay basins	41
Afrotropica	**85**
Congo River basin	34
Nile River basin	26
Western Africa	22
Paleartica	**45**
Japan–Sakhalin	17
Amur–Beringia	14
Europe	11
Indotropica	**219**
Indochina	91
Yangtze–Huang basins	63
India–Burma	54
Australasia	**33**

Note: Major geographic regions (in bold) are followed by example subregions. Totals for subregions do not equal region totals due to overlap in species distributions among subregions and omission of some subregions (adapted from Graf and Cummings 2007).

(plus an additional 16 subspecies) in 51 genera (Williams et al. 1993) to 302 species in 52 genera (Graf and Cummings 2007), but these estimates are provisional owing to our still-imperfect understanding of mussel taxonomy. Unlike many organisms for which species are defined by readily quantifiable characters, most mussel species descriptions are based solely on subjective shell characters. Anatomical features of the animals themselves are used to diagnose higher taxonomic levels (genus and above) but do not provide easily measurable characters useful for differentiating closely related species (Roe and Hoeh 2003; Campbell et al. 2005). In addition to being hard to quantify, shell characters also vary greatly among individuals, along environmental gradients, and among river systems (Section 1.3.B). The nineteenth-century naturalists who described the bulk of North American species dealt with this variation by describing subtle shell variants as separate species, much as if people

Table 3.2. *The 20 most diverse North American river systems from a freshwater mussel perspective*

River system	Mussel species richness	U.S. states
Tennessee	104	AL, GA, KY, MS, NC, TN, VA
Cumberland	89	KY, TN
Wabash	75	IL, IN, OH
Mobile	72	AL, GA, MS, TN
Ohio River[a]	71	IL, IN, KY, OH, PA, WV
Green	70	KY, TN
Scioto	64	OH
Muskingum	62	OH
Kentucky	56	KY
White	56	AR, MO
Licking	54	KY
Kanawha	54	NC, WV, VA
Salt	53	KY
Ouachita	52	AR, LA, OK
Upper Mississippi River[a]	50	IL, IA, MO, MN, WI
St. Francis	50	AR, MO
Illinois	48	IL
Rock	46	IL, WI
Meramec	43	MO
Kaskaskia	43	IL

Note: Data from Haag (2010).

[a] Total includes main stem river fauna only.

with big noses versus small noses were considered different species. This approach resulted in bewildering lists of synonymous names for most currently recognized species. The widespread North American species *Elliptio complanata* has 99 junior synonyms (redundant names applied after the initial description of the species). The situation was even more chaotic in Europe: *Anodonta cygnea* has 549 synonyms (Graf and Cummings 2008). Isaac Lea alone described 838 freshwater mussel species from North America and other parts of the world, but only 28 percent are now considered valid (Section 2.1).

Taxonomists in the early 1900s reduced this synonymy to a more manageable and biologically realistic level (e.g., Simpson 1900a; Ortmann and Walker 1922), resulting in species concepts that have since remained reasonably stable and form the basis of our current estimates of diversity. Sorting through this multitude of species names must have been an onerous chore indeed, and both Simpson and Ortmann expressed great frustration with the overnaming of the previous era: "In 1892 Arnould Locard . . . stated that there were 208 species of [*Unio*] and 250 [*Anodonta*] in France alone. Life is too short and valuable to be wasted in any attempt at deciphering such nonsense"

Table 3.3. *Mussel species richness in North American faunal regions and provinces, with example stream reaches having near-maximum alpha diversity for each province*

Region Province	Total richness	No. endemic species	Source
1.0 Mississippian	**198**	**147 (74%)**	
1.1 Mississippi Embayment	**59**	**1 (2%)**	
Bayou Bartholomew, Morehouse Parish, Louisiana	29		George and Vidrine (1993)
Big Black R., Hinds Co., Mississippi	26		Hartfield and Rummel (1985)
Hatchie R., Tipton Co., Tennessee	26		Manning (1989)
1.2 Upper Mississippi	**55**	**1 (2%)**	
Illinois R., Pike Co., Illinois	40		Starrett (1971)
Meramec R., Jefferson Co., Missouri	40		Buchanan (1980)
Mississippi R., La Crosse Co., Wisconsin	39		Havlik and Stansbery (1978)
1.3 Ohioan	**78**	**2 (3%)**	
Ohio R., Campbell Co., Kentucky	63		OSU, Johnson (1978)
Wabash R., Posey Co., Indiana	52		Goodrich and van der Schalie (1944)
Green R., Hart Co., Kentucky	51		Stansbery (1965)
1.4 Tennessee–Cumberland	**110**	**31 (28%)**	
Tennessee R., Lauderdale Co., Alabama	68		Garner and McGregor (2001)
Clinch R., Anderson Co., Tennessee	51		Ortmann (1918b)
Cumberland R., Russell Co., Kentucky	50		Neel and Allen (1964)
1.5 Interior Highlands	**63**	**9 (14%)**	
Spring R., Lawrence Co., Arkansas	32		OSU
Ouachita R., Montgomery Co., Arkansas	31		Harris and Gordon (1988), OSU
Kiamichi R., Pushmataha Co., Oklahoma	27		OSU
1.6 Great Plains	**37**	**0**	
Kansas R., Douglas Co., Kansas	24		Murray and Leonard (1962)
James R., Hanson Co., South Dakota	16		Coker and Southall (1915), OSU
Grand R., Chariton Co., Missouri	16		Oesch (1995)

(*continued*)

Table 3.3 *(continued)*

	Total richness	No. endemic species	Source
1.7 St. Lawrence–Great Lakes	**47**	**0**	
Sydenham R., Ontario	30		Mackie and Topping (1988)
Maumee R., Defiance Co., Ohio	28		OSU
Lake Erie, Ottawa Co., Ohio	27		OSU
1.8 Western Gulf	**31**	**11 (36%)**	
Brazos R., Coryell Co., Texas	20		Howells et al. (1996)
Guadalupe R., Bexar Co., Texas	18		Howells et al. (1996)
1.9 Sabine-Trinity	**34**	**5 (15%)**	
Sabine R., Sabine Parish, Louisiana	25		OSU
Calcasieu R., Allen Parish, Louisiana	17		OSU
1.10 Pontchartrain–Pearl–Pascagoula	**38**	**2 (5%)**	
Pascagoula R., George Co., Mississippi	24		MMNS
Amite R., E. Feliciana Parish, Louisiana	23		Brown and Curole (1997)
1.11 Mobile Basin	**72**	**32 (44%)**	
Coosa R., St. Clair Co., Alabama	38		Williams et al. (2008)
Cahaba R., Bibb Co., Alabama	36		Williams et al. (2008)
Tombigbee R., Pickens Co., Alabama	35		Williams et al. (2008)
2.0 Eastern Gulf	**58**	**40 (69%)**	
2.1 Escambia–Choctawhatchee	**33**	**11 (33%)**	
Choctawhatchee R., Walton Co., Florida	18		Blalock-Herod et al. (2005)
Patsaliga Creek, Covington Co., Alabama	16		Pilarczyk et al. (2006)
2.2 Apalachicolan	**37**	**15 (41%)**	
Chipola R., Calhoun Co., Florida	27		Brim Box and Williams (2000)
Chattahoochee R., Muscogee Co., Georgia	26		Brim Box and Williams (2000)
Apalachicola R., Liberty Co., Florida	25		Brim Box and Williams (2000)
2.3 Peninsular Florida	**12**	**5 (33%)**	
St. Johns R., Seminole Co., Florida	10		Johnson (1972)
Withlacoochee R., Hernando Co., Florida	9		Johnson (1972)

	Total richness	No. endemic species	Source
3.0 Atlantic	**52**	**37 (71%)**	
3.1 Southern Atlantic	**46**	**27 (59%)**	
Tar R., Nash Co., North Carolina	15		OSU
Lake Waccamaw, Columbus Co., North Carolina	12		Johnson (1984)
Altamaha R., Appling Co., Georgia	10		Sickel (1980)
3.2 Northern Atlantic	**20**	**1 (5%)**	
Hudson R., Rensselaer Co., New York	11		Strayer and Jirka (1997)
Penobscot R., Penobscot Co., Maine	10		Nedeau et al. (2000)
Susquehanna R., Otsego Co., New York	8		Strayer and Fetterman (1999)
4.0 Pacific	**7**	**7 (100%)**	
4.1 Pacific	**7**	**7 (100%)**	
Pit R., Shasta Co., California	5		Haley et al. (2007)
Middle Fork John Day R., Grant Co., Oregon	4		Brim-Box et al. (2006)

Note: Table organized by regions, which are further divided into provinces and then stream reaches. Numbers reference Figure 3.1. OSU = Ohio State University Museum of Biological Diversity online bivalve database (http://www.biosci.ohio-state.edu/~molluscs/main/biv_database.html). MMNS = Mississippi Museum of Natural Science, Natural Heritage Database, Jackson. Species richness data after Haag (2010).

(Simpson 1900a); "species-making within this form [*Elliptio complanata*] has gone beyond all bounds, and in a number of Lea's 'species' . . . the question may be raised whether Lea was actually in earnest, when proposing them, or whether he only wanted to mystify contemporaneous and subsequent students of naiadology. Great credit is due to Simpson for straightening out the worst of this tangle" (Ortmann 1919, 105).

The classifications of Simpson and Ortmann resembled modern species concepts more closely than those of previous workers but continued to be based primarily on subjective, personal ideas about the range of morphological variation that defined species. This approach works reasonably well for species with unambiguous shell characters that overlap little with other species. However, shell characters alone are untenable for defining species in groups with variable and overlapping shell morphology such as sympatric species flocks or closely related allopatric taxa. These problems exist in many genera in the southeastern United States, notably *Pleurobema*, *Uniomerus*, and *Villosa* (e.g., see Section 3.3.A.11). The most intractable taxonomic problem in North America is the genus *Elliptio* in eastern Gulf Coast and Atlantic

Coast rivers. Shell morphology of this genus is wildly variable within and among river systems; consequently, hundreds of names have been applied to the group. Recent assessments based on shell morphology recognized about 30–40 species (Williams et al. 1993; Graf and Cummings 2007; Watters 2008a), but these opinions differ greatly and show little consensus about species concepts or geographic ranges. Surprisingly, the practice of naming new species or resurrecting previously synonymized names based solely on shell morphology continues to the present day (e.g., Gordon 1995; Cicerello and Schuster 2003; Gangloff et al. 2006; Williams et al. 2008). These studies vary in the degree of support given for taxonomic revisions (from no to moderate support) but are alike in being based mostly on personal opinion and offering no falsifiable hypotheses.

A scientifically defensible estimate of North American mussel diversity awaits rigorous phylogenetic study based on quantifiable, heritable attributes such as DNA sequence data (Lydeard and Roe 1998). Such efforts have already yielded surprising departures from traditional classifications. In some cases, studies failed to find genetic differences between populations formerly considered separate species (Mulvey et al. 1997; Campbell et al. 2008; Campbell and Lydeard 2012b), suggesting that diversity estimates based on shell morphology remain inflated to some extent. More commonly, molecular studies have uncovered a high degree of cryptic variation not reflected by shell morphology. These studies show that several currently recognized species include multiple evolutionary units (Mulvey et al. 1997; Roe and Lydeard 1998a; King et al. 1999; Jones et al. 2006a; Serb 2006), suggesting that diversity of North American mussels is underestimated.

It is not surprising that mussel diversity should be higher than current estimates based on shell morphology. Perhaps in response to the excesses of previous workers, Simpson and Ortmann were rather conservative in their classifications, but both described considerable variation among and within populations of many recognized species. In the last 30 years, modern systematic methods have resulted in the description of many previously unrecognized species of freshwater fishes, crayfishes, and salamanders in North America (Petranka 1998; Nelson et al. 2004; Taylor et al. 2007). The limited dispersal capability of fishes such as darters and minnows has resulted in a high degree of cryptic variation. For example, the orangethroat darter (*Etheostoma spectabile*) was formerly considered a single, widely distributed species but is now recognized to consist of more than seven distinct species, some with highly restricted ranges (Ceas and Page 1997). In the southeastern United States, neighboring river systems often contain closely related but distinct fish species (e.g., Wood and Mayden 1993; Clabaugh et al. 1996). Much additional variation within North American fishes is recognized but awaits formal description (Butler and Mayden 2003), and estimates of fish diversity will continue to increase. Because mussel dispersal occurs primarily by transport of glochidia on fish hosts, cryptic variation should be similarly high for mussels.

In-depth, phylogeographic studies of mussel species are generally lacking, but the few existing studies have revealed patterns of cryptic variation similar to fishes. Populations of the oystermussel, *Epioblasma capsaeformis*, in the upper and lower Tennessee River system represent highly divergent, distinct species (Jones et al. 2006a), mirroring patterns of several fish taxa (e.g., Powers et al. 2004; George et al. 2006). Several mussel taxa widespread in the Mobile basin appear to consist of sister species restricted to either the western or eastern portions of the basin (Roe et al. 2001; Campbell et al. 2008; Williams et al. 2008), a pattern characteristic of many fishes (Boschung and Mayden 2004). Some mussel populations in the Interior Highlands of Arkansas and Missouri are distinct from populations east of the Mississippi River (snuffbox, *Epioblasma triquetra*; Zanatta and Murphy 2008) and among rivers within the Interior Highlands (western fanshell, *Cyprogenia aberti*; Serb 2006), a pattern shared with several fish species (e.g., Ceas and Page 1997; Lang and Mayden 2007).

These first fine-scale glimpses of mussel speciation patterns strongly suggest that mussel diversity is substantially underestimated. Our current knowledge of mussel systematics is similar to that of fishes at least 30 years ago. A large percentage of North American freshwater fish species were described subsequent to modern phylogenetic methods. Of the 187 species of darters (Percidae) currently recognized, 57 were described in the last 30 years, representing a 44 percent increase, and the number of madtom catfishes (*Noturus*) has more than doubled since 1969 (Nelson et al. 2004). Overall, the number of recognized fish species in the United States and Canada increased from 2,131 in 1970 to 2,635 in 2004, representing a 24 percent increase (Bailey et al. 1970; Nelson et al. 2004). Assuming that future systematic studies will reveal diversity in mussels 24 percent higher than current estimates, the number of mussel species in North America may approach or even exceed 375.

3.3. Faunal regions and the distribution of mussel diversity in North America

Freshwater mussels occur in every state and province in North America, but diversity is concentrated east of the Great Plains. The 20 rivers with the most diverse mussel faunas all are found in the southeastern and central United States; all but one (Mobile basin) are in the Mississippi River basin, and over half are in the Ohio River system (Table 3.2). Rivers of the Atlantic Coast have lower diversity but highly distinctive faunas. Pacific Coast rivers have low diversity but contain species found nowhere else in North America. Rivers flowing into the Arctic Ocean have few or no mussel species, with the exception of the southern portion of the Nelson–Churchill basin of Hudson Bay, which was colonized by several species from the Mississippi River basin.

Over the past 100 years, there have been several attempts to categorize North American mussel diversity into biogeographical faunal regions. These efforts initially divided the fauna according to the three major drainage realms of North America: Gulf of Mexico, Atlantic Ocean, and Pacific Ocean; successive efforts subdivided

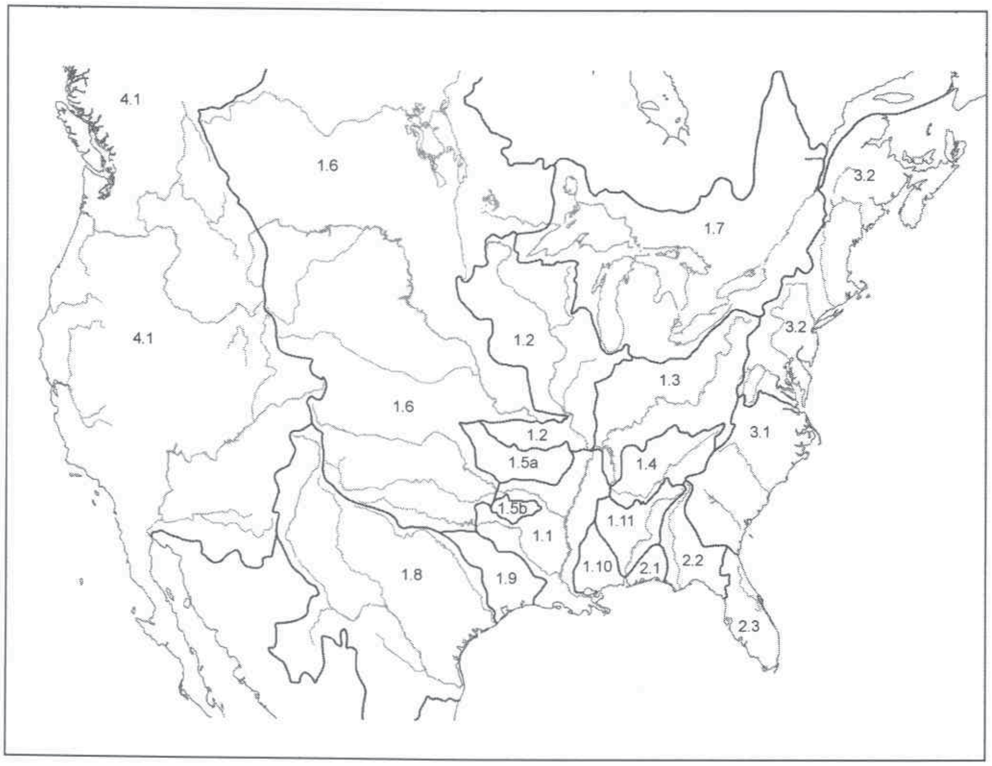

Figure 3.1. Freshwater mussel faunal regions and provinces of North America. Regions are composed of all provinces with the same integer; province numbers follow Table 3.3. For the Interior Highlands province (1.5), letters represent two disjunct units within the Ozark (a) and Ouachita (b) uplands (from Haag 2010).

these realms more finely as better distributional information became available (see Parmalee and Bogan 1998; Haag 2010 for a history of biogeographic schemes). The most recent biogeographical scheme classifies mussel diversity hierarchically among 17 faunal provinces within four major faunal regions (Haag 2010; Figure 3.1; Table 3.3). This hierarchy depicts a large and relatively homogeneous Mississippian region sharing many species, an Eastern Gulf region sharing a moderate number of species with the Mississippian region, and highly distinctive Atlantic and Pacific regions (Figure 3.2). I use this classification throughout the remainder of the book. In the following sections, I present a description of the mussel fauna of each region and province based on the data set of Haag (2010). These descriptions are supported by Tables 3.3 and 3.4 and Figure 3.1, except where otherwise noted. Readers should note that the composition of regional and provincial faunas is based on species distributions prior to major, human modification of streams in the twentieth century. In many cases, species that were widespread historically are now rare or absent from some or all provinces (see Chapter 10).

Table 3.4. *Distribution of mussel species among biogeographical regions and provinces of North America*

	Mississippian region											Eastern Gulf region			Atlantic region		Pacific region
	Miss. Embay.	Upper Miss.	Ohioan	Tenn.–Cumb.	Int. Highlands	Great Plains	St. Lawrence	Western Gulf	Sabine–Trinity	Pont.–Pearl–Pasc.	Mobile Basin	Escambia–Choc.	Apalachicolan	Peninsular Fla.	S. Atlantic	N. Atlantic	Pacific
Margaritifera hembeli	×																
Arkansia wheeleri	×				×												
Actinonaias ligamentina	×	×	×	×	×	×	×										
Amblema plicata	×	×	×	×	×	×	×	×	×	×	×	×					
Anodonta suborbiculata	×	×	×	×	×	×		×	×	×	×	×					
Arcidens confragosus	×	×	×	×	×	×		×	×	×	×						
Cumberlandia monodonta	×	×	×	×	×												
Cyclonaias tuberculata	×	×	×	×	×		×										
Ellipsaria lineolata	×	×	×	×	×						×						
Elliptio crassidens	×	×	×	×						×	×	×	×				
Elliptio dilatata	×	×	×	×	×	×	×										
Epioblasma triquetra	×	×	×	×	×	×	×										
Fusconaia flava	×	×	×	×	×	×	×		×								
Lampsilis abrupta	×	×	×	×	×												
Lampsilis cardium	×	×	×	×	×	×	×		×								
Lampsilis siliquoidea	×	×	×		×	×	×	×	×								
Lampsilis teres	×	×	×	×	×	×		×	×	×	×						
Lasmigona complanata	×	×	×	×	×	×	×			×							
Lasmigona costata	×	×	×	×	×		×									×	
Leptodea fragilis	×	×	×	×	×	×	×	×	×	×	×						
Leptodea leptodon	×	×	×	×	×	×											
Ligumia recta	×	×	×	×	×	×	×			×	×						
Ligumia subrostrata	×	×	×		×	×		×	×	×	×						
Megalonaias nervosa	×	×	×	×	×	×		×	×	×	×	×	×				
Obliquaria reflexa	×	×	×	×	×	×	×		×	×	×						
Obovaria jacksoniana	×				×				×	×	×						
Obovaria olivaria	×	×	×	×	×	×	×										
Obovaria subrotunda	×		×	×			×										
Plectomerus dombeyanus	×		×		×				×	×	×	×					
Plethobasus cyphyus	×	×	×	×													
Pleurobema sintoxia	×	×	×	×	×	×	×										
Pleurobema rubrum	×	×	×	×	×												
Potamilus alatus	×	×	×	×		×	×										
Potamilus capax	×	×	×		×												
Potamilus ohiensis	×	×	×	×	×	×		×									
Potamilus purpuratus	×				×	×		×	×	×	×						
Pyganodon grandis	×	×	×	×	×	×	×	×	×	×	×	×	×				
Quadrula apiculata	×							×	×	×	×						
Quadrula cylindrica	×		×	×	×		×										
Quadrula fragosa	×	×	×	×	×	×											
Quadrula metanevra	×	×	×	×	×	×					×						
Quadrula nodulata	×	×	×	×	×				×								
Quadrula pustulosa	×	×	×	×	×	×	×		×								
Quadrula quadrula	×	×	×	×	×	×	×		×								
Quadrula verrucosa	×	×	×	×	×	×	×	×	×	×	×						
Reginaia ebena	×	×	×	×	×					×	×						
Strophitus undulatus	×	×	×	×	×	×	×	×	×						×	×	
Toxolasma parva	×	×	×	×	×	×	×	×	×	×	×	×					

(continued)

Table 3.4 *(continued)*

	Mississippian region											Eastern Gulf region			Atlantic region		Pacific region
	Miss. Embay.	Upper Miss.	Ohioan	Tenn.–Cumb.	Int. Highlands	Great Plains	St. Lawrence	Western Gulf	Sabine–Trinity	Pont.–Pearl–Pasc.	Mobile Basin	Escambia–Choc.	Apalachicolan	Peninsular Fla.	S. Atlantic	N. Atlantic	Pacific
Toxolasma texasensis	×		×		×			×	×	×	×						
Truncilla donaciformis	×	×	×	×	×	×	×		×	×	×						
Truncilla truncata	×	×	×	×	×	×	×		×								
Uniomerus spp.	×	×	×		×	×		×	×	×	×	×	×	×	×		
Utterbackia imbecillis	×	×	×	×	×	×	×	×	×	×	×	×	×		×		
Villosa lienosa	×	×	×	×	×				×	×	×	×	×				
Alasmidonta marginata		×	×	×	×	×	×									×	
Alasmidonta viridis		×	×	×	×		×										
Anodontoides ferrusacianus		×	×	×		×	×									×	
Lampsilis higginsi		×															
Lasmigona compressa		×	×			×	×									×	
Simpsonaias ambigua		×	×	×			×										
Venustaconcha ellipsiformis		×			×		×										
Villosa iris		×	×	×	×		×										
Cyprogenia stegaria			×	×													
Epioblasma flexuosa			×	×													
Epioblasma obliquata			×	×			×										
Epioblasma personata			×	×													
Epioblasma propinqua			×	×													
Epioblasma sampsoni			×														
Epioblasma torulosa			×	×			×										
Fusconaia subrotunda			×	×													
Hemistena lata			×	×													
Lampsilis fasciola			×	×			×										
Lampsilis ovata			×	×													
Obovaria retusa			×	×													
Plethobasus cicatricosus			×	×													
Plethobasus cooperianus			×	×													
Pleurobema clava			×	×			×										
Pleurobema cordatum			×	×													
Pleurobema plenum			×	×													
Ptychobranchus fasciolaris			×	×			×										
Toxolasma lividus			×	×	×												
Villosa fabalis			×	×			×										
Villosa ortmanni			×														
Actinonaias pectorosa				×													
Alasmidonta atropurpurea				×													
Alasmidonta raveneliana				×													
Dromus dromas				×													
Epioblasma ahlstedti				×													
Epioblasma arcaeformis				×													
Epioblasma biemarginata				×													
Epioblasma brevidens				×													
Epioblasma capsaeformis				×													
Epioblasma florentina				×	×												
Epioblasma haysiana				×													
Epioblasma lenior				×													
Epioblasma lewisi				×													
Epioblasma stewardsoni				×													
Epioblasma turgidula				×	×												
Fusconaia cor				×													
Fusconaia cuneolus				×													

	Mississippian region											Eastern Gulf region			Atlantic region		Pacific region
	Miss. Embay.	Upper Miss.	Ohioan	Tenn.–Cumb.	Int. Highlands	Great Plains	St. Lawrence	Western Gulf	Sabine–Trinity	Pont.–Pearl–Pasc.	Mobile Basin	Escambia–Choc.	Apalachicolan	Peninsular Fla.	S. Atlantic	N. Atlantic	Pacific
Lampsilis virescens				×													
Lasmigona holstonia				×													
Lemiox rimosus				×													
Medionidus conradicus				×													
Pegias fabula				×													
Pleurobema oviforme				×													
Pleuronaia barnesiana				×													
Pleuronaia dolabelloides				×													
Pleuronaia gibberum				×													
Ptychobranchus subtentum				×													
Quadrula intermedia				×													
Quadrula sparsa				×													
Toxolasma cylindrellus				×													
Villosa perpurpurea				×													
Villosa taeniata				×													
Villosa trabalis				×													
Villosa vanuxemensis				×													
Cyprogenia aberti	×				×												
Fusconaia ozarkensis		×			×												
Lampsilis powelli					×												
Lampsilis streckeri					×												
Lampsilis rafinesqueana					×												
Lampsilis reeviana		×			×												
Ptychobranchus occidentalis	×				×												
Venustaconcha pleasi					×												
Villosa arkansasensis					×												
Cyrtonaias tampicoensis								×									
Fusconaia askewi								×	×								
Lampsilis bracteata								×									
Popenaias popei								×									
Potamilus salinasensis								×									
Quadrula aurea								×									
Quadrula couchiana								×									
Quadrula houstonensis								×									
Quadrula petrina								×									
Quadrula mitchelli								×									
Truncilla cognatus								×									
Truncilla macrodon								×									
Fusconaia lananensis									×								
Pleurobema riddelli	×								×								
Potamilus amphichaenus									×								
Anodontoides radiatus	×									×	×	×	×				
Elliptio arca										×	×						
Elliptio arctata										×	×	×	×		×		
Fusconaia cerina										×	×						
Glebula rotundata	×							×	×	×	×	×	×				
Lampsilis ornata										×	×	×					
Lampsilis straminea										×	×	×	×				
Obovaria unicolor										×	×						
Pleurobema beadleanum										×							

(*continued*)

Table 3.4 *(continued)*

	Mississippian region											Eastern Gulf region			Atlantic region		Pacific region
	Miss. Embay.	Upper Miss.	Ohioan	Tenn.–Cumb.	Int. Highlands	Great Plains	St. Lawrence	Western Gulf	Sabine–Trinity	Pont.–Pearl–Pasc.	Mobile Basin	Escambia–Choc.	Apalachicolan	Peninsular Fla.	S. Atlantic	N. Atlantic	Pacific
Potamilus inflatus										×	×						
Quadrula refulgens										×							
Strophitus subvexus										×	×	×	×				
Villosa vibex	×									×	×	×	×	×	×		
Alasmidonta mccordi											×						
Amblema elliotti											×						
Epioblamsa metastriata											×						
Epioblasma othcaloogensis											×						
Epioblasma penita											×						
Hamiota altilis											×						
Hamiota perovalis											×						
Lasmigona alabamensis											×						
Lasmigona etowaensis											×						
Margaritifera marrianae											×	×					
Medionidus acutissimus											×						
Medionidus parvulus											×						
Pleurobema athearni											×						
Pleurobema curtum											×						
Pleurobema decisum											×						
Pleurobema fibuloides											×						
Pleurobema georgianmum											×						
Pleurobema hanleyianum											×						
Pleurobema hartmanianum											×						
Pleurobema marshalli											×						
Pleurobema perovatum											×						
Pleurobema rubellum											×						
Pleurobema stabilis											×						
Pleurobema taitianum											×						
Pleurobema verum											×						
Ptychobranchus foremanianus											×						
Ptychobranchus greeni											×						
Quadrula asperata											×						
Quadrula rumphiana											×						
Quadrula stapes											×						
Strophitus connasaugaensis											×						
Toxolasma corvunculus											×						
Villosa nebulosa											×						
Villosa umbrans											×						
Elliptio mcmichaeli												×					
Elliptio pullata												×	×				
Fusconaia burkei												×					
Fusconaia escambia												×					
Hamiota australis												×					
Lampsilis floridensis												×	×	×			
Medionidus penicillatus												×	×				
Obovaria haddletoni												×					
Pleurobema strodeanum												×					
Ptychobranchus jonesi												×					
Quadrula succissa												×					
Reginaia rotulata												×					
Utterbackia peggyae												×	×				
Villosa choctawensis												×					

	Mississippian region											Eastern Gulf region			Atlantic region		Pacific region
	Miss. Embay.	Upper Miss.	Ohioan	Tenn.–Cumb.	Int. Highlands	Great Plains	St. Lawrence	Western Gulf	Sabine–Trinity	Pont.–Pearl–Pasc.	Mobile Basin	Escambia–Choc.	Apalachicolan	Peninsular Fla.	S. Atlantic	N. Atlantic	Pacific
Villosa villosa												×	×	×			
Alasmidonta triangulata													×				
Alasmidonta wrightiana													×				
Amblema neisleri													×				
Anodonta heardi													×				
Elliptio ahenea													×	×			
Elliptio chipolaensis													×				
Elliptio fraterna													×				
Elliptio fumata													×				
Elliptio nigella													×				
Elliptio purpurellus													×				
Elliptoideus sloatianus													×				
Hamiota subangulata													×				
Lampsilis binominata													×				
Medionidus simpsonianus													×				
Medionidus walkeri													×				
Pleurobema pyriforme													×				
Quadrula infucata													×				
Toxolasma paulus													×	×			
Utterbackia peninsularis													×	×			
Anodonta couperiana														×	×		
Elliptio jayensis[a]														×			
Elliptio monroensis														×			
Elliptio waltoni														×			
Villosa amygdala														×			
Alasmidonta arcula															×		
Alasmidonta heterodon															×	×	
Alasmidonta robusta															×		
Alasmidonta undulata							×								×	×	
Alasmidonta varicosa															×	×	
Anodonta implicata															×	×	
Elliptio angustata															×		
Elliptio cistelliformis															×		
Elliptio complanata							×						×		×	×	
Elliptio congarea															×		
Elliptio darienensis															×		
Elliptio errans															×		
Elliptio folliculata															×		
Elliptio hepatica															×		
Elliptio hopetonensis															×		
Elliptio icterina															×		
Elliptio judithae															×		
Elliptio lanceolata															×	×	
Elliptio lugubris															×		
Elliptio marsupiobesa															×		
Elliptio producta															×		
Elliptio raveneli															×		
Elliptio roanokensis															×		
Elliptio shepardiana															×		
Elliptio spinosa															×		
Elliptio steinstansana															×		
Elliptio waccamawensis															×		

(*continued*)

Table 3.4 *(continued)*

	Mississippian region											Eastern Gulf region			Atlantic region		Pacific region
	Miss. Embay.	Upper Miss.	Ohioan	Tenn.–Cumb.	Int. Highlands	Great Plains	St. Lawrence	Western Gulf	Sabine–Trinity	Pont.–Pearl–Pasc.	Mobile Basin	Escambia–Choc.	Apalachicolan	Peninsular Fla.	S. Atlantic	N. Atlantic	Pacific
Fusconaia masoni															×		
Lampsilis cariosa															×	×	
Lampsilis dolabraeformis															×		
Lampsilis fullerkati															×		
Lampsilis radiata							×								×	×	
Lampsilis splendida															×		
Lasmigona decorata															×		
Lasmigona subviridis			×	×									×		×	×	
Leptodea ochracea															×	×	
Ligumia nasuta							×								×	×	
Pleurobema collina															×		
Pyganodon cataracta							×						×		×	×	
Pyganodon gibbosa															×		
Toxolasma pullus															×		
Villosa constricta															×		
Villosa delumbis															×		
Villosa vaughniana															×		
Elliptio fisherianus																×	
Margaritifera margaritifera							×									×	
Pyganodon fragilis																×	
Anodonta beringiana																	×
Anodonta californiensis																	×
Anodonta kennerlyi																	×
Anodonta nuttalliana																	×
Anodonta oregonensis																	×
Gonidea angulata																	×
Margaritifera falcata																	×

Note: Species are sorted alphabetically roughly by region(s) of primary occurrence (data from Haag 2010). Table omits subspecies and the following recognized taxa of uncertain validity or distribution: *Lampsilis hydiana* (combined with *L. siliquoidea*), *L. satura* (combined with *L. cardium*), *Pygandon lacustris* (combined with *P. grandis*), *Quadrula mortoni* (combined with *Q. pustulosa*), *Q. nobilis* (combined with *Q. quadrula*). In addition, all 5 recognized species of *Uniomerus* are combined as *Uniomerus* spp. because of taxonomic and distributional uncertainty.

[a] includes *E. buckleyi* (see Williams et al. 2011).

3.3.A. Mississippian region

The Mississippian region is a large and geographically heterogeneous region made up of 11 faunal provinces. The region includes the entire Mississippi River basin (with the exception of the upper Missouri River system above Great Falls); the Lake Pontchartrain, Pearl, Pascagoula, and Mobile basins; and all Gulf Coast rivers west of the Mississippi River. The region contains 198 species, or about two-thirds of the North American fauna, of which 147 (74%) are endemic to the region. The Mississippi River basin alone contains 133 species, of which 98 (74%) are endemic to the basin.

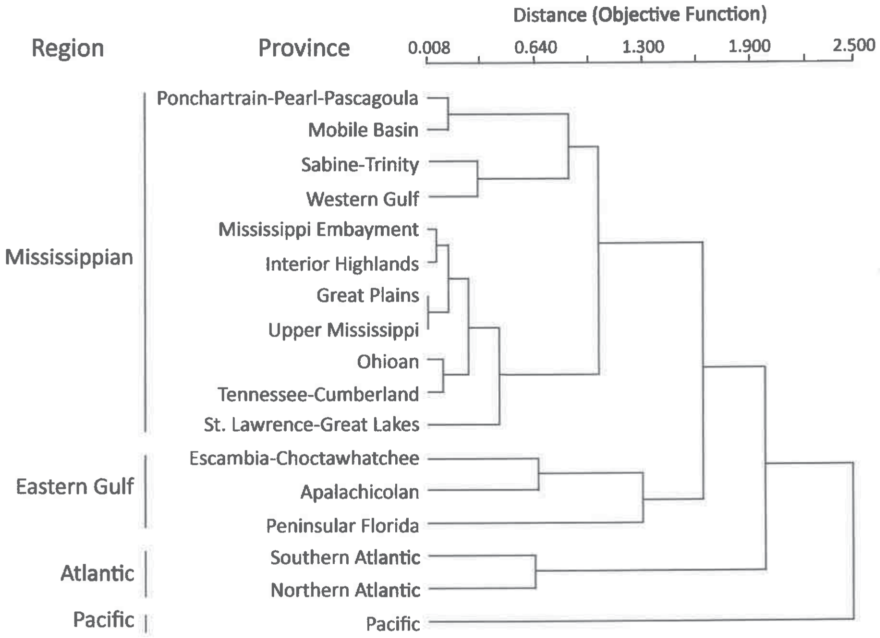

Figure 3.2. Dendrogram depicting relationships among freshwater faunal regions and provinces of North America. Clustering is based on species presence or absence (from Haag 2010).

Despite the basin's geographical heterogeneity, many species are distributed widely in the region, and assemblages in different provinces share a large number of species. Fourteen species occur in 90 percent or more of provinces within the region, and an additional 19 species occur in all six faunal provinces within the Mississippi River basin. Because of the wide distribution of many species, the region is characterized by relatively low beta diversity (the difference in species diversity among sites or habitats). In all provinces, the most diverse sites contain about 50 to 75 percent of total provincial diversity.

The homogeneous nature of much of the fauna suggests that there has been high connectivity and dispersal within this region in recent times. Patterns of genetic variation in several widespread species support high dispersal throughout the region but show evidence of subsequent reproductive isolation in some areas (Berg et al. 1998; Elderkin et al. 2007, 2008). Dispersal between the Mississippi River system and other Gulf Slope rivers likely occurred during glacial periods of low sea level, when many currently isolated river systems had common outlets; in addition, there appears to have been a historical connection between the Mobile basin and the upper Tennessee River (Wiley and Mayden 1985; Conner and Suttkus 1986; Galloway et al. 2011). The subsequent isolation of these river systems is reflected in the major biogeographical split in the Mississippian region between (1) the Mississippi River basin plus the Great

Lakes and (2) all other Gulf of Mexico river basins from and including the Mobile basin west (Figure 3.2). All provinces in the latter group contain distinctive, endemic faunas in addition to widespread Mississippian species. In contrast, endemic faunas in the Mississippi River basin are largely confined to the Tennessee–Cumberland, Ohioan, and Interior Highlands provinces.

3.3.A.1. Mississippi Embayment province

The Mississippi Embayment province encompasses the lower Mississippi River and all tributaries below the mouth of the Ohio River, including most of the lower Red River system and the Atchafalaya basin, and the Mermentau River, which flows directly into the Gulf of Mexico immediately west of the Atchafalaya basin. Within the Mississippi River basin, the distribution of the Mississippi Embayment fauna overlies closely the Coastal Plain physiographic province, a low-lying basin filled with marine and fluvial sediments deposited since the region was inundated by the Gulf of Mexico during the Cretaceous Period (van Arsdale and Cox 2007). Streams may have gravel substrates transported from uplands, but most of the province is characterized by low-gradient streams with fine sediments and an abundance of lentic or wetland habitat. Upland portions of several large, western river systems in the province have distinct mussel assemblages that support their inclusion in other faunal provinces (upper Red and Arkansas river systems, Great Plains province; upper White, Ouachita, and St. Francis rivers, Interior Highlands province).

The fauna of the Mississippi Embayment province is composed of a large number of species widespread in the Mississippian region but is distinguished by the presence of several species adapted to low-gradient streams and wetland habitats, including *Anodonta suborbiculata*, *Arcidens confragosus*, *Lampsilis teres*, *Ligumia subrostrata*, *Plectomerus dombeyanus*, *Potamilus capax*, *P. purpuratus*, and *Toxolasma texasensis*. These species occur in other provinces but are widespread and often ubiquitous in the Mississippi Embayment. Twenty species occur in more than 90 percent of major rivers in the province, and alpha diversity is often high in larger streams.

The Mississippi Embayment province has only a single recognized endemic species, the Louisiana pearlshell, *Margaritifera hembeli*, restricted to several small tributaries of the lower Red River. The Ouachita rock-pocketbook, *Arkansia wheeleri*, has a similarly restricted distribution (lower Ouachita River) but is shared with a few streams in the Interior Highlands province. However, the province is likely to contain cryptic, endemic species, primarily in western river systems in Arkansas and Louisiana. A number of currently recognized taxa are poorly known with respect to their distinctiveness as species and their geographic range (e.g., Louisiana fatmucket, *Lampsilis hydiana*; sandbank pocketbook, *L. satura*; southern mapleleaf, *Quadrula apiculata*) and may represent or contain species endemic to the province (Neel 1941; Valentine and Stansbery 1971). In addition, populations of several widespread taxa in these western river systems may represent distinct species endemic to the

Mississippi Embayment (e.g., southern hickorynut, *Obovaria jacksoniana*; pyramid pigtoe, *Pleurobema rubrum*; *Toxolasma* spp.; J. Harris, personal communication).

The lower Mississippi River itself supports few mussel species due to the highly dynamic nature of this section of the river (van der Schalie and van der Schalie 1950; Brown et al. 2005; see Section 4.1.D.1). However, sloughs, backwaters, and oxbow lakes adjacent to the river support a modest fauna consisting of at least 25 species (Cooper 1984; Cicerello et al. 1991; Jones et al. 2005). The dynamic and unstable nature of the main channel in present times, coupled with repeated inundation by the sea in geologic history, has likely served as a long-standing dispersal barrier to many mussel species and their fish hosts, contributing to the isolation of many taxa west of the Mississippi River.

3.3.A.2. Upper Mississippi province

The Upper Mississippi province includes the entire Mississippi River system upstream of the mouth of the Ohio River but excluding most of the Missouri River system; southern tributaries of the lower Missouri River (Osage and Gasconade rivers) are included in the Upper Mississippi province. Upland stream habitat characterizes most of the province, but wetland and lentic habitats can be found adjacent to larger streams, and abundant glacial moraine and kettle lakes occur in the upper portions of the province (Delong 2005). Nearly the entire province lies within the recently glaciated Central Lowlands physiographic province, with the exception of the Gasconade, Meramec, and Osage rivers on the Ozark Plateau in the southern portion of the province (Delong 2005; Galat et al. 2005).

The Upper Mississippi province contains a diverse mussel fauna with high alpha diversity but has only a single endemic species, the Higgins eye, *Lampsilis higginsi*, which is widely distributed in the province. The ellipse, *Venustaconcha ellipsiformis*, is widespread and characteristic of the province but also occurs in small areas of the Interior Highlands and Great Lakes provinces. The broken-ray, *Lampsilis reeviana*, is restricted to headwaters of the Osage, Gasconade, and Meramec river systems but is widely distributed in the Interior Highlands province. However, populations in the Upper Mississippi province are recognized as a separate subspecies, the northern broken-ray, *L. r. brittsi* (Oesch 1995), suggesting that it may represent an additional endemic taxon. The remainder of the fauna is composed of widespread Mississippian species that colonized the province following Pleistocene glaciation (Burdick and White 2007). A notable exception is the creek heelsplitter, *Lasmigona compressa*, which is widespread in the province but occurs elsewhere in the Mississippi River basin only in northern tributaries of the Ohio River (Ohioan province; see Section 4.1.A). A number of Mississippian species evidently have been unsuccessful in colonizing the province, judging by their absence or restricted distribution (e.g., *Potamilus purpuratus, Plectomerus dombeyanus, Pleurobema rubrum, Quadrula cylindrica, Toxolasma texasensis, Villosa lienosa*).

The fauna of the Upper Mississippi province is relatively homogeneous because of its recent geological history, and, unlike the lower Mississippi, the upper river itself provides habitat for a diverse mussel fauna and therefore serves as a central route of dispersal throughout the province. Twenty-four of 55 total species occur in all major rivers in the province. Rivers in the southern portion of the province have higher species richness likely because they were not glaciated (e.g., Osage, Gasconade, Meramec rivers) or were not directly affected by the most recent glacial advance (e.g., Illinois, Kaskaskia rivers) and because of their proximity to glacial refugia (Haag 2010). Streams in the southern portion of the province, particularly the Osage and Meramec rivers, also are distinguished by their similarities with the Ohioan and Mississippi Embayment provinces, notably the replacement of *Lampsilis higginsi* by *L. abrupta* and the absence of *Lasmigona compressa*.

3.3.A.3. Ohioan province

The Ohioan province includes the Ohio River and all of its tributaries except the upper two-thirds of the Cumberland and Tennessee river systems. Upland stream habitat characterizes most of the province, but streams flow through several geologically distinct regions. The upper Ohio River basin and southern tributaries of the Ohio flow through the unglaciated Appalachian Mountains and Interior Low Plateaus physiographic province (White et al. 2005). Northern tributaries of the middle and lower Ohio River flow through recently glaciated plains of the Central Lowlands physiographic province (White et al. 2005). The lower Ohio River and lower reaches of its tributaries (e.g., Cumberland, Green, Tennessee, Tradewater, Wabash rivers) assume a lowland character and provide habitats similar to those found in the Mississippi Embayment province (Warren and Call 1983; Burr and Warren 1986).

The Ohioan province has a highly diverse fauna, second only to the Tennessee–Cumberland province. Alpha diversity in large streams rivals the Tennessee–Cumberland province. Species richness in the Ohio River in the vicinity of Cincinnati, Ohio (63 species), was nearly as high as the more famous Muscle Shoals on the Tennessee River (68 species; Section 3.3.A.4) but is overshadowed by the latter stream due to the presence of few endemic species in the Ohio. The Ohioan province contains only two endemic species: the Wabash riffleshell, *Epioblasma sampsoni*, and the Kentucky creekshell, *Villosa ortmanni* (occurring only in the Green River system); the Scioto pigtoe, *Pleurobema bournianum*, is known only from the Scioto River system in Ohio, but the validity of this taxon is questionable (Watters et al. 2009). However, 13 species are shared exclusively with the Tennessee–Cumberland province, most of which are widespread in and characteristic of the Ohioan province. An additional six species are mostly restricted to the Ohioan and Tennessee–Cumberland provinces but also occur in western Lake Erie and tributary streams (St. Lawrence–Great Lakes province), which they apparently colonized from the Ohioan province during the Pleistocene (Clarke and Stansbery 1988). The northern riffleshell, *Epioblasma torulosa rangiana*, is shared exclusively with western Lake Erie and likely has a similar dispersal history. The remainder of the fauna of the Ohioan province consists of species widespread in the Mississippi River basin.

Similar to the upper Mississippi River, the Ohio River bisects and provides a dispersal corridor throughout the entire province. For example, populations of the fanshell, *Cyprogenia stegaria*, in three large tributaries showed evidence of high gene flow suggesting that they were essentially panmictic prior to impoundment of the Ohio River (Grobler et al. 2011). Populations in smaller streams tend to show greater genetic population structure indicative of a stepping stone model of isolation by distance (Berg et al. 2007; Elderkin et al. 2008). High historical gene flow coupled with the recent origin of populations in formerly glaciated regions reduces the possibility for cryptic variation in the province; however, population structure of few species has been examined in detail. High connectivity and dispersal has resulted in a relatively homogeneous fauna throughout the province. However, diversity generally increases in a downstream direction, with tributaries of the upper Ohio River having fewer species than those of the middle and lower river. This may be explained in part by a failure of some species to disperse into formerly glaciated areas in the northern and upper portions of the Ohio River system. The fauna of the lower Ohioan province (downstream of and including the Green River) also is somewhat distinct from the upper province due to the addition of lowland species more typical of the Mississippi Embayment province. In contrast to these lowland species that transcend provincial boundaries, the distribution of other Ohioan species ends abruptly at the mouth of the Ohio River. Several species occur within the first few kilometers of the river upstream of its mouth (e.g., *Epioblasma flexuosa, E. torulosa, Plethobasus cooperianus, Pleurobema cordatum*) but are absent beyond the mouth of the river. The distribution of the essentially upland Ohioan fauna is likely truncated by the unstable, lowland nature of the main channel of the lower Mississippi River.

3.3.A.4. Tennessee–Cumberland province

The Tennessee–Cumberland province includes the upper two-thirds of the Tennessee and Cumberland river systems. On the basis of the distribution of endemic species, the downstream boundary of the province is placed in the Tennessee River just downstream of Muscle Shoals in northwestern Alabama and in the Cumberland in the vicinity of Clarksville, Tennessee (Ortmann 1924a, 1925). The province encompasses all tributaries upstream of these points, including Bear Creek (Tennessee River system) and the Red River (Cumberland River system). Characteristic Tennessee–Cumberland endemic species also occur in the Duck River upstream of the vicinity of Centerville, Tennessee, and the upper portion of its tributary, the Buffalo River, but they are absent in the lower sections of these streams. In addition, the Little River, a tributary of the lower Cumberland, also has at least three of these endemic species. The Tennessee and Cumberland rivers flow into the lower Ohio River, and their mouths are separated by only 19 km; at one point near their mouths, the rivers flow within 3 km of each other. Upland stream habitat characterizes the province, which lies predominantly within the Appalachian Mountains and the Interior Low Plateaus physiographic province (White et al. 2005).

The Tennessee–Cumberland province is the most diverse faunal province in North America, with about 110 total species and 32 endemic species. The two river systems have similar faunas, sharing 83 species. Alpha diversity in mid-sized to large streams is spectacular. The highest species richness recorded from a single stream reach anywhere on Earth is from Muscle Shoals on the Tennessee River in Alabama (68 species; Box 10.1), but richness can exceed 50 species in other stream reaches throughout the province (Ortmann 1918b, 1925).

The most notable feature of the province is its high number of endemic species, especially within the genus *Epioblasma*. Many widespread North American genera are represented by endemic species, and the province has four endemic genera (*Dromus, Lemiox, Pegias*, and *Pleuronaia*). Most endemic species are widespread in both the Cumberland and Tennessee river systems, but 11 occur only in the Tennessee (*Alasmidonta raveneliana, Epioblasma ahlstedti, Fusconaia cor, F. cuneolus, Lampsilis virescens, Lemiox rimosus, Pleuronaia barnesiana, Quadrula intermedia, Q. sparsa, Toxolasma cylindrellus*, and *Villosa perpurpurea*), and at least two occur only in the Cumberland (*Alasmidonta atropurpurea, Pleuronaia gibberum*). In addition, four subspecies are endemic to the province, three of which are restricted to the Tennessee River system (*Epioblasma florentina aureola, E. torulosa gubernaculum, Quadrula cylindrica strigillata*), and one is restricted to the Cumberland River system (*E. florentina walkeri*).

The province undoubtedly harbors additional cryptic, endemic species in part because of its complex geologic history and limited gene flow with the Ohioan and other provinces. As recently as the Pleistocene, the upper Tennessee River is thought to have flowed to the Gulf of Mexico through the Mobile basin, but the lower Tennessee and Cumberland rivers had a separate outlet to the west (Galloway et al. 2011). Several endemic taxa that were previously considered widespread in the province were recently found to consist of multiple taxa (e.g., *Epioblasma capsaeformis, E. florentina walkeri*, Jones et al. 2006a, Jones and Neves 2010; *Villosa* spp., K. Kuehnl, personal communication). In these cases, populations in the upper Tennessee system are distinct from those in the lower Tennessee, and Cumberland populations are distinct from the Tennessee. Similarly, populations of the slabside pearlymussel, *Pleuronaia dolabelloides*, in the Duck River (lower Tennessee) were genetically distinct from those in the upper Tennessee system, but these differences were not sufficient to consider them separate species (Grobler et al. 2006). Populations of *Cyprogenia stegaria* throughout the Ohio River system (including the Tennessee River) showed little genetic differentiation, but those in the upper Tennessee River system lacked a mitochondrial DNA haplotype present elsewhere, suggesting that they experienced a significant bottleneck at some point followed by limited gene flow with other populations (Grobler et al. 2011). This finding raises the possibility that some widely distributed species may be represented by distinct taxa in the Tennessee-Cumberland province. For example, *Anodontoides denigratus* and *Venustaconcha sima* are provisionally recognized as distinct species based on their isolation by hundreds of kilometers from populations of similar species (Gordon 1995; Cicerello and Schuster 2003).

Although endemic species largely distinguish this province, the fauna also is characterized by a large number of species shared exclusively with the Ohioan province; the remainder of the fauna is widely distributed throughout the Mississippi River basin. Despite the potential for limited gene flow in some cases, the connection with the Ohio River has resulted in strong similarity between the faunas of the Tennessee–Cumberland and Ohioan provinces (Figure 3.2). Only four taxa in the Ohioan province are absent in the Tennessee–Cumberland (*Epioblasma torulosa rangiana, E. sampsoni, Lasmigona compressa*, and *Villosa ortmanni*). The fauna of the lower third of the Tennessee and Cumberland rivers and the lower Duck River, where endemic species are absent, is essentially identical to the fauna of other large streams in the lower Ohioan province.

The high degree of endemism in the Tennessee–Cumberland province is likely due to its former isolation and long geologic history, during which it has not been affected directly by glaciation or associated sea level changes for millions of years. The upper Tennessee River system has largely occupied its current course since at least the Eocene (56–34 mya), and for much of its history it flowed directly to the Gulf of Mexico, allowing it to follow an evolutionary trajectory largely independent from other North American river systems (Galloway et al. 2011). Similarly, the lower Tennessee and Cumberland systems flowed directly to the Gulf as recently as the Pleistocene. This long history of isolation is likely responsible for the greater number of endemic genera in the province than in any other region of North America. Confluence among these river systems and with the Ohio River system at various times allowed dispersal of endemic species as well as dispersal of species widespread in the Ohio and Mississippi river systems. The curious, abrupt absence of endemic species in the lower Tennessee, Duck, and Cumberland rivers is unexplained. To an extent, this may simply reflect a failure of endemic species to disperse widely subsequent to development of modern river courses since the Pleistocene. However, archaeological evidence shows that some endemic species occurred farther downstream in these rivers, nearly to their mouths, within the last 5,000 years (Casey 1987; Parmalee and Bogan 1998). In modern times, the disappearance of these species coincides roughly with the point at which these rivers begin to assume lowland characteristics as they approach the Coastal Plain. Because endemic species of the Tennessee–Cumberland province typically inhabit upland streams, their present distribution may be truncated by the disappearance of upland stream habitat (Haag 2010).

3.3.A.5. Interior Highlands province

The Interior Highlands province encompasses two geographically discontinuous areas: (1) the upper White and upper St. Francis river systems within the Ozark Plateaus physiographic province plus the adjacent Verdigris, Neosho, and Illinois river systems in the Central Lowlands physiographic province, and (2) streams of the Ouachita physiographic province, including the upper Ouachita, Kiamichi, and Little rivers (Red River system) and the Poteau River (Arkansas River system). Both areas are characterized by upland stream habitat (Brown et al. 2005; Matthews et al. 2005) and are the remnants of an ancient mountain range that may have been continuous with the Appalachians prior to deposition of marine and alluvial sediments in the lower Mississippi River valley (Robison 1986; Mayden 1988). Consequently, these upland habitats are isolated by the extensive lowlands of the Arkansas River valley and the Coastal Plain sections of the lower White and St. Francis river systems, which have characteristic Mississippi Embayment faunas (Section 3.3.A.1). Unlike most other faunal provinces that are circumscribed mainly by river system boundaries, the distribution of the Interior Highlands mussel fauna follows closely the occurrence of upland stream habitat, a pattern that also is seen in the discontinuous distributions of many upland fish species in these areas (Mayden 1988; Strange and Burr 1997).

The Interior Highlands province includes at least nine endemic species, but only two, the western fanshell, *Cyprogenia aberti*, and Ouachita kidneyshell, *Ptychobranchus occidentalis*, occur in both disjunct areas. Both species are widespread and characteristic of the province, but their distributions extend into the Mississippi Embayment province in the Ouachita, St. Francis, and White rivers likely because these rivers transport upland-derived gravel substrates for considerable distances downstream. All other endemic species have highly restricted distributions. The Ozarks proper contain an additional four endemic taxa, all restricted to various portions of the upper White River system (*Epioblasma florentina curtisi, Fusconaia ozarkensis, Lampsilis streckeri*, and *Venustaconcha pleasi*). The Neosho mucket, *Lampsilis rafinesqueana*, occurs only in the Neosho, Verdigris, and Illinois river systems. The Ouachita highlands contain two additional endemic species, the Arkansas fatmucket, *Lampsilis powelli*, and the Ouachita creekshell, *Villosa arkansasensis*. *Lampsilis reeviana* is shared exclusively with the Upper Mississippi province, but Interior Highlands populations are recognized as separate subspecies, the Arkansas broken-ray, *L. r. reeviana* (upper White River), and the Ozark broken-ray, *L. r. brevicula* (upper White and St. Francis river systems; Oesch 1995), suggesting that they may represent distinct taxa endemic to the province.

The Interior Highlands province likely contains additional, cryptic endemic species. The isolation of most river systems in the province from each other and from other upland regions appears to have strongly limited dispersal and gene flow among mussel populations (Turner et al. 2000; Elderkin et al. 2007, 2008). Populations of *Cyprogenia aberti* in different river systems represent several genetically distinct lineages (Serb 2006). In addition, Interior Highland populations of several widespread species (e.g., *Epioblasma triquetra, Fusconaia flava, Pleurobema* spp., *Toxolasma* spp., *Villosa iris*) are genetically or morphologically distinct from populations elsewhere in the Mississippi River basin (e.g., Burdick and White 2007; Zanatta and Murphy 2008; Campbell and Lydeard 2012b).

In addition to endemic species, the Interior Highlands province is characterized by species widespread throughout the Mississippi River basin. Because all streams flow ultimately onto the Gulf Coastal Plain, the province has strong affinities to the Mississippi Embayment province, despite its upland characteristics (Figure 3.2). These affinities are illustrated by the occurrence in all river systems of characteristic Mississippi Embayment species such as *Potamilus purpuratus, Lampsilis teres*, and *Ligumia subrostrata*. However, the fauna also contains several upland species that are absent or rare in the Mississippi Embayment, including *Alasmidonta marginata, A. viridis*, *Cyclonaias tuberculata*, and *Epioblasma triquetra*. In addition, the occurrence of *Cyprogenia, Epioblasma turgidula, Ptychobranchus*, and *Toxolasma lividus* suggests past faunal exchange with the Ohio River basin via the ancient mountain range connection with the Appalachians.

3.3.A.6. Great Plains province

The Great Plains province includes all river systems east of the Rocky Mountains in the Great Plains and adjacent portions of the Central Lowlands physiographic provinces, from the upper Red River of Texas and Oklahoma, north to the Nelson–Churchill basins in south central Canada (Saskatchewan, Assiniboine, and Red rivers; Galat et al. 2005; Matthews et al. 2005; Rosenberg et al. 2005). The province includes the entire Missouri River system with the exception of the Osage and Gasconade rivers (Upper Mississippi province) and the extreme upper portion of the Missouri River above Great Falls within the Rocky Mountains (Pacific province). With the exception of the Nelson–Churchill basins (flowing into Hudson Bay), all river systems in the province are in the Mississippi River basin. Rivers flowing into James Bay (southern Hudson Bay) evidently were colonized from the St. Lawrence–Great Lakes province and are therefore included in that province (Section 3.3.A.7).

The Great Plains province includes no known endemic species. The fauna bears strong affinity to the Upper Mississippi province (Figure 3.2) but is a depauperate subset of that fauna. Like the Upper Mississippi province, the northern portion of the Great Plains was extensively glaciated in the Pleistocene, and the present fauna is limited to species that dispersed from glacial refugia. Dispersal and species persistence also are limited by arid conditions and hydrologic variability, which result in unstable stream habitats (Hoke 2005; Matthews et al. 2005). Characteristic species are short-lived or fast-growing species that can adapt to these challenges (e.g., *Anodontoides ferrusacianus, Lampsilis* spp., *Lasmigona complanata, Leptodea fragilis, Ligumia subrostrata, Potamilus* spp., *Pyganodon grandis, Strophitus undulatus, Uniomerus* sp., *Utterbackia imbecillis*; see Chapters 6 and 8). In the Hudson Bay portion of the province, the fauna is further limited by extreme conditions imposed by the northern climate as well as now defunct post-Pleistocene dispersal routes from the Mississippi River basin (Cvancara 1970; Graf 1997).

Because of variable physical conditions and dispersal history, mussel communities are heterogeneous across the province. No species occur in all major river systems, and only 13 of 37 species occur in more than 50 percent of rivers in the province. Highest diversity is found in larger streams in the eastern portion of the province, where more stable conditions and proximity to the Upper Mississippi province allow development of richer mussel assemblages (e.g., Kansas, James rivers).

3.3.A.7. St. Lawrence–Great Lakes province

The St. Lawrence–Great Lakes province includes all five Great Lakes and Lake St. Clair and their watersheds as well as the St. Lawrence and Ottawa river systems and rivers flowing into James Bay (Albany and Moose rivers). The lakes themselves provide a diverse array of habitats, including deep, oligotrophic lakes; shallow bays and wetlands; and shallow, rocky reefs that resemble stream habitats (primarily in western Lake Erie and Lake St. Clair; Fuller et al. 1995; Ludsin et al. 2001; see Section 4.1.D.2). Tributaries to the Great Lakes provide habitats similar to streams in the Upper Mississippi province and northern portions of the Ohioan province. Highest diversity is found in tributary streams of the lakes, but a comparably diverse fauna occurs in western Lake Erie and Lake St. Clair.

The St. Lawrence–Great Lakes province contains no known endemic species, but some species may show shell stunting or other morphological differences relative to their counterparts in other provinces (Clark and Wilson 1912; Clarke and Stansbery 1988). This is a faunistically heterogeneous province because the lakes and their watersheds were colonized from multiple sources following Pleistocene glaciation. The fauna is composed of species from both the Atlantic and Mississippian regions. Most Atlantic region species are restricted to the Lake Ontario and St. Lawrence River basins because upstream dispersal was truncated by Niagara Falls. The eastern elliptio, *Elliptio complanata*, reached the Lake Huron basin and James Bay drainages via past and current connections with the Ottawa River system (van der Schalie 1963; Clarke 1973). Subsequently, *E. complanata* may have reached Lake Superior by headwater exchange with James Bay drainages along with several Mississippian species (*Lampsilis siliquoidea, Lasmigona compressa, Pyganodon grandis*; Clarke 1973). *Elliptio complanata* may have reached upper Lake Michigan via interlake dispersal but is absent from Lake Erie and Lake St. Clair.

Although the waters of the Great Lakes currently flow into the Atlantic Ocean, the fauna of the province is dominated by species of the Mississippi River basin (Figure 3.2) because this was the primary source of post-Pleistocene colonization. The Lake Erie and Lake St. Clair basins have the most diverse fauna in the province (39 species) owing to a former connection between the Maumee and Wabash rivers (Ortmann 1924b; van der Schalie 1963; Clarke and Stansbery 1988). This route allowed colonization by six species otherwise endemic to the Ohioan and Tennessee–Cumberland provinces as well as Mississippian species; Ohioan species are absent elsewhere in the province. In addition to the Maumee-Wabash connection, genetic evidence suggests that some species reached the Lake Erie watershed via multiple routes (Elderkin et al. 2007; 2008). The Lake Michigan basin (31 species) was colonized via a former connection with the Wisconsin River (van der Schalie 1963), allowing dispersal of a diverse array of Upper Mississippi province species, including the ellipse, *Venustaconcha ellipsiformis*, which is absent in Lakes Erie and St. Clair. Lake Superior has the least diverse fauna in the province (seven species) because it was colonized primarily by a late Pleistocene connection with the Mississippi River system above St. Anthony Falls, which limited the distribution of many Mississippian species (Graf 1997). Mississippian species likely reached other parts of the upper Great Lakes by interlake basin dispersal in postglacial times.

3.3.A.8. Western Gulf province

The Western Gulf province encompasses all rivers flowing into the Gulf of Mexico from the Brazos south to the Rio Grande. Streams in the province traverse a variety of geologic features. The lower sections of major streams lie within the Coastal Plain, but most arise in the Great Plains or Central Lowlands physiographic provinces (Dahm et al. 2005). Headwaters of the Rio Grande originate in the Rocky Mountains and Sierra Madre.

This province represents a transitional zone between the Mississippian region mussel fauna of North America and the fauna of northern Mexico and Mesoamerica and is characterized by a mingling of these faunas. The northern limit of the province (Brazos River) is indicated by the sudden absence of many Mississippian taxa that reach their southernmost distribution in the adjacent Trinity River. The number of Mississippian species continues to decline southward in river systems along the Texas coast, with only eight Mississippian species occurring in the Rio Grande system. Simultaneously, Mississippian species are replaced by endemic species with probable Mississippian affinity (*Lampsilis bracteata, Quadrula aurea, Q. couchiana, Q. houstonensis, Q. petrina, Truncilla cognata*, and *T. macrodon*) or species of Mexican origin (e.g., *Cyrtonaias tampicoensis, Potamilus salinasensis, Popenaias popei, Quadrula mitchelli*). A distinguishing characteristic of the Western Gulf province fauna is the occurrence of the Mexican species, the Tampico pearlymussel, *Cyrtonaias tampicoensis*, in all river systems. This species occurs north of the Rio Grande only in the Western Gulf province, but it is widespread in Mexico (Howells et al. 1996).

Endemic species in the Western Gulf province have restricted distributions encompassing only one or two river systems. Only the golden orb, *Quadrula aurea*, and false spike, *Quadrula mitchelli*, occur in more than 50 percent of river systems in the province. Like the Interior Highlands province, the restricted distribution of most species suggests limited gene flow among rivers and the likely occurrence of unrecognized cryptic endemic species. For example, populations of *Potamilus purpuratus* in the Western Gulf province may represent a separate species (*P. coloradoensis*) distinct from populations elsewhere in the Mississippian Region (Roe and Lydeard 1998). In addition, the Rio Grande and adjacent Nueces River may represent a biographical entity unique from the remainder of the Western Gulf province (Haag 2010). These rivers have five species not found elsewhere in the province, and much of the fauna appears to have strong Mexican or Mesoamerican affinity. However, the phylogenetic relationships of all endemic species in the province are poorly known, as is the distribution of these species south of the Rio Grande. Because most Western Gulf species have declined precipitously in recent years, information necessary to better resolve biogeographical patterns in this province may be hard to come by.

3.3.A.9. Sabine–Trinity province

The Sabine–Trinity province encompasses rivers of the central Gulf Coast, including the San Jacinto, Trinity, Neches, Sabine, and Calcasieu rivers. Rivers in the province lie almost exclusively within the Coastal Plain, except for headwaters of the Trinity River, which arise in the Central Lowlands and Great Plains physiographic provinces (Dahm et al. 2005). Streams are lowland in character, with wetland and lentic habitats adjacent to main channels.

The Sabine–Trinity province contains at least three endemic species. The Louisiana pigtoe, *Pleurobema riddelli*, occurs in all river systems in the province, and the Texas heelsplitter, *Potamilus amphichaenus*, and triangle pigtoe, *Fusconaia lananensis*, occur in all rivers, except the Calcasieu. *Pleurobema riddelli* also may occur in a few streams of the adjacent lower Red River system as a result of headwater stream capture, but the identity of these specimens is uncertain (Vidrine 1993). The Texas pigtoe, *Fusconaia askewi*, occurs in all river systems in the province but also in a small section of the Brazos River system (Howells et al. 1996). Phylogenetic relationships of these and other species in these isolated river systems are poorly known (see Campbell and Lydeard 2012b), and the province likely contains additional endemic species. The western pimpleback, *Quadrula mortoni*, is reported from all rivers in the province (Vidrine 1993; Howells et al. 1996) and is genetically distinct from *Q. pustulosa* of the Mississippi River basin (Serb et al. 2003). Although *Q. mortoni* is likely endemic to the province, because of its morphological similarity to *Q. pustulosa*, it is unknown if it occurs elsewhere, particularly in the adjacent Red River system (Vidrine 1993). Other poorly known taxa may contain species endemic to the Sabine–Trinity province (e.g., *Lampsilis hydiana, L. satura, Obovaria jacksoniana, Quadrula apiculata, Strophitus, Uniomerus*).

Apart from endemic species, the fauna of the Sabine–Trinity province is homogeneous and composed of a depauperate subset of the Mississippi Embayment province fauna. Of 29 nonendemic species in the province, all occur in the Mississippi Embayment, and 22 occur in all rivers in the province, indicating a high level of past faunal exchange.

3.3.A.10. Pontchartrain–Pearl–Pascagoula province

The Pontchartrain–Pearl–Pascagoula province encompasses the Pearl and Pascagoula river systems and all streams flowing into Lakes Pontchartrain and Maurepas (Amite, Tangipahoa, Tchefuncte, and Tickfaw rivers). The province lies entirely within the Coastal Plain physiographic province (Ward et al. 2005). Streams are sandy and lowland in character, with wetland and lentic habitats adjacent to main channels.

The province contains at least two endemic species, the Mississippi pigtoe, *Pleurobema beadleanum*, and purple pimpleback, *Quadrula refulgens*. A third species, the inflated heelsplitter, *Potamilus inflatus*, is shared with the Mobile Basin province, but genetic evidence suggests that populations in each province represent distinct species (Roe and Lydeard 1998b). Three other species, *Elliptio arca, Fusconaia cerina*, and *Obovaria unicolor*, are shared exclusively with the Mobile basin. Apart from endemic species, the faunas of the Pontchartrain–Pearl–Pascagoula and Mobile Basin provinces are virtually identical. Of 37 nonendemic species in the Mobile Basin, the Pontchartrain–Pearl–Pascagoula province contains all but the butterfly, *Ellipsaria lineolata*, and monkeyface, *Quadrula metanevra*, and has no species that are absent in the Mobile Basin. Of 35 nonendemic species in the Pontchartrain–Pearl–Pascagoula province, all but seven occur in the Mississippi River basin. The fauna is homogeneous throughout the province. All species known from the province occur in the Pearl River, and the Lake Pontchartrain and Pascagoula systems lack only four and six species, respectively.

3.3.A.11. Mobile Basin province

The Mobile Basin province encompasses all rivers flowing into Mobile Bay in the Gulf of Mexico. The Mobile Basin province consists of two major river systems, the Alabama (including the Cahaba, Coosa, and Tallapoosa river systems) and the Tombigbee (including the Black Warrior River system). The faunas of these systems are similar, sharing 55 of 72 total species in the province. The province has great physical heterogeneity as many streams arise in the uplands of the Cumberland Plateau, Valley and Ridge, or Piedmont Plateau physiographic provinces and then become lowland streams as they flow onto the Coastal Plain (Ward et al. 2005). Many species transcend these different habitats, but others are strictly limited to either upland or lowland habitats (Section 4.1.D.3).

The Mobile Basin province is characterized by its large number of endemic species (more than 30), which rivals that of the Tennessee–Cumberland province. Approximately 14 endemic species are shared by the Alabama and Tombigbee river systems. At least seven additional species are restricted to the Alabama system (*Alasmidonta mccordi, Amblema elliotti, Epioblasma othcaloogensis, Hamiota altilis, Pleurobema georgianum, Ptychobranchus foremanianus, Villosa umbrans*), and six are restricted to the Tombigbee (*Hamiota perovalis, Pleurobema curtum, P. rubellum, P. marshalli, Ptychobranchus greenii, Quadrula stapes*). Two other species are shared with a single, adjacent province: the Alabama pearlshell, *Margaratifera marrianae* (with the Escambia–Choctawhatchee province), and *Potamilus inflatus* (with the Pontchartrain–Pearl–Pascagoula province).

The province likely contains additional cryptic, endemic mussel species, but the taxonomic status of many remains unclear. Mobile Basin *Pleurobema* have long perplexed taxonomists because of their highly variable shell morphology, and 46 species are described from the province. A recent reevaluation of this group winnowed the number of recognized species to 13 (Campbell et al. 2008; Williams et al. 2008), but several of the most problematic nominal species are extinct and represented only by shells in museum collections, leaving their taxonomic status dependent on subjective assessments of shell morphology. *Potamilus inflatus* in the Mobile Basin is genetically distinct from populations in the Pontchartrain–Pearl-Pascagoula province, but these species remain undescribed (Roe and Lydeard 1998b). Mobile Basin populations of several other species shared with adjacent river systems have recently been proposed as distinct species (Williams et al. 2008). The Mobile Basin province has spectacular fish diversity, with many endemic species occupying extremely limited ranges, and new species continue to be described (Boschung and Mayden 2004). Likewise, additional research will surely reveal additional, unrecognized mussel diversity in the province.

The majority of the Mobile Basin fauna – including endemic and nonendemic species – is clearly of Mississippian origin. Of 37 nonendemic species in the province, 30 are shared with the Mississippi River basin, including characteristic Mississippi Embayment species such as the bankclimber, *Plectomerus dombeyanus*, and bleufer, *Potamilus purpuratus*. Several Mobile Basin species are sister to widespread Mississippian species, including the gulf pigtoe, *Fusconaia cerina* (sister to *F. flava*; Campbell et al. 2005), Alabama hickorynut, *Obovaria unicolor* (sister to *O. subrotunda*; Campbell et al. 2005), and ridged mapleleaf, *Quadrula rumphiana* (sister to *Q. quadrula*; Serb et al. 2003). In addition, the closest relatives of many endemic species are upland species of the upper Tennessee River system (e.g., *Epioblasma*, *Lasmigona etowaensis*, *Ptychobranchus*, *Villosa umbrans*), which is explained by a former connection between these watersheds (Galloway et al. 2011). However, the diversity and heterogeneous composition of the Mobile Basin fauna, which also includes many lowland species, supports colonization from the Mississippi River basin via multiple routes (see Section 3.3.A). The Mobile Basin shows surprisingly weak affinity to the adjacent Escambia River and other rivers to the east. The Mobile Basin shares 20 species with the Escambia River, but only one species (*Margaritifera marrianae*) and one genus (*Hamiota*) do not also occur in the Mississippian region.

3.3.B. Eastern Gulf region

The Eastern Gulf region includes three provinces that encompass all river systems of the Gulf of Mexico from the Escambia River east and all river systems of the Florida peninsula, north to the St. Mary's River on the Atlantic Coast. The region contains 58 species, 69 percent of which are endemic to the region. The fauna is highly heterogeneous, and only four species are shared by all three provinces (Florida sandshell, *Lampsilis floridensis*; *Uniomerus* sp.; southern rainbow, *Villosa vibex*; downy rainbow, *V. villosa*); 19 species are shared by two or more provinces.

This region represents a transitional zone between the Mississippian and Atlantic regions. Seventeen species (30%) are shared with the Mississippian region, and of these, 14 are shared with the Mississippi River basin. The number of Mississippian species declines eastward, with 16 species in the Escambia–Choctawhatchee province, 11 in the Apalachicolan province, and 2 in the Peninsular Florida province. Simultaneously, the number of species shared with the Atlantic region increases from west to east, but these species are limited to *Pyganodon cataracta*, *Lasmigona subviridis*, *Anodonta couperiana*, and potentially *Elliptio complanata*. However, mussel assemblages in the Eastern Gulf region are similar to those in the Atlantic region in often being dominated by several species of *Elliptio*.

Dispersal between the Eastern Gulf and Mississippian regions appears to have occurred in part across the Coastal Plain at low sea level during glacial advances (Swift et al. 1986). This is supported by the presence of several lowland or large-stream Mississippian taxa (e.g., *Amblema*, *Anodonta suborbiculata*, *Megalonaias*, *Pyganodon grandis*) and the Mississippian affinity of several endemic large-stream taxa (e.g., *Fusconaia*, *Pleurobema*, *Quadrula*, *Reginaia*). Nevertheless, there is an abrupt and profound faunal shift between the Mobile River basin in the Mississippian region and the adjacent Escambia River and other rivers of the Eastern Gulf region (Figure 3.2). The Mobile Basin and Eastern Gulf regions share only a single genus (*Hamiota*) that is not also present elsewhere in the Mississippian region. In contrast, a large number of genera shared by the Mobile and Mississippi river basins are absent in the Eastern Gulf region, but they occur in western Gulf Coast river systems, further supporting the inclusiveness of the Mississippian region and its distinctiveness from the Eastern Gulf region.

3.3.B.1. Escambia–Choctawhatchee province

The Escambia–Choctawhatchee province includes the Escambia, Yellow, and Choctawhatchee river systems. The nearby Perdido River and the Blackwater River (Yellow River system) are not known to support mussels (Williams et al. 2008). All of these watersheds lie entirely on the Coastal Plain physiographic province and are composed of low-gradient, lowland streams with wetland and lentic habitats adjacent to main channels.

This province has 11 endemic species, 6 of which are widely distributed. Two species are restricted to the Escambia or Yellow river systems (narrow pigtoe, *Fusconaia escambia*, and round ebonyshell, *Reginaia rotulata*) and three to the Choctawhatchee River system (fluted elephant-ear, *Elliptio mcmichaeli*; tapered pigtoe, *Fusconaia burkei*; Haddleton lampmussel, *Obovaria haddletoni*). The Alabama pearlshell, *Margaritifera marrianae*, occurs only in the Escambia River system and two adjacent, small streams in the Mobile Basin. The province likely harbors additional, cryptic endemic species. Populations of *Toxolasma parva* and *Medionidus penicillatus* may represent distinct, endemic species (Williams et al. 2008), and Eastern Gulf *Elliptio crassidens* have been regarded as a separate subspecies (*E. c. incrassatus*; Clench and Turner 1956). In addition to endemic species, rivers in the province show considerable faunal heterogeneity with only nine species occurring in all river systems, suggesting limited dispersal and gene flow.

3.3.B.2. Apalachicolan province

The Apalachicolan province includes the Apalachicola, Ochlockonee, and Suwannee river systems and Econfina Creek, a small stream flowing directly to the Gulf of Mexico. Several other small, direct Gulf tributaries (St. Marks, Aucilla, and Steinhatchee rivers) have limited faunas composed of widespread Eastern Gulf region species (e.g., *Elliptio pullata, Villosa villosa*). The Apalachicola River system arises in the uplands of the Blue Ridge and Piedmont Plateau physiographic provinces but flows onto the Coastal Plain, where streams assume a lowland character (Ward et al. 2005). All other river systems lie entirely within the Coastal Plain physiographic province.

The province has at least 15 endemic species. Two species, the oval pigtoe, *Pleurobema pyriforme*, and sculptured pigtoe, *Quadrula infucata*, occur in all major river systems, and the purple bankclimber, *Elliptiodeus sloatianus*, and shiny-rayed pocketbook, *Hamiota subangulata*, occur in both the Apalachicola and Ochlockonee rivers. The remaining endemic species are restricted to single river systems. Eight species are endemic to the Apalachicola River system (*Alasmidonta triangulata, Amblema neislerii, Anodonta heardi, Elliptio chipolaensis, E. fraterna, E. fumata, E. nigella, Lampsilis binominata*), two to the Ochlockonee River (*Alasmidonta wrightiana, Medionidus simpsonianus*), and one to the Suwannee River (*Medionidus walkeri*). Four additional species are shared with only one other faunal province: *Elliptio* *ahenea*, *Toxolasma paulus*, and *Utterbackia peninsularis* (with Peninsular Florida province) and *Utterbackia peggyae* (with Escambia–Choctawhatchee province).

The province likely harbors additional, cryptic endemic species. Populations of *Quadrula infucata* in the Suwannee River system are genetically distinct from those elsewhere in the province (Campbell and Lydeard 2012b). The gulf moccasinshell, *Medionidus penicillatus*, may be endemic to the Apalachicola province if populations in the Escambia–Choctawhatchee province represent a separate species (Williams et al. 2008). Similar to the Atlantic region, the Apalachicolan province harbors a high diversity of shell forms within the genus *Elliptio*. Although the taxonomy of this group is understood poorly, molecular genetics techniques may reveal the presence of additional, endemic species of *Elliptio* in the province (e.g., Brim Box and Williams 2000; Williams et al. 2008).

In addition to *Pleurobema pyriforme* and *Quadrula infucata*, only seven species occur in all major river systems in the province. Species richness is highest in the Apalachicola River system (33 species) owing to its large size and greater variety of habitats. Although most species are distributed widely in the system, at least two are restricted to upland streams (*Lampsilis binominata, Lasmigona subviridis*), and others occur predominantly in lowland streams of the Coastal Plain (e.g., *Amblema neislerii, Elliptio crassidens, Lampsilis straminea*; Brim Box and Williams 2000). Richness of the Ochlockonee River system is lower, but the system shares a high percentage of species with the Apalachicola (18 of 20). The fauna of the Suwannee River is similar to the faunas of the Apalachicola and Ochlockonee rivers (sharing 10 of 13 total species) but also contains two species otherwise restricted to the adjacent Peninsular Florida province (*Elliptio ahenea* and *Utterbackia peninsularis*).

3.3.B.3. Peninsular Florida province

The Peninsular Florida province extends from the Waccasassa River on the Florida Gulf Coast, south and around the Florida Peninsula, then north to and including the St. Mary's River. Major river systems include the Hillsborough, Myakka, Peace, Kissimmee–Okeechobee, St. John's, and Withlacoochee systems. Several smaller rivers have only limited mussel faunas (e.g., Alafia, Caloosahatchee, St. Mary's, Waccasassa; Johnson 1972; Butler 1989). Because of the extremely low geographic relief in the Florida Peninsula, all streams are lowland in character and may be associated with extensive networks of wetlands and shallow lakes (Smock et al. 2005).

This province has low diversity (12 species) but contains a distinctive fauna. At least four species are endemic to the province, and most are widely distributed. Three other species are shared with only one other province (southern lance, *Elliptio ahenea*; iridescent lilliput, *Toxolasma paulus*; Peninsular floater, *Utterbackia peninsularis*; with the Apalachicolan province). The province may contain unrecognized, cryptic diversity. Populations of *Uniomerus* in the Peninsular Florida province may represent distinct species (Williams et al. 2008). As elsewhere in the Eastern Gulf and Atlantic regions, the taxonomic status of *Elliptio* in the province is in disarray. Currently recognized species are highly variable, both within and among populations, and many shell forms have been described (e.g., Watters 2008a; Williams et al. 2011). However, it is unknown whether this variation is due to the presence of undescribed species or simply extreme phenotypic plasticity among a few species. The fauna of the province is fairly homogeneous, with half of the species occurring in 80 percent or more of major river systems.

3.3.C. Atlantic region

The Atlantic region contains two provinces, encompassing all streams flowing into the Atlantic Ocean from the Satilla River system of Georgia north to Newfoundland. The region contains 52 species, 71 percent of which are endemic to the region (37 species). The region as a whole is characterized by the near-ubiquity of the eastern elliptio, *Elliptio complanata*, which is reported from all Atlantic Coast river systems and is the dominant species in many areas (Strayer and Jirka 1997; Nedeau et al. 2000; Savidge 2006). Otherwise, few other species (about seven) occur throughout the Atlantic region, but other species of *Elliptio* also usually dominate assemblages in the Southern Atlantic province.

The Atlantic region has long been considered to consist of two distinct faunas: a northern and a southern fauna. The Southern and Northern Atlantic provinces are distinguished primarily by the large number of endemic species, many of which have highly restricted ranges, in the Southern province contrasted with the low degree of endemism and relative homogeneity among river systems in the Northern province. The boundary between the Southern and Northern provinces is traditionally placed in the vicinity of Chesapeake Bay. For fishes, the boundary is placed between the Chowan–Roanoke river basins and the James River (Jenkins and Burkhead 1994). For mussels, Johnson (1970) placed the boundary between the James (Southern) and York (Northern) river systems. The existence of a biogeographic boundary in this region is further supported by a major split in DNA genotypes between populations of the green floater, *Lasmigona subviridis*, in the Rappahannock and James river basins (King et al. 1999). The clustering analysis presented by Haag (2010) supported the boundary proposed for fishes by Jenkins and Burkhead (1994), placing the James River within the Northern Atlantic province. However, because distributions of species of *Elliptio* play a large role in characterizing faunal differences among rivers in this region, the current taxonomic uncertainty surrounding these species precludes precise placement of a boundary at this time. For this discussion, I follow Johnson (1970) and King et al. (1999) in defining the Southern Atlantic province as from and including the James River south. Further phylogenetic research in Atlantic Coast rivers, especially within the genus *Elliptio*, is needed to confirm the boundaries of the Southern and Northern Atlantic provinces.

Past dispersal between the Atlantic and Mississippian regions appears limited to headwater exchanges with the Mississippi River basin or Mobile basin (Johnson 1970; Hocutt et al. 1986; Swift et al. 1986). Consequently, species shared between the regions are limited to small-stream species (e.g., *Lasmigona subviridis*, *Strophitus undulatus*), and endemic Atlantic species are members of genera characteristic of small streams in the Mississippian region (e.g., *Alasmidonta, Elliptio, Lampsilis, Villosa*). This suggests that, apart from headwater exchange, the Atlantic region has had little connection with the Mississippian and Eastern Gulf regions and has followed a largely independent evolutionary trajectory. However, the fauna is clearly of North American origin as the only Atlantic species of probable Eurasian affinity is the Holarctic species *Margaritifera margaritifera*.

3.3.C.1. Southern Atlantic province

The Southern Atlantic province extends from the Satilla River north to (provisionally) the James River. Most larger river systems arise on uplands of the Blue Ridge, Valley and Ridge, or Piedmont Plateau physiographic provinces then flow onto the Coastal Plain (e.g., Altamaha, James, Cape Fear, Pee Dee, Roanoke, Santee, Savannah), but several lie predominantly or entirely within the Coastal Plain (e.g., Chowan, Neuse, Ogeechee, Satilla, Tar, Waccamaw; Smock et al. 2005).

The Southern Atlantic province has the highest percentage of endemic species of any province in eastern North America (59%). Of 27 endemic species, 14 are in the genus *Elliptio*. Despite high endemism and total diversity, alpha diversity is low compared to most other regions; even the most diverse stream reaches harbor less than 30 percent of total province richness. This is due to the restricted ranges of most endemic species, resulting in great faunal heterogeneity among rivers. Consequently, few species are characteristic of the entire province. In addition to species characteristic of the Atlantic region as a whole, species occurring in over half of Southern Atlantic province rivers include *Elliptio icterina*, *E. roanokensis*, *Fusconaia masoni*, *Toxolasma pullus*, *Uniomerus* sp., *Villosa constricta*, *V. delumbis*, *V. vibex*, and *Utterbackia imbecillis*.

Several major centers of endemism exist within the province, notably the Altamaha River system, which has about seven endemic species. However, endemism in this province as a whole is poorly understood and likely underestimated. Although Sepkoski and Rex (1974) postulated that glochidia could move on fishes among coastal rivers, based on genetic evidence, King et al. (1999) concluded that many populations distributed among isolated Atlantic coast rivers are evolutionarily distinct units that experience little gene flow. Differences among river systems are exemplified by the bewildering diversity of the genus *Elliptio* within the province. Mussel assemblages in most Southern Atlantic province rivers are dominated by members of this genus. Within the several recognized species groups of *Elliptio*, each river system often has a highly distinctive form or several forms (Bogan 2002;

Savidge 2006; Watters 2008a), and many forms defy placement in species groups based on shell morphology. Phylogenetic studies of this group may reveal a large number of cryptic, endemic species, but at this time, no consensus exists for estimates of species richness within Atlantic *Elliptio*. Populations of other species may be distinct from populations beyond the Atlantic region (e.g., *Strophitus undulatus, Uniomerus* sp., *Villosa vibex*), and these and other species also may show differences among river systems within the Southern Atlantic province (e.g., King et al. 1999).

The great heterogeneity among rivers in the Southern Atlantic province suggests that this province is composed of additional biogeographical groups. On the basis of a clustering analysis, Sepkoski and Rex (1974) recognized a Middle Atlantic province that extended from the Susquehanna to the Tar River. Similarly, the clustering results of Haag (2010) showed a deep split in this area between the Neuse and Cape Fear rivers. However, until phylogenetic relationships among the myriad forms of *Elliptio* are better known, it is impossible to provide a finer division of the Southern Atlantic province.

3.3.C.2. Northern Atlantic province

The Northern Atlantic province extends from the York River system of Chesapeake Bay (provisionally) to Newfoundland. Most river systems in the southern half of the province lie within the Adirondack or Appalachian mountains and the Piedmont Plateau physiographic province (e.g., Delaware, Potomac, Hudson, Rappahannock, Susquehanna; Jackson et al. 2005). In the northern half of the province, most rivers lie entirely within the New England–Maritime physiographic province (Jackson et al. 2005). Mussel populations are found primarily in upland streams and natural lakes and ponds, especially in the northern portion of the province, but a few species, such as the alewife floater, *Anodonta implicata*, tidewater mucket, *Leptodea ochracea*, and eastern pondmussel, *Ligumia nasuta*, are largely restricted to tidal sections of rivers (Strayer 1993; Section 4.1.B).

The Northern Atlantic province has a low-diversity, homogeneous fauna with few endemic species. Only one species is considered endemic to the province, the Newfoundland floater, *Pyganodon fragilis*; this species is restricted to Canadian rivers in the northern portion of the province (Cyr et al. 2007). The northern lance, *Elliptio fisheriana*, is potentially endemic to the southern portion of the province from the Rappahannock to the Susquehanna rivers, but the relationship of this species to other *Elliptio* in the Southern Atlantic province is unknown (NatureServe 2010). The eastern pearlshell, *Margaritifera margaritifera*, occurs in North America only in the Northern Atlantic province, where it is widespread from the Delaware River north, but also occurs in Europe and northern Asia. All other species in the province are widespread throughout the Atlantic region. However, *Anodonta implicata* and the eastern lampmussel, *Lampsilis radiata*, are widespread in the Northern Atlantic province but occur only sporadically in the Southern Atlantic province. Mississippian species (e.g., *Alasmidonta marginata, Anodontoides ferrusacianus, Lasmigona compressa, L. costata*) occur in portions of river systems from the Susquehanna to the Hudson, but at least some may have only recently colonized the province via the Erie Canal or by glochidia that arrived on stocked fishes (Strayer and Jirka 1997).

3.3.D. Pacific region

The Pacific region contains a single province, the Pacific province. The Pacific province encompasses all river systems of North America flowing into the Pacific Ocean, including the Gulf of California (Colorado River), Bering Sea (e.g., Yukon River), and the Arctic Ocean (e.g., McKenzie River) and the endorheic river systems of the Great Basin (e.g., Bear, Humboldt, and Truckee rivers). The only portion of the Mississippi River basin represented in the province are the headwaters of the upper Missouri River above Great Falls, where Pleistocene stream capture from the upper Columbia River system allowed colonization by the western pearlshell, *Margaritifera falcata* (Gangloff and Gustafson 2000). A wide variety of aquatic habitats in the province support mussel populations, including high-gradient mountain streams, lowland rivers and sloughs, and lakes (Nedeau et al. 2005).

The Pacific province has the lowest number of species (seven) but is the most distinctive of any mussel faunal province in North America. All species are endemic, none being shared with any other North American province. The faunas of major river systems from the Sacramento River to the Columbia River are nearly identical, each having five species. The Fraser River has a similar fauna but apparently lacks the California floater, *Anodonta californiensis*, and western ridgemussel, *Gonidea angulata*. The Columbia and Fraser river systems also include the western floater, *Anodonta kennerlyi*, which is absent in rivers to the south. Streams in the Great Basin vary in faunal composition but in total contain four species, and the Colorado River contains only *A. californiensis*. Rivers of the far north contain few or no mussel species. *Margaritifera falcata* and potentially the Oregon floater, *Anodonta oregonensis*, occur in southeastern Alaska (Nedeau et al. 2005). Other rivers in Alaska and northwest Canada contain only a single species, the Yukon floater, *Anodonta beringiana*, which is widespread but absent in southern river systems. The only other species in these northern river systems is *A. kennerlyi*, which is restricted to the Peace River in the southern McKenzie River system (Nedeau et al. 2005).

The Pacific province fauna appears to be Eurasian in origin and has followed an evolutionary trajectory largely independent from the remainder of North America. *Gonidea angulata* and *Margaritifera falcata* appear more closely related to Eurasian species than to any North American species (Smith 2001; Campbell et al. 2005). Similarly, *Anodonta beringiana* occurs also in Kamchatka in eastern Asia

(Nedeau et al. 2005) and is more closely related to the Asian species *Sinanodonta woodiana* than to North American *Anodonta* (Chong et al. 2008). The relationships of other Pacific *Anodonta* remain uncertain, but their affinity to the Eurasian *Pseudanodonta complanata* suggests an evolutionary connection to Eurasia for these species as well (Chong et al. 2008).

Chapter 4

Aquatic habitats and mussel assemblages

Freshwater mussels occur in a wide variety of habitats, from small, ephemeral streams and wetlands to large rivers and lakes, and assemblages vary markedly within and among these habitats. Mussel distributions are related to many of the same habitat factors that determine the distribution of fishes and other aquatic organisms. However, in many ways, mussel habitat use is best considered like that of plants rather than more mobile animals. Mobile animals actively select habitats, and habitat use can change dramatically over time (e.g., fish use of flow refuges during floods) or over the course of an animal's life (e.g., different habitats for juvenile vs. adult fish, spawning migrations). Adult mussels are mostly sedentary (Section 1.4.B), and their ability to select and move among habitats is minimal. The lack of habitat selection greatly simplifies a discussion of mussel habitat, but it limits mussel occurrence in many areas. Mussels are mostly stuck wherever the juveniles happen to fall off their host fish. Therefore mussels may accumulate in large numbers in favorable habitats and be consistently absent from unfavorable ones.

The physical factors that influence ecological assemblages can be classified as macrohabitat or microhabitat factors. Macrohabitat factors describe differences in habitats at large scales, say, between headwater streams and large rivers, between lakes and streams, or among climatic or geological zones. Microhabitat factors describe small-scale habitat differences within a specific locality, for example, differences among riffles, runs, and pools at a stream site. These factors often are interrelated within a spatial hierarchy. For example, macrohabitat factors like watershed geology may primarily determine local substrate composition and current velocity, and local characteristics of streamside vegetation can influence other microhabitat factors like channel stability (Gordon et al. 1992; Stalnaker et al. 1995). However, effects also may be manifested independently of scale. For example, water chemistry as a function of watershed geology may influence mussel distribution regardless of local habitat features (Strayer 1993).

In this chapter, I examine how macrohabitat and microhabitat factors influence mussel assemblages. I focus primarily on natural factors, and the effects of human alteration of aquatic habitats are discussed in Chapter 10. However, the physical and chemical processes set into motion by human alteration of streams and lakes often have similar effects on mussels as natural factors. Some mussel species seem to have rather specific habitat requirements, but many are able to adapt to a wide range of habitats. Concerning the eastern elliptio, *Elliptio complanata*, a species ubiquitous in Atlantic Coast rivers, Ortmann (1919, 109) wrote, "It apparently has no ecological preferences, being found practically in any permanent body of water; in canals and reservoirs . . . in large rivers . . . and very far into the headwaters." Many other species exhibit similarly catholic tastes in habitat, making it difficult to specify their requirements and leading to famously vague characterizations of habitat use such as "found on gravel bars and in mud" (Call 1900 as cited in Strayer 2008, 44).

Another difficulty is that mussel habitat use can differ substantially among regions or even among nearby sites. Throughout the Gulf Coastal Plain, the little spectaclecase, *Villosa lienosa*, is one of the most ubiquitous mussel species, occurring in habitats ranging from headwater streams to large rivers and reservoirs (Williams et al. 2008), but in the Ohio river system, it is largely restricted to gravel substrates in clear, upland streams and is considered a species of conservation concern (Cummings and Mayer 1992; Watters et al. 2009). It also is necessary to consider the often overriding effects of biogeographical factors or limits on dispersal. In addition to the availability of suitable habitat, distributions of many aquatic species are limited by their inability to disperse over land among watersheds. Even within a river system, dispersal may be limited by stretches of unsuitable habitat. For example, dispersal of species in small, upland streams may be restricted by lowland, large-stream habitat in the lower portion of a watershed. Despite these difficulties, a number of pervasive patterns in mussel habitat use exist, and examining these patterns is the first step in understanding how mussel assemblages are put together.

4.1. Macrohabitat factors

4.1.A. Climate

Climate is a fundamental determinant of the distribution of many organisms. Among numerous examples, this effect is illustrated in the southern Appalachian Mountains, where northern plant and animal species occur only at higher elevations, where the climate mimics that of more northerly latitudes. There are few such striking examples of the influence of climate on mussel distributions. The northern distributional limit for most mussel species in central Canada occurs between the 15°–18°C isotherms for mean July air temperature, suggesting that colder climates limit mussel distributions (Clarke 1973), but ice scour also may be a limiting factor (Matteson 1955; Burlakova et al. 1998; Kurth et al. 2007). Not surprisingly, arid regions in the western United

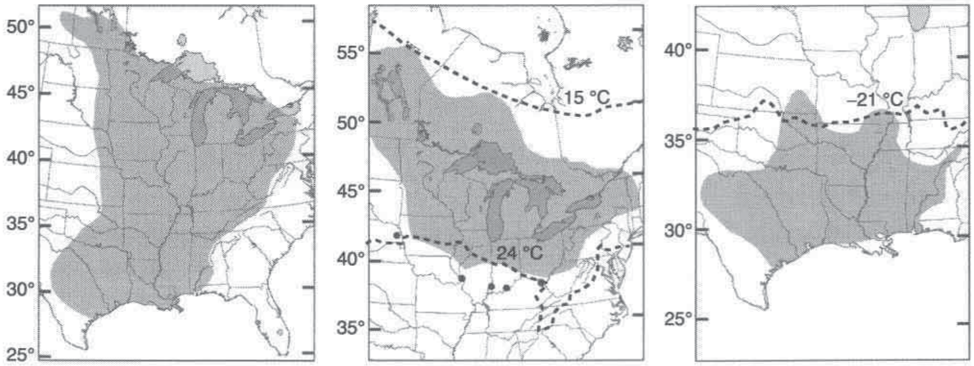

Figure 4.1. Three different types of distributional patterns of freshwater mussels. (left) The threeridge, *Amblema plicata*, a species that has dispersed widely across latitudinal and habitat gradients. (middle) The creek heelsplitter, *Lasmigona compressa*, a species whose southern distribution may be limited by warm temperatures. Dots are isolated records of the species beyond its core range. Isotherms (dotted lines) are mean daily July air temperature (converted from 5°F isotherms; data from the U.S. National Climatic Data Center, http://www.ncdc.noaa.gov/, and the Atlas of Canada, Natural Resources Canada, http://atlas.nrcan.gc.ca/). (right) The bleufer, *Potamilus purpuratus*, a species whose northern distribution may be limited by cool temperatures. The isotherm is mean annual minimum air temperature (converted from 5°F isotherms, data from U.S. Department of Agriculture Plant Hardiness Zone Map, http://www.usna.usda.gov/). All latitudes are north (distributional data from Clarke 1981b, 1985; Cummings and Mayer 1992; Oesch 1995; Howells et al. 1996; Parmalee and Bogan 1998; Cicerello and Schuster 2003; Watters et al. 2009).

States with few permanent streams harbor few or no mussel species. Apart from limitations imposed by extremely harsh climates, the broad-scale distributions of many mussel species in North America can be explained well by biogeographical factors (Chapter 3) or other macrohabitat factors unrelated to climate. Nevertheless, a few examples suggest that climate may play a role in determining the distribution of some species.

With the exception of the Interior Highlands and Tennessee–Cumberland provinces, most mussel species in the Mississippi River system have dispersed widely across climatic gradients (Figure 4.1; Chapter 3). However, the distributions of at least three species are truncated in a manner suggesting an influence of climate. The cylindrical papershell, *Anodontoides ferussacianus*, and the creek heelsplitter, *Lasmigona compressa*, are widespread and abundant in the upper Mississippi River system and northern tributaries of the Ohio River system but become abruptly absent (*L. compressa*), or localized and rare (*A. ferussacianus*), south of about 39°N latitude (Figure 4.1; Cummings and Mayer 1992; Watters et al. 2009). The southern limit of *L. compressa* in the western portion of its range also corresponds closely to the 24°C isotherm for mean daily July air temperature (Figure 4.1). Apparently relictual populations of

Anodontoides exist in cool, upland streams in southeastern Kentucky and adjacent Tennessee and may have diverged as a distinct species (Cicerello and Schuster 2003), perhaps when post-Pleistocene warming isolated them from northern populations. Similarly, the ellipse, *Venustaconcha ellipsiformis*, is restricted to the upper Mississippi River system north of about 40°N latitude, except for isolated populations in the Ozark Mountains (Cummings and Mayer 1992; Oesch 1995). The ranges of these species are not restricted by drainage divides or obvious changes in habitat availability. For example, mussel assemblages in northern tributaries of the Ohio River in Ohio are nearly identical to those in southern tributaries in Kentucky, except for the absence or rarity of *A. ferussacianus* and *L. compressa* in the latter streams (Chapter 3). These distributional patterns suggest that warm temperatures are a limiting factor for these species.

There are few examples of southern species that may be limited by cooler northern climates. The southern distribution of several species in the Mississippi River system may simply reflect the rarity of lowland or lentic habitats beyond the Mississippi Embayment physiographic province (Section 4.1.D.3). This is supported by the northern expansion of the flat floater, *Anodonta suborbiculata*, following widespread impoundment of streams (Watters et al. 2009). The northern limit of the bleufer, *Potamilus purpuratus*, occurs at about 37°N latitude, near the confluence of the Mississippi and Ohio rivers, corresponding to a mean annual minimum air temperature isotherm of about −21°C (Figure 4.1). This point also represents the northernmost extension of the Mississippi Embayment physiographic province, but lowland habitats and lowland species extend a considerable distance beyond this boundary (Chapter 3). Furthermore, *P. purpuratus* is not restricted to lowland habitats and occurs widely in upland streams (Harris and Gordon 1990; Williams et al. 2008). The absence of *P. purpuratus* in the Tennessee and Cumberland river systems south of 37°N may be because these streams enter the Ohio River at a point north of the species' thermal limit. Apart from this potential example, the restricted distributions of the numerous species endemic to the southeastern United States are explained well by dispersal barriers and vicariance biogeography (Chapter 3) and need not invoke climate as a limiting factor.

The mechanisms by which climate may limit mussel distributions are poorly known because physiological tolerance has been studied for few species. Many species may have fairly broad temperature tolerance. Mortality of glochidia and juveniles of eight species was low at water temperatures less than 33°C and increased sharply above this temperature, but lethal temperatures for glochidia varied widely among species (Pandolfo et al. 2010). The southern distribution of two nonnative bivalves, *Dreissena bugensis* and *D. polymorpha*, in North America appears limited by mortality at high temperatures, and the more northerly distribution of *D. bugensis* may be explained by its lower thermal tolerance (Thorp et al. 1998). *Anodontoides ferussacianus* had higher mortality at 29°C than the more widespread fatmucket, *Lampsilis siliquoidea*, and giant floater, *Pyganodon grandis* (Salbenblatt and Edgar 1964), potentially explaining its rarity south of 39°N latitude. Similarly, the mucket, *Actinonaias ligamentina*, had decreased resource assimilation and higher mortality at 35°C compared to co-occurring *Amblema plicata, Fusconaia flava*, and *Obliquaria reflexa* (Spooner and Vaughn 2008; Allen and Vaughn 2009). These species share similar habitats and biogeographical affinities, but *A. ligamentina* is absent south of about 33°N latitude (Miller et al. 1992a; Vidrine 1993), a point that does not coincide with dispersal barriers or obvious changes in habitat availability. The other three species occur south to about 29°N (Howells et al. 1996), where they appear limited by a biogeographical boundary (Chapter 3). These distributional patterns suggest that physiological sensitivity to high temperature may limit the southern distribution of *A. ligamentina* and perhaps other species.

The northern distributional limit of mussel species also may be determined by physiological tolerance, especially related to reproduction. Gametogenesis and glochidial production were curtailed in a mussel population subjected to depressed water temperature (under 20°C) caused by hypolimnetic dam discharge (Heinricher and Layzer 1999). In a northern population of the eastern elliptio, *Elliptio complanata*, gamete development and glochidial production were retarded during an exceptionally cool summer (Matteson 1955). The northern distribution of zebra mussels (*Dreissena polymorpha*) is thought to be limited by temperatures below the minimum threshold for reproduction (about 12°C; Borcherding 1991). Accordingly, the restriction of most mussel species in Canada to south of the 15°–18°C isotherms for July air temperature (Clarke 1973) suggests that climate effects on reproduction dictate the range of these species. However, the range of *Lampsilis siliquoidea* and *Pyganodon grandis* extends well north of this point, suggesting that species vary in cold tolerance.

The role of climate in determining mussel distribution and abundance remains poorly known, especially with regard to specific effects on feeding, reproduction, and long-term population persistence. Factors unrelated to climate also may influence the distributional patterns I have discussed. In Pennsylvania, the distribution of *Lasmigona compressa* follows closely the occurrence of Pleistocene glacial deposits (Ortmann 1919), which could explain its absence in unglaciated areas south of the Ohio River; however, in Ohio, the species occurs widely in glaciated and unglaciated areas (Watters et al. 2009). In addition to its direct effect on aquatic organisms, climate – especially rainfall – also affects physical and chemical characteristics of aquatic habitats. Across much of eastern North America, rainfall is adequate to provide permanent streamflow and probably explains few mussel distributional patterns. In contrast to the paucity of demonstrated or potential climate relationships and the generally large scale of these effects, other macrohabitat factors have strong effects on mussel distributions at a variety of scales.

4.1.B. Salinity and tidal effects

Most North American mussels occur strictly in freshwater. Only one species, the round pearlshell, *Glebula rotundata*, is tolerant of brackish water to an appreciable extent. This species occurs in both fresh and brackish water but is restricted primarily to within about 150 km of the coast (Vidrine 1993; Howells et al. 1996; Brim Box and Williams 2000; Williams et al. 2008). In brackish water, *G. rotundata* commonly occurs alongside euryhaline marine bivalves such as *Mytilopsis leucophaeata* and *Rangia cuneata* (Vidrine 1993; Williams et al. 2008) and may even co-occur with oysters (*Crassostrea virginica*; Shelton 2006). In 2005, intrusion of saltwater into the Pearl River, Louisiana, from Hurricane Katrina shifted the mussel assemblage from dominance of salinity-intolerant species to dominance of *G. rotundata* (Brown et al. 2010). Although salinity tolerance explains its occurrence in estuarine waters, its restriction to coastal areas is unexplained because apparently suitable lowland habitat occurs throughout the Gulf Coastal Plain. Unlike most Gulf Coast species, which have strong biogeographical affinities (Chapter 3), *G. rotundata* is widely distributed in coastal drainages from Texas to the Ochlockonee River, Florida, transcending several biogeographical boundaries (Brim Box and Williams 2000). Host use of *G. rotundata* is poorly known, but specialization on estuarine fish species that do not deeply penetrate fresh waters could explain its coastal distribution (Parker et al. 1984; Section 8.3.A).

The Atlantic Coast species *Anodonta implicata, Leptodea ochracea*, and *Ligumia nasuta* occur predominantly in tidally influenced streams (Ortmann 1913; Strayer 1993; Nedeau et al. 2000) but do not occur in brackish water (D. Strayer, personal communication). The coastal distribution of the alewife floater, *A. implicata*, is explained well by its apparent host specialization on the anadromous alewife (*Alosa pseudoharengus*; Johnson 1946; Davenport and Warmuth 1965). Host use of the tidewater mucket, *L. ochracea*, and the eastern pondmussel, *L. nasuta*, is unknown, but use of anadromous fishes also has been proposed to explain their coastal distributions (Johnson 1947; Nedeau et al. 2000). Alternatively, the coastal distributions of these two species may reflect a preference for fine sediments in low-gradient streams (Johnson 1947; Strayer and Jirka 1997; Nedeau et al. 2000; Section 4.1.D.3). Inland populations of *L. nasuta* occur in similar habitats in the Great Lakes province (Clarke 1981a; Watters et al. 2009), but lowland habitats are largely confined to coastal areas in the North Atlantic province (Jackson et al. 2005). Similarly, the winged floater, *Anodonta nuttalliana*, of the Pacific province, is restricted to low-gradient, depositional habitats in coastal areas (Nedeau et al. 2005), but whether this is due to the distribution of host fishes, suitable habitat, or other factors is unknown.

4.1.C. Physiography and water chemistry

Water chemistry of fresh waters is highly variable and determined primarily by the physiographical and geological composition of a watershed (Webb and Walling 1992; Allan 1995). The buffering capacity of water, as determined by its bicarbonate content, is of particular importance as it regulates the acidity–alkalinity balance (pH). The primary source of bicarbonate is dissolution of sedimentary rocks, especially limestone and other carbonates, and watersheds with these rocks have well-buffered, hard waters with neutral or slightly alkaline pH (~6.9–8.3). Watersheds with primarily metamorphic or igneous rocks typically have poorly buffered, soft waters with lower pH. Low pH also can be caused or exacerbated by high concentrations of humic acids from decomposition of plant material. Extremely alkaline waters ($pH > 9.0$) are rare.

Acidic conditions can negatively affect the ability of aquatic organisms to obtain and regulate ions (including calcium, Ca^{2+}) and can mobilize toxic metals, and productivity is typically lower than in more neutral waters. Consequently, diversity and abundance of aquatic organisms often decrease with increasing acidity (Allan 1995). Because they produce a calcareous shell, buffering capacity and pH are especially important to mollusks (Section 1.3.A). Dissolved Ca^{2+} necessary for shell growth and maintenance is present mostly as bicarbonate; therefore poorly buffered waters with low pH typically have low Ca^{2+} concentrations (Nduku and Harrison 1976). Freshwater bivalves are physiologically capable of taking up Ca^{2+} at extremely low concentrations (0.02 mg/L) but are apparently limited to waters where uptake rates exceed loss from shell dissolution and diffusion; minimum concentrations likely vary widely among species and habitats (Heming et al. 1988; McMahon and Bogan 2001).

Many snails and fingernail clams (Sphaeriidae) can tolerate low pH and soft waters (Økland 1983; Rooke and Mackie 1984), but most mussel species are intolerant of these conditions. In a region of otherwise spectacular mussel diversity, most species are rare or absent in the Tennessee and Coosa river systems within the Blue Ridge physiographic province, where streams flow through metamorphic rocks and have soft water (Parmalee and Bogan 1998). Similarly, in the Cumberland River system, mussel diversity is low in poorly buffered streams flowing through Pennsylvanian sandstone but increases dramatically in streams that have cut through this layer into underlying Mississippian limestone (Parmalee and Bogan 1998). Mussels are absent in the Blackwater, Escatawpa, and Perdido rivers in Alabama and Florida, and diversity is low in the Satilla and St. Mary's rivers in Georgia, even though neighboring streams have diverse and abundant mussel faunas (Sepkoski and Rex 1974; Williams et al. 2008). The absence or low diversity of mussels in these coastal blackwater streams is attributed to their low pH (4–6) caused by humic acids and an absence of carbonate-bearing rocks. The absence or rarity of mussels in much of central Canada was explained in part by the poorly buffered waters of the Canadian Shield (a region underlain by igneous rocks) (Clarke 1973), and mussels were absent in poorly buffered streams in New York ($CaCO_3 < 47$ ppm; Clarke and Berg 1959).

At least two species are specifically adapted to soft waters. The eastern pearlshell, *Margaritifera margaritifera*, is almost completely restricted to soft, low-productivity waters and "is very impatient of water that holds lime" (Ortmann 1919, 5). This species occurs only in streams with less than 10 mg Ca^{2+}/L or less than 45 ppm $CaCO_3$ (Harman 1970; Strayer 1993) and is usually the only species present, suggesting that these low concentrations exclude other mussel species (Ortmann 1919; Bauer et al. 1991). In turn, *M. margaritifera* apparently is excluded from well-buffered and more productive streams. European populations had increased mortality in human-impacted streams with increasing nitrate concentrations and had fewer young individuals in enriched streams with higher productivity, conductivity, and Ca^{2+} concentrations (Bauer 1988). It is unknown whether intolerance of *M. margaritifera* to productive habitats is due to nitrate toxicity itself or a related factor (e.g., lower oxygen in enriched streams; Bauer 1988). The Louisiana pearlshell, *Margaritifera hembeli*, is similarly restricted to nutrient-poor, slightly acidic waters (pH 6.0–6.9) with low conductivity that support few other mussel species (Johnson and Brown 1998, 2000), but other margaritiferids are not restricted to soft waters (Chesney et al. 1993; Williams et al. 2008).

A few other species either show some affinity for soft waters or exhibit wide tolerance to water hardness. The dwarf wedgemussel, *Alasmidonta heterodon*, and brook floater, *A. varicosa*, occurred most frequently in streams with low Ca^{2+} concentrations (less than 20 mg/L), but, unlike *M. margaritifera*, they also occurred in streams with higher concentrations and with other mussel species (Strayer 1993). In Atlantic coast streams, *Elliptio complanata* occurs in a wide range of water hardness (21 to more than 300 ppm alkalinity; Harman 1970) and is one of the only species that occurs widely on the Canadian Shield, where it can occur at Ca^{2+} concentrations of 2.5 mg/L (Clarke 1973; Rooke and Mackie 1984). Two other Atlantic coast species, the triangle floater, *Alasmidonta undulata*, and the creeper, *Strophitus undulatus*, also have wide tolerance to water hardness (Harman 1969; Strayer 1993). In the Cumberland and Tennessee river systems, the Cumberland elktoe, *Alasmidonta atropurpurea*, and Appalachian elktoe, *A. raveneliana*, occur almost exclusively in poorly buffered and species-poor headwater streams but are absent from streams with well-buffered waters and greater species diversity (Parmalee and Bogan 1998). The Etowah heelsplitter, *Lasmigona etowaensis*, and Tennessee heelsplitter, *L. holstonia*, are more widely distributed in the Coosa and Tennessee river systems, respectively, but can occur in very small, poorly buffered streams where no other species occur (Williams et al. 2008). Specialization for soft waters or a wide tolerance to water hardness may be a relatively widespread adaptation allowing some species – particularly within the Anodontini – to colonize poorly buffered headwater or coastal streams that are inhospitable to most other species.

The other chemical constituent of water of obvious importance to mussels is oxygen. In the absence of human-caused eutrophication, dissolved oxygen concentration (DO) is high in most surface waters but can be low seasonally, especially in wetlands and isolated bodies of standing water (Walling and Webb 1992; Allan 1995). Oxygen requirements of mussels are surprisingly poorly known but appear to vary among species. In the laboratory, species that typically inhabit flowing streams exclusively (*Pleurobema cordatum, Villosa iris, V. contricta*) were more sensitive to low DO than species occurring in a wider range of habitats (*Amblema plicata, Elliptio* spp., *Pyganodon grandis, Quadrula pustulosa*); the minimum DO at which species were able to regulate oxygen consumption at 24.5°C ranged among species from about 2 to 7 mg/L (Chen et al. 2001). The lentic species *Utterbackia imbecillis* can respire normally at DO of 0.7 mg/L (Hiestand 1938). During an extreme drought, two lentic species (*Toxolasma paulus* and *Uniomerus carolinianus*) experienced no increase in mortality at DO greater than 5 mg/L, but stream species experienced either moderately (*Elliptio* spp., *Villosa lienosa, V. vibex*) or greatly increased mortality (*E. crassidens, Hamiota subangulata, Medionidus penicillatus, Pleurobema pyriforme*; Johnson 2001). During the same drought, mussel abundance declined significantly in small upland streams that ceased to flow (and presumably had low DO) but did not change in large streams that maintained flow (Haag and Warren 2008). These observations suggest that DO is important in determining species composition in some habitats. Mussel assemblage composition in isolated lentic habitats may be limited to species that can tolerate seasonally low DO, and periodic drought and associated low DO may be a major factor limiting diversity and abundance in headwater streams (Section 4.1.D.1).

Apart from anthropogenic effects on water quality (Chapter 10), there is little information about how other aspects of water chemistry influence mussel distribution and abundance. Mussels appear highly sensitive to concentrations of potassium greater than 4–7 ppm (Imlay 1973). Naturally high potassium concentrations occur in North America primarily in the Great Plains and the southwestern United States. Although the absence or low diversity of mussels in those regions is attributed to harsh and unstable aquatic habitats and biogeographical factors (Chapter 3), potassium toxicity also may restrict mussel distributions (Imlay 1973); evidently, this interesting hypothesis has not been pursued further (see Keller et al. 2007). In a Great Plains stream in North Dakota, the absence of mussels was attributed to naturally high chloride concentrations (Cvancara and Harrison 1965). However, mussels are much less sensitive to chloride, and high potassium is usually coincident with high chloride, suggesting that potassium toxicity is the mechanism restricting mussel occurrence in this and other streams (Imlay 1973).

4.1.D. Physiography and physical habitat

Physiography also directly determines the physical nature of aquatic habitats. Landscape characteristics, such as erodibility and permeability of bedrock, soil thickness and infiltration capacity, topography, and vegetation cover, dictate stream channel morphology and the morphology and occurrence of lentic habitats. These factors, along with catchment size and rainfall, also determine the size of streams and their hydrological and physical stability (Church 1992; Gordon et al. 1992). At large scales, physical habitat influences mussel distribution and abundance in several ways.

4.1.D.1. Stability and disturbance at the macrohabitat scale

Habitat stability is a major factor influencing the composition of all ecological assemblages. Unstable aquatic habitats are inhabited primarily by highly mobile organisms such as fishes and support few benthic macroinvertebrates (Allan 1995). As relatively long-lived and sedentary organisms that live buried in the sediment, habitat stability is especially important to mussels. In streams, mussels can be dislodged or buried during floods or stranded and emersed during drought, both of which can result in high mortality (Tucker 1996; Hastie et al. 2001; Gagnon et al. 2004; Haag and Warren 2008). Consequently, diverse and abundant mussel assemblages occur primarily in stable stream habitats (e.g., Vannote and Minshall 1982; Layzer and Madison 1995; Strayer 1999a; Howard and Cuffey 2003).

At a large scale, habitat stability is influenced primarily by physiographical characteristics of a watershed. Streams flowing through bedrock in areas of high topographic relief are relatively stable because channels are laterally and vertically constrained and have coarse sediments that are not easily transported (Church 1992). In regions of low relief and without surface bedrock, stream channels have few lateral constraints and meander actively. Sand bed streams are particularly dynamic because sediment load is large relative to transport capacity and sand is carried as bed load, resulting in highly mobile, shifting substrates even at moderate flows (Gordon et al. 1992; Allan 1995). Lowland, alluvial rivers with silt and clay sediments are more stable than sand bed streams because the cohesive nature of these sediments makes them less easily erodible than sand, and fine sediments are carried primarily in suspension rather than as bed load (Church 1992; Allan 1995). Alluvial rivers also typically have extensive marginal wetlands and other associated lentic habitats that are not scoured by high flows. In addition to channel stability, watershed geology (especially soil permeability and thickness) influences flow variability by determining whether water enters a stream gradually via groundwater or rapidly via surface runoff. Similarly, areas of grassland or sparse vegetation may exhibit more rapid runoff and greater variability in flow compared to wooded landscapes (Gordon et al. 1992).

Habitat instability is a critical limiting factor for mussels throughout large portions of North America. The Missouri River, Red River (Oklahoma and Texas), and other streams of the Great Plains have dynamic channels with high sediment loads and shifting sand substrate, and these harsh conditions are compounded by climatic extremes and unpredictable drought and flooding (Galat et al. 2005; Matthews et al. 2005). The Mississippi River below the mouth of the Missouri River has a highly dynamic and unstable channel because of massive inputs of sediments from the Great Plains. Suspended sediment concentrations in the upper Mississippi River are less than 20 mg/L but average 340 mg/L below the mouth of the Missouri River (DeLong 2005), and submerged, mobile sand dunes up to 10 m high occur across the streambed in much of the lower river (Brown et al. 2005). These habitats supported few mussels even historically (Say 1830–1838; Isely 1914; Coker and Southall 1915; Bartsch 1916;

Coker et al. 1921; van der Schalie and van der Schalie 1950). Where they do occur, mussels are found in these rivers primarily in side channels and sloughs that are protected from scour in the main channel (Isely 1924; Section 4.2.B). Local occurrence of unstable, sandy substrates also limits mussel occurrence at smaller landscape scales (e.g., Hartfield and Ebert 1986).

Traditionally, streams with stable gravel substrates, clear water, and well-developed riffle-pool sequences are considered optimal mussel habitats, and indeed, streams of this type often conspicuously support abundant and diverse faunas. It is less widely recognized that meandering, lowland streams with fine sediments and turbid water also can support substantial mussel faunas. These alluvial rivers may contain gravel transported from upland areas, and these substrates often support high mussel abundance and diversity (e.g., Hartfield and Rummel 1985; Ahlstedt and Jenkinson 1991; George and Vidrine 1993). However, high abundance and diversity also occurs in rivers having fine sediments exclusively. In the Cache River, Arkansas, mussel beds composed of 26 species and abundance up to 44 mussels/m^2 occurred in clay substrate (Christian et al. 2005). In the Tensas River, Louisiana, which originates entirely on fine alluvial sediments, "the beds . . . were literally massed with live mussels touching and even overlying one another" (Coker 1915, 3). Many other lowland streams with few coarse sediments support high abundance and diversity (e.g., Manning 1989; Miller et al. 1992a; Kesler et al. 2001) comparable to stream types more commonly considered suitable for mussels, attesting to the stability of these alluvial streams.

Habitat stability also is affected by the size of a stream or lake and its position in a watershed. Small streams are considered more unstable or variable habitats than larger streams (Horwitz 1978; Schlosser 1982a, 1990). In small streams, especially those with steep catchments, flow responds quickly to rainfall, resulting in highly variable, flashy hydrographs, and subsequent brief floods are highly turbulent and violent because of the irregular nature of the streambed (Gordon et al. 1992). These events can radically reconfigure small streams and cause massive mussel mortality (Matthews 1998; Hastie et al. 2001). In larger streams, flood pulses are attenuated and of longer duration and typically involve less turbulence because of the more uniform streambed profile (Gordon et al. 1992). The record flood of 1993 in the upper Mississippi River resulted in no detectable decrease in mussel richness, abundance, or recruitment (Miller and Payne 1998). Small streams also are more vulnerable to drought. Flow in large streams is sustained even during severe drought by the large size of the catchment, but small streams often dry completely or are reduced to isolated pools. Consequently, severe drought can nearly eliminate mussels from small streams, but assemblages in larger streams may be relatively unaffected (Gagnon et al. 2004; Golladay et al. 2004; Haag and Warren 2008). Similarly, large lakes, or those fed by streams, provide more stable habitats than small, isolated wetlands or floodplain sloughs that may experience seasonal periods of anoxia or dry completely.

Other, more subtle factors related to habitat stability influence mussel assemblages at large scales. In an agricultural landscape in Iowa, mussel abundance and species richness were highest in low-gradient watersheds underlain by alluvial deposits, an effect attributed to increased groundwater flux and hydrologic stability. Watersheds with higher gradients and associated higher hydrologic variability supported few mussels (Arbuckle and Downing 2002; Poole and Downing 2004). Similarly, lower gradients and associated lower shear stress (the force exerted by flowing water that moves objects in the substrate) at high flow were the most important physical factors predicting the occurrence of mussel assemblages in the Coosa River system in Alabama, Georgia, and Tennessee (Gangloff and Feminella 2007). However, the power to predict mussel occurrence based solely on habitat stability was low in these studies because of widespread human impacts in the watersheds.

Few studies have examined how mussel assemblage composition is affected by habitat stability. In Great Lakes tributary streams in Michigan, mussel assemblages differed among three major glacial formations: outwash plains, moraines, and lake plains (Strayer 1983). Streams on outwash plains had low flow variability because of high soil infiltration, and those on lake plains were prone to flooding and drying owing to their more compact sediments; moraines were intermediate in hydrological stability but were characterized by higher gradients. Di Maio and Corkum (1995) concluded that Great Lakes tributary streams in Ontario classified a priori as either "event responsive" (i.e., hydrologically variable) or hydrologically stable each had distinct and characteristic assemblages that reflected variable species responses to stability. However, these patterns appear driven primarily by differences between only two streams (one in each flow type) with the highest mussel abundance. Moreover, of the six species identified as strongly associated with one or the other flow type, four occurred only in one stream in that type, precluding strong generalizations about associations between assemblage structure and flow variability.

Despite the lack of empirical data, several consistent patterns suggest an important role of habitat stability in determining assemblage composition at large scales. In chronically unstable streams, such as in the Great Plains, assemblages are composed of a characteristic subset of the regional fauna that can tolerate these conditions (Chapter 3). Many of the same species also adapt to streams that are destabilized by channelization (Section 10.5.A). Lentic habitats support distinctive assemblages that differ markedly from those in stable streams (Section 4.1.D.2). These assemblages share many species with unstable streams, suggesting that lentic habitats also represent unstable or highly variable habitats for mussels.

Our knowledge of ecological attributes that allow species to survive in unstable habitats primarily concerns responses to drought (but see Chapter 8). Despite characterizations of mussels in general as tolerant to emersion and drought (McMahon and Bogan 2001), this generalization appears to apply to few species. The pondhorn, *Uniomerus tetralasmus*, and other members of the genus are well known for their ability to withstand complete drying of their habitat by burrowing into and essentially aestivating in the substrate (Simpson 1899; van der Schalie 1940b). Early reports describe live *Uniomerus* being brought to the surface by plows worked through previously drained ponds and wetlands (Frierson 1903b; Isely 1914). *Uniomerus tetralasmus* can survive emersion in the laboratory for up to *2 years* at 100 percent relative humidity (RH) and 15°C, more than 200 days at 50 percent RH and 25°C, and more than 50 days even at 35°C (Holland 1991). *Uniomerus* often is found in small streams or ephemeral ponds with no other mussel species, suggesting that this extreme tolerance to emersion is unique among North American mussels (but see Dance 1958 for an African example).

Other wetland or lentic species may have modest drought survival ability. The giant floater, *Pyganodon grandis*, and the lilliput, *Toxolasma parva*, survived emersion in the laboratory for about 150 and 30 days at 100 percent RH, respectively, and about 25 days at 50 percent RH (Holland 1991). The pondmussel, *Ligumia subrostrata*, and Texas lilliput, *T. texasensis*, were reported "aestivating" in exposed, dried sediments similar to *U. tetralasmus* (van der Schalie 1940b). In drained hatchery ponds, *P. grandis* and *L. subrostrata* survived for more than 3 months buried about 5 cm in damp mud (J. Stoeckel and W. R. Haag, unpublished data). In drought-impacted streams in Georgia, *Toxolasma paulus* and *Uniomerus carolinianus* experienced no increase in mortality when DO fell below 5 mg/L (Johnson 2001). However, these species do not appear to depend on aestivation for drought survival to the extent of *Uniomerus*. In lowland streams in Alabama, *Pyganodon grandis* responded to receding water level by moving to deeper water, but *Uniomerus* simply burrowed into the substrate (J. Stoeckel personal communication).

Most stream species appear poorly adapted to cope with drought. In the same Georgia study, species typically restricted to streams experienced moderately or greatly increased mortality at low DO (Section 4.1.C). Similarly, mussels in small upland streams survived drought only in sections of the streambed that retained standing water; sections that dried completely had numerous dead mussels in situ but no live mussels (Haag and Warren 2008). After 2 weeks of exposure in an impounded river dewatered for dam maintenance, no mussels survived in the sediment, even though it remained moist and the water table was only 40 cm deep. Furthermore, dead mussels were not found more than 5 cm deep in the sediment, indicating that they did not exhibit deep burrowing as a drought survival strategy (W. R. Haag, unpublished data[1]). These observations suggest that drought and flow variability are important limiting factors for mussels, especially in small streams.

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[1] Twelve 0.25 m^2 quadrats excavated in 5 cm layers to a depth of 40 cm (the depth of the water table) in sand substrate. Mean density of dead shells = 14/m^2. Species represented were *Quadrula pustulosa, Obliquaria reflexa, Amblema plicata, Truncilla donaciformis*, and *Plectomerus dombeyanus* (Lower Lake, Little Tallahatchie River, Panola Co., Mississippi, September 28, 2006).

Table 4.1. *Phylogenetic patterns of mussel occurrence in streams and lakes in North America*

Family tribe	Streams only	Streams + riverine lake systems	Isolated lentic systems only	All three habitat types
Margaritiferidae	5 (0.10)	0	0	0
Unionidae				
Amblemini	1 (0.25)	3 (0.75)	0	0
Anodontini	19 (0.44)	7 (0.16)	0	17 (0.40)
Lampsilini	74 (0.66)	23 (0.20)	0	16 (0.14)
Pleurobemini	55 (0.75)	11 (0.15)	0	7 (0.10)
Quadrulini	9 (0.38)	11 (0.46)	0	4 (0.17)
Totals	163 (0.64)	55 (0.20)	0	44 (0.16)

Note: Table entries are approximate number of species followed by (in parentheses) the proportion of species in each tribe that occur in each habitat category. Subspecies are not included. Habitat use for species was obtained from Cummings and Mayer (1992), Brim Box and Williams (2000), Nedeau et al. (2000, 2005), Strayer and Jirka (1997), Williams et al. (2008), and NatureServe (2010).

4.1.D.2. Stream versus lake mussel assemblages

The most obvious physical dichotomy in freshwater habitats is between streams (lotic habitats) and lakes (lentic habitats), and mussel assemblages often differ radically between these two major habitat types. Mussels are usually thought of as riverine animals, and indeed, diversity is usually much greater in streams. In all North American biogeographical provinces, highest mussel diversity occurs in streams (Table 3.3), and with few exceptions, lentic habitats support only a fraction of regional diversity. Of the 42 mussel species in the Sipsey River system, Alabama, only about 5 are found in floodplain lakes or other lentic habitats (Haag and Warren 2010; W. R. Haag, observations). Notable exceptions include Lake Waccamaw in North Carolina, Lake St. Clair and western Lake Erie, and Lake Pepin on the upper Mississippi River. These natural lakes support assemblages similar to those in the most diverse streams in their respective biogeographical provinces (Table 3.3; Coker et al. 1921; Hart et al. 2002). In addition, some impounded streams have both lotic and lentic characteristics and support faunas consisting of riverine and lentic elements.

About two-thirds of North American mussel species occur primarily in streams and rarely, or never, in lentic habitats (Table 4.1). In sharp contrast, no species occur exclusively in lakes. Of the one-third of the fauna that occurs in lakes, many species occur in lakes only rarely or in only specific types of lentic habitats (see subsequent discussion). Several species are characteristic components of lake assemblages (e.g., *Anodonta*, *Elliptio jayensis* (including *E. buckleyi*), *E. complanata*, *Lampsilis cariosa*, *Ligumia nasuta*, *Pyganodon*, *Toxolasma*, *Utterbackia*), but all also occur in streams, where they may or may not be restricted to pools or other microhabitats that resemble lentic conditions (Section 4.2.B). Two narrowly endemic species, the Waccamaw spike, *Elliptio waccamawensis*, and the Waccamaw fatmucket, *Lampsilis fullerkati*, are associated closely with lentic habitats in Lake Waccamaw, but they also occur in streams in the Waccamaw River system (Bogan 2002). Highly diverse and endemic assemblages of lake mollusks occur in other parts of the world, primarily in ancient lakes (e.g., Lake Baikal, African Great Lakes). North America lacks a unique lake mussel fauna, probably because most lakes are relatively recent in origin (e.g., Pleistocene). This suggests that ancestors of North American freshwater mussels were primarily riverine animals that secondarily colonized lentic habitats to varying extents, similar to some fishes (Kitchell et al. 1977).

Despite lower diversity and the absence of an obligate lake fauna, mussels are important components of lake ecosystems in much of North America, and the composition of lentic assemblages is usually distinct from those in streams. High-density mussel assemblages are most often associated with large rivers (e.g., more than 20 individuals/m^2; Section 4.1.D.4.), but densities from 20 to 100/m^2 occur in many North American lakes (Downing and Downing 1992; Cyr 2009), and densities of 200/m^2 were reported in a lake in Finland (Englund and Heino 1994a). The distinctiveness of lentic mussel assemblages has long been recognized (e.g., Baker 1898; Headlee and Simonton 1904), but these assemblages are highly variable and influenced strongly by physical characteristics of lentic habitats.

Lentic habitats can be classified into numerous types based on geomorphological characteristics (e.g., Hutchinson 1957). For this discussion, I classify lentic habitats into two categories: (1) riverine lakes and (2) isolated lentic habitats. Riverine lakes are closely associated with and influenced by rivers and have riverine characteristics. An example is Lake Pepin, an 80-km-long natural impoundment of the Mississippi River formed behind a sediment dam from the Chippewa River and other tributaries (Blumentritt et al. 2009). Other examples of natural lakes directly interpolated within river courses include Caddo Lake (Red River system) in Louisiana and Texas and many of the interconnected lake systems in formerly glaciated regions of the United States and Canada. These lakes include areas resembling lotic habitats, especially near lake outlets and the mouths of tributary streams (Wilson and Danglade 1912; Coker et al. 1921). Similarly, Lake St. Clair and western Lake Erie can be considered riverine lakes. These areas are shallower, have shorter water retention times, and are more productive than the other Great Lakes; they receive input from and are in close proximity to a concentration of sizable rivers; and they have numerous shallow, rocky reefs and shoals that are kept silt-free by winds and currents (Fuller et al. 1995; Ludsin et al. 2001). Portions of run-of-the-river reservoirs created primarily for navigation also retain substantial riverine characteristics (e.g., Ohio, Tennessee, upper Mississippi rivers). These impoundments are created by relatively low dams (usually less than 20 m) and have short retention times and substrates that are kept silt-free by currents (Voightlander and Poppe 1989).

Isolated lentic habitats are either isolated from or influenced to a lesser extent by rivers and consequently lack riverine habitats. Examples include most hydroelectric and storage reservoirs, most of the Great Lakes, many glacial lakes (e.g., kettle lakes), and smaller features such as farm ponds and borrow pits (formed by excavation of soil for road construction). Lentic habitats associated with river floodplains may be either isolated or riverine, depending on their degree of connectivity with the river. For example, Lake Chicot, an oxbow of the Mississippi River in Arkansas, can be considered a riverine lake because it has a unidirectional current originating from tributary inflow and exiting into the Mississippi River, and this current keeps much of the sandy substrate silt-free; other nearby oxbow lakes are more isolated from riverine influence and primarily lentic in nature, lacking currents and having substrates composed of fine sediments (Cooper 1984).

Because they have physical similarities and close connectivity with lotic habitats, riverine lakes have mussel assemblages that resemble and are a predictable subset of the riverine fauna from which they are derived. I examined patterns of assemblage composition among isolated lentic habitats, riverine lakes, and unimpounded streams in the lower Mississippi River and lower Ohio River basins in Arkansas, Kentucky, Mississippi, and Tennessee (Figure 4.2). Mussel assemblages in riverine lakes clustered closely with those in unimpounded streams despite the wide range of stream sizes represented in the data set (small streams to the Mississippi River). Unimpounded streams and riverine lakes were well separated from isolated lentic habitats on ordination axis 1, which described a gradient from sites having a phylogenetically diverse group of primarily riverine species (*Actinonaias, Amblema, Arcidens, Cyclonaias, Ellipsaria, Elliptio*, *Fusconaia*, *Lampsilis, Lasmigona complanata, Leptodea fragilis, Ligumia recta, Megalonaias, Obliquaria, Quadrula, Plectomerus, Pleurobema, Potamilus*, *Truncilla*, *Villosa lienosa*) to sites that lacked these species. No species occurred only in lakes, but seven, mostly in the Anodontini and Lampsilini (*Anodonta suborbiculata, Ligumia subrostrata, Pyganodon grandis, Toxolasma parva, T. texasensis, Uniomerus tetralasmus* (Quadrulini), and *Utterbackia imbecillis*), were shared widely by all three habitat types, as indicated by their central placement on the ordination plot.

High mussel diversity is found in riverine lakes throughout the Mississippian region. Lake Pepin historically supported at least 32 mussel species (Hart et al. 2002), representing the majority of the 39 species that occurred in lotic sections of the upper Mississippi River (Table 3.3). In contrast, isolated lentic habitats in the upper Midwest have much lower diversity and lack riverine species (Coker et al. 1921). Western Lake Erie supported more than 50 percent of total species richness of the St. Lawrence–Great Lakes province (Table 3.3), and portions of the Alabama, Cumberland, Mississippi, Ohio, and Tennessee rivers that are impounded for navigation continue to support diverse mussel assemblages (Section 10.5.A). In the Mississippian region, assemblages in riverine lakes are distinguished from those in streams

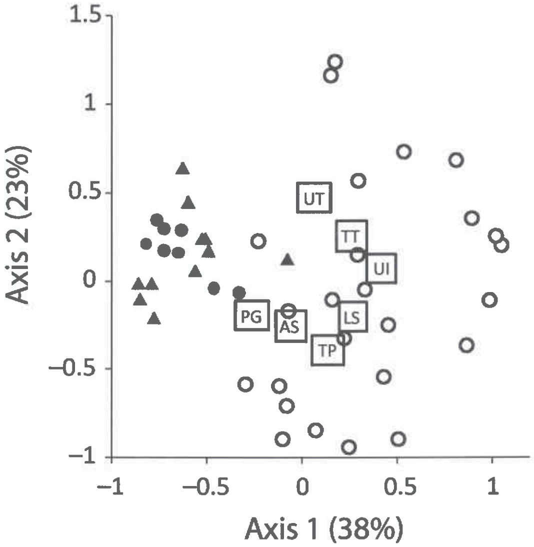

Figure 4.2. Ordination of mussel assemblages in three habitat types (isolated lentic habitats, open circles, $n = 34$ sites; riverine lakes, solid circles, $n = 8$ sites; unimpounded streams, triangles, $n = 11$ sites) based on species presence or absence (nonmetric multidimensional scaling, Sørensen distance, 53 sites × 36 species, PC-ORD; McCune and Mefford 1999). Numbers in parentheses on axis titles give the percentage of variation explained by that axis. Best solution was three-dimensional (third axis not shown, 19% of variance) with final stress = 16.75 and instability = 0.00045. Two-letter abbreviations indicate coordinates for the seven species with the highest positive correlations on axis 1 as well as species at both extremes of the gradient described by axis 2 (see text); species abbreviations are given in Table 4.2. A large number of primarily riverine species (not plotted; see text) formed a tight cluster that overlaid closely the cluster of riverine lakes and unimpounded streams; scores for riverine species on axis 1 ranged from about −0.5 to −0.7 and on axis 2 from 0.1 to 0.3.

primarily by the absence or rarity of species dependent on shallow, shoal habitat (e.g., *Cyprogenia, Dromus, Epioblasma, Ptychobranchus*; Section 4.2.C).

Mussel assemblages in isolated lentic habitats are a more limited subset of regional faunas and consist mostly of the Anodontini and Lampsilini. In the lower Mississippi and lower Ohio River basins, only about seven species occur commonly in these habitats (see Figure 4.2 and previous discussion), and an equal number occur primarily in riverine habitats but only sporadically in isolated lentic habitats (*Lampsilis siliquoidea, L. teres, Leptodea fragilis, Potamilus ohiensis, Quadrula pustulosa, Q. quadrula, Villosa lienosa*). Mussel assemblages of isolated lentic habitats contain similar species throughout the Mississippian region (e.g., Evermann and Clark 1918; Coker et al. 1921), except for several southern species that are absent or rare in northern areas (e.g., *Anodonta suborbiculata, Ligumia subrostrata, Toxolasma texasensis*). However, unlike riverine faunas, assemblage composition in isolated lentic habitats is

Table 4.2. *Mussel assemblage composition in isolated lentic habitats in the Mississippi River Alluvial Plain in Bolivar, Sharkey, Sunflower, and Washington Counties, Mississippi*

Lake	*Anodonta suborbiculata* (AS)	*Leptodea fragilis*	*Ligumia subrostrata* (LS)	*Pyganodon grandis* (PG)	*Quadrula quadrula*	*Toxolasma parva* (TP)	*Toxolasma texasensis* (TT)	*Uniomerus tetralasmus* (UT)	*Utterbackia imbecillis* (UI)
Blue							x		
Bolivar	x			x					
Ferguson	x	x		x	x	x			
Fish							x		
Lost	x			x			x		x
Thighman	x		x	x			x		x
Washington	x		x	x	x	x			
Unnamed								x	
Unnamed								x	
Unnamed				x					
Unnamed								x	
Unnamed				x					
Unnamed	x			x				x	
Unnamed							x	x	
Unnamed							x		x

Note: Species abbreviations reference Figure 4.2 (data from Cooper 1984; W. R. Haag, unpublished data).

highly variable and unpredictable. The wide scatter of isolated lentic habitats on both axes of Figure 4.2 depicts this heterogeneity. The only detectable pattern among these sites is a weak gradient on axis 2 of increasing occurrence of *Uniomerus tetralasmus* coincident with a decrease in *A. suborbiculata, L. subrostrata, P. grandis*, and *T. parva*, perhaps reflecting the greater tolerance of *U. tetralasmus* to ephemeral habitats (Section 4.1.D.1). Part of this heterogeneity could be caused by physical habitat differences among sites. However, even in physically similar habitats within a small area, assemblages appear to be drawn essentially at random from a common species pool (Table 4.2). The unpredictable composition of assemblages in isolated lentic habitats is in part likely reflective of the stochastic nature of colonization of these habitats by fishes infected with mussel glochidia (e.g., floods, fish stocking by humans).

Differences between lentic and riverine mussel assemblages show broadly similar patterns across North America, but they vary in some regions. In the Atlantic and Eastern Gulf regions, about two-thirds of mussel species occur primarily in streams, and few are widespread in isolated lentic habitats, reflecting proportional habitat affinities for the North American fauna as a whole (Table 4.1). Furthermore, species characteristic of isolated lentic habitats in these regions are composed largely of Anodontini and Lampsilini (e.g., *Anodonta, Lampsilis radiata, Ligumia nasuta, Pyganodon, Toxolasma, Utterbackia*), similar to the lentic assemblages in the Mississippian region. A distinctive feature of lentic mussel assemblages in the Atlantic region is the ubiquitous occurrence of *Elliptio complanata* (Pleurobemini) (Nedeau et al. 2000); in contrast, Pleurobemini are virtually absent in isolated lentic habitats in the Mississippian region. In Maine, where most rivers flow through series of natural lakes, highest diversity is found in streams, but 8 of 10 species in the state also occur in lakes to some extent (Nedeau et al. 2000). In the Pacific region, only two species occur predominantly in streams (western ridgemussel, *Gonidea angulata*, and western pearlshell, *Margaritifera falcata*), and the remaining five species (*Anodonta*) occur in lakes and streams (Nedeau et al. 2005). Differences between lentic and lotic mussel assemblages are least pronounced in the Peninsular Florida province, where streams are strongly coupled with extensive networks of wetlands and shallow lakes (Smock et al. 2005); in this province, all species occur in lakes or similar lentic habitats in sluggish streams (Johnson 1972; Butler 1989). These regional differences in habitat affinity reflect both landscape features (e.g., lack of upland stream habitat in the Florida Peninsula) and historical artifacts (e.g., colonization of the Pacific region primarily by lentic species).

The uneven phylogenetic representation in lentic assemblages suggests that mussel lineages differ in their ecological or historical preadaptation for lentic conditions. Assemblages in lentic habitats include representatives of all major phylogenetic groups, except the Margaritiferidae (Table 4.1). However, most Amblemini, Lampsilini, Pleurobemini, and Quadrulini in lentic habitats are restricted to riverine lakes, and few (0%–17%) occur in isolated lentic habitats. In contrast, about 40 percent of the Anodontini occur in isolated lentic habitats. Furthermore, although all Anodontini occur also in streams, many are restricted to lentic microhabitats (Section 4.2.B). These traits could indicate that the Anodontini originated in lentic habitats, unlike other, primarily riverine mussel groups. However, nearly half of anodontine species are restricted to lotic habitats (e.g., most *Alasmidonta*, most *Lasmigona*, *Pegias, Strophitus*). An equally plausible explanation for the predominance of anodontines in lentic habitats is that life history traits of many of these species allowed them to colonize largely vacant lentic niches to a greater extent than other groups.

4.1.D.3. Upland versus lowland mussel assemblages

Uplands and lowlands provide vastly different aquatic habitats and can support distinctive mussel assemblages. I refer to uplands as areas underlain by continental bedrock or glacial deposits and lowlands as areas of extensive alluvial deposits or recent marine sediments. In regions of North America with significant mussel faunas, extensive lowland areas occur primarily in the Atlantic and Gulf Coastal Plains. Upland streams generally have high gradients, coarse substrates, turbulent flow, clear water, cool temperatures, and consistently high oxygen levels. Lowland streams represent the opposite end of this continuum: low gradients, preponderance of fine substrates (except where coarse materials are transported from uplands), less turbulent flow, more turbid water (from suspended sediment or phytoplankton), warmer water, and seasonally low oxygen in some cases. In addition, lowland streams are associated with extensive lentic and wetland habitats, but these habitats are rare in most upland watersheds.

The transition between uplands and lowlands is demarcated by the *fall line*, so named because streams crossing this boundary have waterfalls or rapids as they descend to the Coastal Plain. As streams cross the fall line, physical characteristics can change from upland to lowland within a few kilometers. This change is especially abrupt in Alabama, where streams flow directly off the Appalachian Plateaus onto the Gulf Coastal Plain (e.g., Cahaba River). Farther east along the Gulf Coast (e.g., Apalachicola River) and on the Atlantic Coast, Appalachian uplands are separated from the Coastal Plain by the Piedmont, a region of low, rolling hills, which provides aquatic habitats intermediate between lowlands and uplands. However, resistant metamorphic rocks along the eastern and southern edge of the Piedmont create steep gradients and rapids at the fall line, which are ecological barriers to the upstream distribution of many lowland aquatic species (Jenkins and Burkhead 1994). West of the Mississippi River, the upland–lowland transition is also distinct and abrupt, occurring at the Coastal Plain boundary with the Ozark and Ouachita mountains in Arkansas, Missouri, and Oklahoma (Matthews et al. 2005) and the Balcones Escarpment in Texas (Dahm et al. 2005). The upland–lowland boundary is least distinct in the Mississippi and lower Ohio river systems in the northern portion of the Gulf Coastal Plain. The boundary between the Coastal Plain and adjacent uplands occurs about 100 km upstream from the mouth of the Ohio River, but lowland habitats extend northward in the Mississippi River system and upriver in the Ohio River system for more than 300 km and into the lower reaches of tributaries (Chapter 3).

Many mussel species are generalists with regard to uplands and lowlands, but the distribution of others corresponds to the upland–lowland boundary to a remarkable degree (Figure 4.3). In the Mobile Basin province, about half of the species (53%) are generalists, but the rest are strictly limited to either upland (24%) or lowland streams (23%) (see Williams et al. 2008). These affinities do not have a strong phylogenetic component. Nearly all Mobile Basin species restricted to either uplands or lowlands have congeners that are generalists or are restricted to the opposite stream type (e.g., *Epioblasma, Ligumia, Medionidus, Pleurobema, Potamilus, Quadrula, Villosa*; Figure 4.3). Similar, sharp boundaries in species distributions occur at the fall line in Arkansas, where, again, many species are generalists but about an equal number are

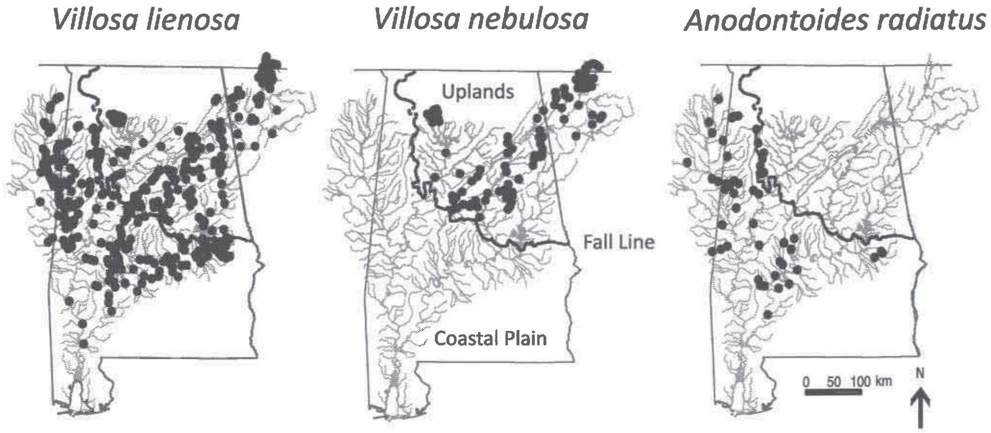

Figure 4.3. Distribution of three mussel species with regard to the upland–lowland boundary in Alabama, including a generalist, the little spectaclecase (*Villosa lienosa*), an upland specialist, the Alabama rainbow (*V. nebulosa*), and a lowland specialist, the rayed creekshell (*Anodontoides radiatus*). The fall line represents the abrupt boundary between uplands of the Appalachian and Piedmont plateaus and the lowlands of the Gulf Coastal Plain (redrawn from Williams et al. 2008).

restricted to either lowlands or uplands (Harris et al. 2009). In this region, the western fanshell, *Cyprogenia aberti*, and Ouachita kidneyshell, *Ptychobranchus occidentalis*, are restricted primarily to uplands, but their distributions extend onto the Coastal Plain for a considerable distance in large rivers that flow off of uplands and presumably transport coarse substrates or other features of upland habitats; these species are absent in streams that originate on the Coastal Plain.

The transition between upland and lowland faunas is more gradual in other areas. In the lower Ohio River system, several lowland species extend variable distances beyond the Coastal Plain (e.g., *Anodonta suborbiculata*, *Ligumia subrostrata, Potamilus capax, Toxolasma texasensis, Uniomerus tetralasmus*) in accordance with the diffuse nature of the lowland–upland boundary in this region. However, lowland characteristics may more strongly limit the downstream distribution of upland species (van der Schalie 1939b; Section 3.3.A.3). In the Apalachicola River system, only two species (6% of the fauna) are restricted to Piedmont streams above the fall line and 5 (15%) to lowlands (Brim Box and Williams 2000). The low degree of specialization in this river may be due to the transitional nature of Piedmont streams with regard to upland or lowland characteristics.

Upland or lowland affinities are poorly understood in the Atlantic region. The Piedmont and Coastal Plain narrow northward along the Atlantic Coast, and both terminate in New Jersey. Consequently, mussel and fish assemblages in the North Atlantic province are progressively dominated northward by upland species (Jenkins and Burkhead 1994, Strayer and Jirka 1997). In the South Atlantic province, several species appear restricted to upland streams (e.g., *Alasmidonta varicosa*, *Lasmigona* *decorata, Elliptio collina, Strophitus undulatus, Villosa vaughniana*), and others transcend the upland–lowland boundary (e.g., *Elliptio complanata, E. icterina, Fusconaia masoni, Pyganodon cataracta, Villosa delumbis*) (A. Bogan and T. Savidge, personal communication). Our ability to assess these affinities, particularly for potential lowland species, is limited for several reasons. First, comprehensive distributional studies of the South Atlantic province are not yet available. Second, apparent lowland affinities of some species (*Anodonta implicata, Leptodea ochracea*, and *Ligumia nasuta*) may reflect affinity for tidally influenced streams rather than lowland habitats (Section 4.1.B). Third, other apparent lowland specialists are endemic to river systems lying solely on the Coastal Plain (e.g., Waccamaw River), potentially reflecting biogeographical rather than habitat affinities. Fourth, the transitional nature of Piedmont streams may allow colonization by species with lowland affinities. Finally, our poor understanding of mussel systematics in this region limits conclusions about habitat affinities. The eastern lampmussel, *Lampsilis radiata*, and several species of *Elliptio* have distinct shell morphologies above and below the fall line (T. Savidge, personal communication), which could represent ecophenotypic variation or separate upland and lowland species. The fall line represents a profound distributional barrier for many fish species in the Atlantic region (Jenkins and Burkhead 1994), and further study will likely show similar strong patterns for mussels.

Many North American species are strictly specialized for either lowland or upland habitats. For some species, restriction to lowlands may be because of their dependence on lentic or wetland habitats. For example, *Anodonta suborbiculata* has expanded its range into upland areas in response to stream impoundment (Williams et al. 2008; Watters et al. 2009). However, many species restricted to lowlands are also restricted to riverine habitats. The ecological processes that produce these distributional patterns are unknown, but they clearly have a profound effect on mussel assemblages.

4.1.D.4. Stream size

An increase in species richness with increasing habitat area (the species–area relationship) is a fundamental pattern in ecology. Larger areas support more species presumably because they have a greater diversity of habitats and can support larger populations that have lower probabilities of local extinction (Rosenzweig 1995; Gotelli and Graves 1996). Streams and lakes are particularly amenable for examining species–area relationships because the boundaries of these ecosystems are clearly defined, unlike for many terrestrial ecosystems (Sepkoski and Rex 1974). Stream size can be measured in a variety of ways, including stream order and link magnitude, but watershed area is a straightforward and useful proxy for size (Hughes and Omernik 1983). Fish species richness generally increases with increasing watershed area, stream size, or lake size, and these variables often are the best predictors of fish diversity; however, these relationships can vary substantially at a number of scales (reviewed in Matthews 1998).

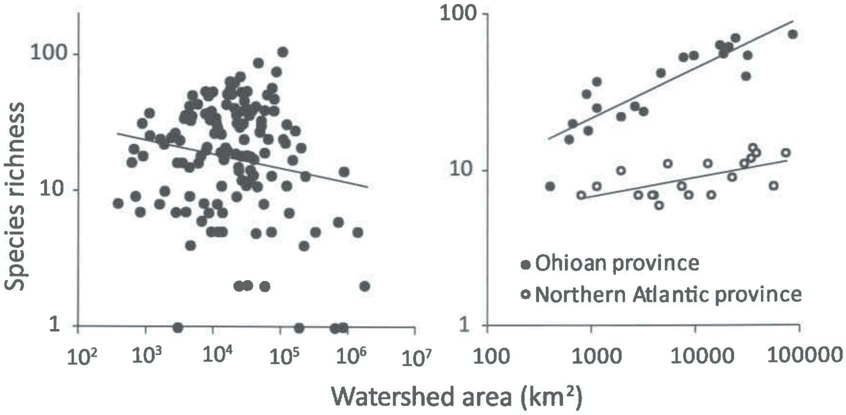

Figure 4.4. Mussel species–area relationships at different scales and in different regions of North America. (left) Relationship between species richness and watershed area for river systems throughout North America (137 river systems; log richness = $-0.102(\log \text{area}) + 1.680$, $R^2 = 0.029$, $p < 0.045$). (right) Species–area relationships for the Ohioan and Northern Atlantic provinces (see Table 4.3 for regression statistics; data from Haag 2010).

A positive relationship between stream size and mussel species richness has been recognized for many years and has been ascribed the status of an ecological "law" (Ortmann 1913; Coker et al. 1921; Baker 1926). In many streams, species richness indeed increases with stream size, and assemblages show predictable changes along this gradient (van der Schalie 1938a; Strayer 1983). However, assemblages are influenced by many other factors, and the generality of these patterns has not been examined carefully. For example, at the continental scale, there is a weak, *negative* relationship between watershed area and mussel richness (Figure 4.4). The negative form of this relationship is driven by several large western or northern river systems with low mussel diversity (e.g., McKenzie, Yukon, Churchill, Columbia, Colorado); regardless, it is clear that at this scale, watershed area is of no use in predicting mussel diversity. This is not surprising because biogeographical history, not stream size nor any other habitat variable, is the most fundamental factor influencing the mussel assemblage of a particular stream (Chapter 3). To examine stream size relationships, it is necessary to focus on specific regions or watersheds, thus removing or reducing confounding biogeographical effects.

A positive relationship between species richness and stream size is a strong and pervasive phenomenon in the Mississippian region. In the Ohioan province, watershed area explains 77 percent of the variation in species richness among major river systems (Table 4.3). This relationship predicts a doubling of richness for every 10 times increase in watershed area, resulting in a predicted 21 species in a 1,000 km^2 watershed and 75 species in a 50,000 km^2 watershed (Figure 4.4). Strong species–area relationships are evident at spatial scales ranging from small tributary systems to the

Table 4.3. *Mussel species–area relationships for various faunal provinces*

Faunal Group	z	R^2	p	N
Significant relationships				
Ohioan province	0.322	0.767	<0.001	20
Upper Mississippi province	0.261	0.385	0.017	14
Interior Highlands province	0.166	0.641	0.017	8
Northern Atlantic province	0.121	0.373	0.005	19
Nonsignificant relationships				
Southern Atlantic province	0.118	0.085	0.336	13
Pacific province	−0.158	0.233	0.226	8
Great Plains province	−0.117	0.027	0.558	16
Peninsular Florida province	0.389	0.260	0.132	10

Note: Relationships were not tested for provinces for which data were available for fewer than eight river systems (e.g., Apalachicola, Choctawhatchee–Escambia); z is the slope of the species–area relationship (both variables log-transformed), and N is the number of river systems in each province in the data set.

entire Ohio River system ($R^2 = 0.616$–0.892; Watters 1992). Similar relationships exist throughout much of the Mississippian region, including the Upper Mississippi and Interior Highlands provinces (Table 4.3), the Tennessee–Cumberland and Mobile Basin provinces (Ortmann 1918b, 1925; Haag and Warren 1998), and tributaries to Lake St. Clair and western Lake Erie (St. Lawrence–Great Lakes province; van der Schalie 1938a; Strayer 1983). Only the Great Plains province has no apparent relationship between species richness and watershed area (Table 4.3).

Increases in richness along stream size gradients represent orderly and predictable patterns of assemblage succession. The Cumberland River system in Kentucky and Tennessee provides a characteristic example of this succession in a diverse Mississippian fauna. Watershed area explained more than 80 percent of variation in species richness among sites in this example (Figure 4.5). Although a linear function provides a good fit to these data, the rate of increase in richness appears to vary at several points along this gradient. The smallest site (27 km^2) had no mussels, but the next downstream site had a distinctive but depauperate assemblage of four species (Table 4.4). All but one of these species (*Lampsilis fasciola*) were absent in larger streams, and this site shared no species with the most downstream site in the system (Table 4.4). Beyond the extreme headwaters, richness increased rapidly, and most species remained widespread in subsequently larger streams. The lower section of a fourth-order tributary of only 150 km^2 (Horse Lick Creek) had nearly half the richness of the much larger Cumberland River and shared about half of its species with the most downstream site. The rate of increase in richness appears to decline in mid-sized streams (Figure 4.5). To an extent, the apparent similarity of these sites based on richness alone (lower and upper Rockcastle River, 28 vs. 27 species) is belied by the loss of small-stream species (*Alasmidonta viridis, Pleurobema oviforme, Pegias fabula*)

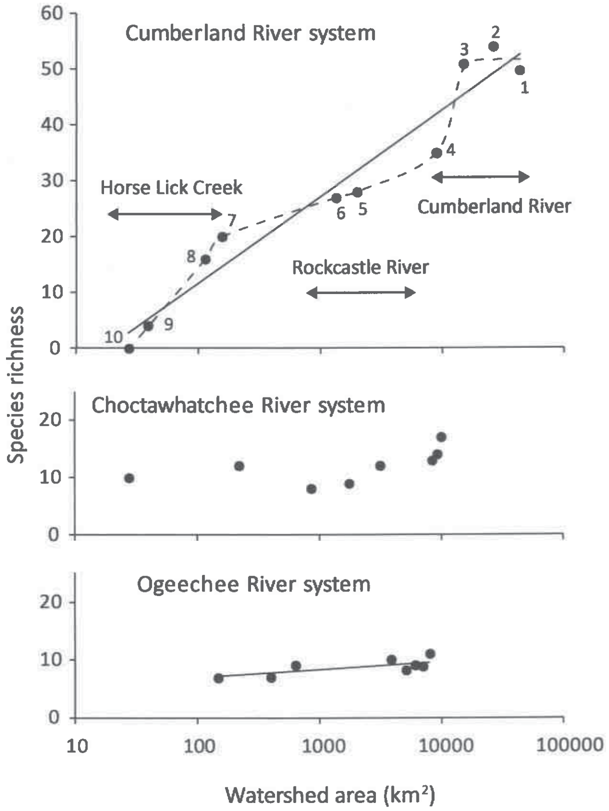

Figure 4.5. Changes in species richness along a stream size gradient in three river systems. Solid lines are regression lines. The dotted line for the Cumberland River was fit by eye, and numbers correspond to sites in Figure 4.6 and Table 4.4. Regression statistics (based on log–log transformed data) are as follows: Cumberland River system, slope (z) = 0.287, $R^2 = 0.814$, $p < 0.001$; Choctawhatchee River system, no significant relationship; Ogeechee River system, slope (z) = 0.050, $R^2 = 0.559$, $p < 0.05$ (data from Williamson 1905; Wilson and Clark 1914; Neel and Allen 1964; Harker et al. 1979; Parmalee et al. 1980; DiStefano 1984; Casey 1987; Cicerello 1993, 1994; Sickel and Chandler 1996, Cumberland River system; Blalock-Herod et al. 2005, Choctawhatchee River system; J. Williams, unpublished data, Ogeechee River system).

and the addition of larger-stream species (*Obliquaria reflexa, Obovaria subrotunda*) in a downstream direction. Nevertheless, richness and assemblage composition is similar overall among mid-sized-stream sites (i.e., sites 4–7; Table 4.4). Richness again increased sharply in large streams, nearly doubling from the lower reaches of a mid-sized tributary (Rockcastle River, site 5) to the main stem Cumberland River (site 3; Figure 4.6). This abrupt increase in richness is due to the appearance of a distinctive group of obligate large-river species (Table 4.4). Subsequently, even though a few species continue to be lost or gained, richness leveled off throughout the remainder of the main stem (about 50 species/site), and these sites shared a high percentage

Table 4.4. *Mussel assemblage succession along a stream-size gradient in the Cumberland River system*

	Site Watershed Area (km^2)									
	10	9	8	7	6	5	4	3	2	1
Species	27	39	114	157	1,343	1,977	8,902	14,861	26,517	43,395
Alasmidonta viridis	x	x	x	x						
Medionidus conradicus		x	x	x	x	x				
Villosa taeniata		x	x	x	x	x	x			
Lampsilis fasciola		x	x	x	x	x	x	x	x	
Pegias fabula			x	x	x					
Pleurobema oviforme			x	x	x					
Actinonaias pectorosa			x	x	x	x	x	x		
Toxolasma lividus			x	x	x	x		x		
Villosa trabalis			x	x	x	x	x	x		
Alasmidonta marginata			x	x	x	x	x	x	x	
Ptychobranchus subtentum				x	x		x	x		
Elliptio dilatata			x	x	x	x	x	x	x	x
Lasmigona costata			x	x	x	x	x	x	x	x
Lampsilis cardium			x	x	x	x	x	x	x	x
Ligumia recta			x	x	x	x	x	x	x	x
Ptychobranchus fasciolaris			x	x	x	x	x	x	x	x
Strophitus undulatus			x	x	x	x	x	x	x	x
Villosa iris				x	x	x			x	
Actinonaias ligamentina				x	x	x	x	x	x	x
Amblema plicata				x	x	x		x	x	x
Pleurobema sintoxia				x	x	x	x	x	x	x
Cyclonaias tuberculata					x	x	x	x	x	x
Leptodea fragilis					x	x	x	x	x	x
Potamilus alatus					x	x	x	x	x	x
Quadrula cylindrica					x		x	x	x	x
Quadrula pustulosa, Q. verrucosa					x	x	x	x	x	x
Epioblasma brevidens, E. capsaeformis						x	x	x	x	
Epioblasma triquetra						x		x	x	
Elliptio crassidens						x	x	x	x	x
Fusconaia subrotunda						x	x	x	x	x
Obliquaria reflexa						x	x	x	x	x
Obovaria subrotunda						x	x	x	x	x
Dromus dromas							x	x	x	x
Epioblasma arcaeformis							x		x	x
Epioblasma haysiana							x	x	x	x
Ellipsaria lineolata							x	x	x	x
Hemistena lata							x	x	x	
Pleurobema plenum, P. rubrum							x	x	x	x
Truncilla truncata							x	x	x	x
Cumberlandia monodonta								x	x	x
Cyprogenia stegaria								x	x	x
Epioblasma florentina								x	x	
Epioblasma lewisi, E. obliquata								x	x	x
Lampsilis abrupta								x	x	x
Leptodea leptodon								x		
Megalonaias nervosa								x	x	x
Obovaria olivaria, O. retusa								x	x	x
Plethobasus cooperianus, P. cyphyus								x	x	x
Pleurobema cordatum								x	x	x
Potamilus ohiensis								x		x
Quadrula metanevra								x	x	x
Truncilla donaciformis								x	x	x
Epioblasma torulosa									x	x
Reginaia ebena									x	x
Lampsilis teres									x	x
Arcidens confragosus										x
Plethobasus cicatricosus										x
Totals[a]	0	4	16	21	27	28	34	51	53	50

Note: Lines were fit by eye to illustrate the relative rates of species loss (upper line) and gain (lower line) with increasing stream size. See Figure 4.6 for site locations and Figure 4.5 for data sources.

[a] Some species with identical occurrences are combined on a single row and others with limited distributions are omitted, but column totals are total reported species richness at each site.

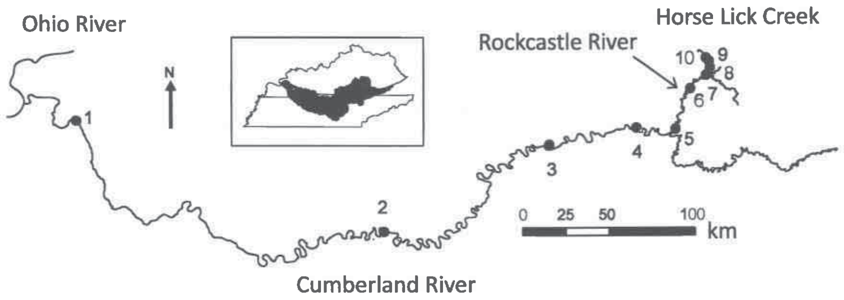

Figure 4.6. Map of the Cumberland River system, Kentucky and Tennessee, showing sites referenced in Figure 4.5 and Table 4.4. Other tributaries in the system are not shown.

of species despite a distance of more than 500 km and a tripling of watershed area between sites 1 and 3.

The successional patterns described in this example are repeated throughout the Mississippian region. Headwaters are characterized by depauperate but distinctive assemblages that share few species with larger streams (Warren 1991; Myers-Kinzie et al. 2001; Strayer 2008). Apart from these distinctive headwater faunas, subsequent changes in richness occur primarily as species additions, and few species are lost in larger streams, causing richness to increase with stream size (Ortmann 1913; Strayer 2008). A higher rate of increase in richness in small streams relative to mid-sized streams is seen in the Scioto River system (Ohio River drainage), where the slope of species–area relationships (z) decreased in increasingly larger watersheds (Watters 1992). In larger streams, the presence and composition of a distinctive guild of obligate large-river species is one of the most characteristic and predictable features of mussel assemblages throughout the Mississippian region.

The large-river guild represents nearly 30 percent of the Mississippian fauna and includes members of all major phylogenetic groups, except the Amblemini (Table 4.5). The representation of large-river species among phylogenetic groups is similar to the representation in these groups for the fauna as a whole, indicating that specialization for large-river habitats has little or no phylogenetic component but has occurred evenly across the fauna. Moreover, specialization has not occurred along generic lines to an appreciable extent as several genera have both large-river specialists and stream-size generalists (e.g., *Epioblasma, Fusconaia, Lampsilis, Pleurobema, Quadrula*). With the exception of a few large-river specialists endemic to the Tennessee–Cumberland or Mobile Basin provinces, most large-river species are widely distributed in the Mississippian region (e.g., *Arcidens confragosus, Ellipsaria lineolata, Lampsilis abrupta/higginsi, Leptodea leptodon, Megalonaias nervosa, Obovaria olivaria, Plethobasus cyphyus, Quadrula nodulata, Reginaia ebena*). Some large-river specialists may occur a short distance into the lowermost reaches of tributaries, but the distribution of others may stop abruptly at the mouths of smaller

Table 4.5. *Distribution of mussel species among stream-size guilds in North America*

Biogeographical region/ phylogenetic group	Total richness	Large-river specialists	Headwater specialists	Stream-size generalists
Mississippian	181	52 (0.29)	11 (0.06)	119 (0.66)
Margaritiferidae	3 (0.02)	1 (0.02)	2 (0.18)	0
Amblemini	3 (0.02)	0	0	3 (0.03)
Anodontini	21 (0.12)	4 (0.08)	7 (0.64)	11 (0.08)
Lampsilini	96 (0.53)	28 (0.54)	2 (0.18)	66 (0.56)
Pleurobemini	37 (0.20)	14 (0.27)	0	23 (0.19)
Quadrulini	21 (0.12)	5 (0.10)	0	16 (0.14)
Eastern Gulf	53	6 (0.11)	2 (0.04)	45 (0.85)
Atlantic	51	1 (0.02)	1 (0.02)	49 (0.96)
Pacific	7	0	0	7 (1.00)

Note: Table entries are numbers of species followed by proportions (in parentheses). For biogeographical regions, proportions are the representation of species in each stream-size guild across the region such that row totals = 1. In the Mississippian region, proportions for phylogenetic groups are the representation of each group within a particular habitat guild such that column totals = 1. Total richness includes only species for which stream-size affinity could be assessed (data sources given in Table 4.1).

streams (e.g., Neel and Allen 1964). The prominence of this large-river guild in the Mississippian region suggests that large rivers present unique and important habitats that have been exploited extensively by a broad cross section of the regional fauna.

About two-thirds of Mississippian species are stream-size generalists (Table 4.5). Although some generalists occur most often or in higher abundance in either mid-sized to large streams (e.g., *Actinonaias ligamentina, Cyclonaias tuberculata, Leptodea fragilis, Quadrula* spp.) or small streams (e.g., *Fusconaia ozarkensis, Medionidus* spp., *Villosa* spp.), many others show no evident stream-size preference, occurring in all but the smallest streams (see Table 4.4). Few species occur exclusively in headwater streams, but these represent a distinctive guild that, unlike the large-river guild, has a strong phylogenetic component. The headwater guild is composed disproportionately of Anodontini and Margaritiferidae, as well as a few Lampsilini, and lacks members of other groups (Table 4.5). Headwater specialists in the Margaritiferidae in the Mississippian region (*Margaritifera hembeli* and *M. marrianae*) have extremely restricted ranges that are likely relicts of formerly wide distributions (Smith 2001). Other headwater specialists are widely distributed (e.g., *Alasmidonta viridis, Anodontoides* spp., *Lasmigona compressa*), suggesting that life history traits or other characteristics of these lineages allow them to penetrate very small streams but also limit their occurrence in larger streams. The headwater guild is less strictly limited by stream size than the large-river guild. For example, there are isolated historical records of the slippershell mussel, *Alasmidonta viridis*, in several large rivers, but the vast majority of occurrences are in small streams (Clarke 1981b). Isolation in headwater streams has apparently led to divergence of several endemic taxa in these lineages in the southeastern United States (*Alasmidonta atropurpurea, A. raveneliana, Anodontoides "denigratus," Lasmigona etowaensis, L. holstonia*).

Despite the pervasive and consistent nature of stream-size relationships in most of the Mississippian region, these relationships are surprisingly absent or at most weak throughout the remainder of North America. In the Atlantic, Eastern Gulf, and Pacific regions, there was no relationship between watershed area and species richness for most provinces (Table 4.3). There was a significant, positive species–area relationship among river systems only in the Northern Atlantic province, but the relationship explains a low percentage of variation in richness, and the slope (z) is low. In contrast to the Ohioan province, this relationship predicts an increase of only 1.3 species for every 10 times increase in watershed area, resulting in a predicted 7 species in a 1,000 km^2 watershed and only 11 species in a 50,000 km^2 watershed (Figure 4.4). Sepkoski and Rex (1974) reported a significant species–area relationship for the Atlantic Coast with a slope similar to the Ohioan province ($z = 0.32$), but this analysis apparently conflated several biogeographical regions.

The lack of strong species–area relationships in these provinces also is apparent within river systems. There was a significant, positive species–area relationship among sites in the Delaware, Hudson, and Susquehanna river systems, but similar to the Northern Atlantic province as a whole, this relationship explained only 19 percent of the variation in richness among sites and predicted an increase of only one species for every 10 times increase in watershed area (Strayer 1993). In the Choctawhatchee River system (Escambia–Choctawhatchee province), there was no species–area relationship, and in the Ogeechee River system (Southern Atlantic province), there was a weak relationship that predicted only a small increase in richness with increasing watershed area (Figure 4.5). In both of these river systems, all sites shared more than 70 percent of their species with the most downstream site, indicating that assemblage composition was relatively homogeneous throughout, and there was little evidence of distinctive headwater or large-stream assemblages. In Patterson Creek, a 733 km^2 tributary of the Potomac river system (Northern Atlantic province), species richness and assemblage composition was similar near the mouth of the creek and in its upper headwaters (six and five species, respectively; Clayton et al. 2001). Headwater sites in the Chipola river system (Apalachicolan province) have nearly 70 percent of the species richness of sites on the lower main stem and share all species but one (rayed creekshell, *Anodontoides radiatus*) with larger streams (Brim Box and Williams 2000; Garner et al. 2009). In the Pacific province, there are no readily available data sets with which to evaluate stream-size patterns of assemblage succession, and the low diversity would make detecting patterns difficult. However, most or all species occur in habitats ranging from large, main stem rivers to small creeks, with the exception that *Margaritifera falcata* may penetrate farther into headwater streams than other species (Nedeau et al. 2005; Brim Box et al. 2006; Haley et al. 2007).

The fundamental differences in stream-size relationships between the Mississippian and other regions were noted by Ortmann (1913, 360): "the fauna of the Atlantic streams is rather uniform, in each system, [and] . . . the fauna does not deteriorate, or very little so, in an upstream direction. This differs strikingly from [the Ohio River system] . . . where a gradual decrease of the number of species toward the sources is the rule" (see also Strayer 1993). In addition to the lack of strong species–area relationships, a large-river faunal guild – so conspicuous in the Mississippian region – is nearly absent elsewhere in North America (Table 4.5). In the North Atlantic province, only *Elliptio fisheriana* and *Lampsilis cariosa* occur primarily in larger streams (Ortmann 1913; Johnson 1947; Strayer 1993). A distinctive large-river guild occurs only in the Apalachicolan province but contains few species (*Amblema neislerii, Elliptio fraterna, Elliptoideus sloatianus*, and *Megalonaias nervosa*). Other species are restricted to the lower reaches of coastal tributaries (*Anodonta implicata, Glebula rotundata, Leptodea ochracea*, and *Ligumia nasuta*), giving the impression of a large-river assemblage, but these distributions may be related to tidal influence or other habitat factors rather than stream size (Section 4.1.B). The lack of strong species–area relationships in other regions is striking, and these fundamental differences suggest several mechanisms governing assemblage structure at a macroscale.

On the basis of predictions of species diversity theory and island biogeography (e.g., Rosenzweig 1995), I propose the following explanation for richness patterns seen in the Mississippian region. Rapid accumulation of species in small tributaries occurs because these streams function as islands in the sense that (1) an increase in size results in a rapid increase in habitat diversity, which can support a wider variety of species; (2) species colonize these streams by immigration from larger streams, and colonization rate is a function of the diversity and size of available habitats; and (3) as stream size increases in headwaters, streams can support larger populations that have lower probabilities of extinction. In mid-sized streams, species diversity increases only modestly because (1) habitat diversity does not increase appreciably until large-river habitats are encountered, (2) immigration of large-river specialists is precluded by the absence of large-river habitat, and (3) population sizes for most species reach a minimum size for persistence above which increases do not appreciably reduce extinction. The abrupt increase in richness in large rivers occurs because these streams present a unique set of habitats, in addition to many of the same habitats found in mid-sized streams, therefore allowing the coexistence of large-river specialists along with stream-size generalists. Richness reaches an asymptote in large rivers for similar reasons as in mid-sized streams: habitat diversity does not increase appreciably, there are limited sources for immigration of additional species (because large streams contain most of the regional species pool), and population sizes are sufficiently large for long-term persistence.

Ortmann (1913) concluded that the uniformity of Atlantic region assemblages arises because these streams have lower habitat diversity than streams in the interior, an explanation that is consistent with species richness theory. This idea was based on the premise that habitat diversity is low because Atlantic Coast streams have uniformly low gradients, flowing mostly through the Piedmont and Coastal Plain physiographic provinces. Although several river systems in the Atlantic region have consistently low gradients (e.g., Altamaha, Cape Fear, Ogeechee), many others flow primarily on uplands (most rivers in the North Atlantic province) or across a variety of physiographies (e.g., James, Roanoke, Savannah). Even streams restricted to the Piedmont and Coastal Plain have topographic basin relief similar to or exceeding that of streams in the Ohioan and Upper Mississippi provinces (Benke and Cushing 2005). Physiography and topographic relief of stream systems in the Eastern Gulf and Pacific regions also is highly variable and shows no clear pattern compared to the Mississippian region. Furthermore, it is not clear that low gradient translates to low habitat diversity. Many low-gradient streams present an array of aquatic habitats ranging from deep, main-channel runs to extensive marginal wetlands. Finally, low-gradient streams in the Mississippian region that lie largely or entirely within the Coastal Plain show stream-size assemblage succession similar to streams in uplands (Haag and Warren 2010; W. R. Haag, observations). Consequently, it is difficult to conclude that differences in stream gradient or related differences in habitat diversity explain fundamental differences in mussel assemblages among regions.

Biogeographical and disturbance histories provide more compelling explanations for these divergent patterns. Much of the aquatic fauna of the Atlantic and Eastern Gulf regions appears derived from headwater exchange with the Mississippi River basin or Mobile basin (Johnson 1970; Hocutt et al. 1986; Swift et al. 1986). Consequently, large-river mussel species are absent from the Atlantic region and poorly represented in the Eastern Gulf region. Dispersal of large-river taxa was restricted to the Coastal Plain between the Mobile Basin and Gulf Coast rivers to the east at low sea level (Swift et al. 1986), which is likely responsible for the presence of taxa such as *Amblema* and *Megalonaias* in the Eastern Gulf. In addition to restricted dispersal of large-river taxa, fluctuations in sea level over the last 20 million years repeatedly inundated the lower sections of Atlantic and Gulf Coast rivers. A rise of as much as 80 m about 4 million years ago would have completely obliterated all large-river habitats in the Eastern Gulf region and much of the South Atlantic region. Similarly, Pleistocene glaciation obliterated most current watersheds in the North Atlantic province (Schmidt 1986). These events would have disrupted previously established richness gradients, including the extinction of large-river specialists that may have developed previously, and left behind assemblages composed exclusively of headwater specialists or stream-size generalists. Because of the relatively short time since these events, patterns of species richness may remain in disequilibrium (Sepkoski and Rex 1974). In the Atlantic region, this idea is supported by the sporadic distribution of many species within and among drainages (Ortmann 1913; Strayer 1993) and the presence of apparent incipient species flocks in the genus *Elliptio* in the South Atlantic province, including a potential large-river guild that may be restricted to deep, main-channel habitats (Savidge 2006). The lack of strong stream-size richness gradients in the Pacific region may likewise be explained by its dynamic, recent tectonic history and the derivation of its aquatic fauna primarily from Beringia and arid western portions of the Mississippi River basin (Minckley et al. 1986), two areas with depauperate mussel faunas.

The dynamic nature of these regions contrasts with the long, geologically stable history of much of the Mississippian region (Briggs 1986; Robison 1986), which has allowed extensive development of species richness gradients, including evolution of a distinctive large-river guild. Specialization for large-river habitats to an extent that varies among species may be a primary explanation for the strong species–area relationships that characterize the region. Unlike isolated river systems of the Atlantic and Gulf coasts, formerly glaciated portions of the Mississippian region were readily colonized from refugia to the south, including large-river specialists, headwater specialists, and stream-size generalists. These colonists evidently took their habitat preferences with them, judging by the similarity of large-river faunas in the upper Mississippi River with those in unglaciated regions. However, even within this region, richness patterns may be disrupted by chronic disturbance. The Great Plains province is notable within the Mississippian region for its lack of a species–area relationship. Throughout much of the province, mussel assemblages may be kept in disequilibrium by arid conditions and unpredictable stream habitats (Galat et al. 2005; Hoke 2005; Matthews et al. 2005). Within this heterogeneous area, richness is likely better predicted by east–west gradients of rainfall, disturbance intensity or frequency, and distance from source populations.

In addition to patterns of species richness, mussel abundance appears related to stream size in some areas. In the Mississippian region, dense aggregations, known as mussel beds, are found primarily in large or mid-sized streams (Figure 4.7, 4.8). Mussel beds are characterized by average densities of more than 10–20 individuals/m^2 but often exceeding 100/m^2 and can have maximum local densities greater than 700/m^2 (Christian and Harris 2005; Allen and Vaughn 2009; C. Davidson, personal communication). Mussel beds are composed predominantly of large-river specialists and some stream-size generalists (Section 8.1); Ortmann (1919) referred to these as "bed-forming" species. In contrast, mussel density in small streams rarely exceeds 10/m^2 and is typically much lower (Figure 4.7). The only exception to this pattern of which I am aware is the Louisiana pearlshell, *Margaritifera hembeli*, which is restricted to small streams in Louisiana, where it occurs in dense beds of more than 300 individuals/m^2 (Johnson and Brown 1998).

Apart from this coarse categorization of streams as large or small, relationships between stream size and mussel abundance have not been studied. For example, it unknown what the form of this relationship may be on a continuous gradient of stream size. The degree to which this relationship holds across North America also is unknown

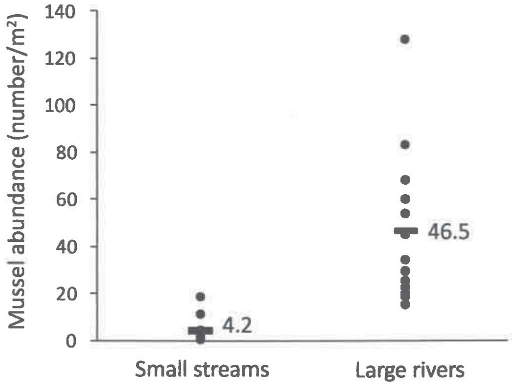

Figure 4.7. Mussel abundance in small versus large streams. Horizontal bar is the mean abundance in each stream type. Small streams are defined as fourth order or smaller (small streams, $n = 11$; large rivers, $n = 13$; see Chapter 8 for details about this data set).

because there are fewer quantitative data sets from other biogeographical regions. In the Atlantic region, the ubiquitous eastern elliptio, *Elliptio complanata*, often occurs at very high abundance, with local densities approaching 1,000/m^2 (Nedeau 2008; W. Lellis, personal communication; Figure 4.8). It is unclear if these high densities are restricted to larger streams, but density of *E. complanata* in smaller streams is often less than 10/m^2 (Balfour and Smock 1995; Strayer et al. 1996a). Like *Margaritifera hembeli* of the Mississippian region, *M. margaritifera* is largely restricted to small streams in the North Atlantic province, where it can occur at densities greater than 100/m^2 (Harman 1970). The relationship of stream size to mussel abundance has important implications for understanding the processes that structure mussel assemblages (Chapter 8), and an examination of this relationship in other areas is needed.

4.2. Microhabitat factors

For many organisms, local assemblages are structured spatially by small-scale variations in habitat, and differences in microhabitat use allow coexistence of multiple species. For example, within a stream reach, fish species finely partition physical habitat space (e.g., depth, current, substrate), which limits overlap in habitat use (Moyle and Vondracek 1985). Attempts to find similar patterns of habitat partitioning within mussel assemblages have been largely unsuccessful (e.g., Strayer and Ralley 1993). Consequently, ecologists seem to have thrown up their hands on this issue and resorted to statements such as "most mussel species thus far examined have shown no obvious differences in their adult habitat preference" (Cummings and Graf 2009, 348). With 300 species in the North American fauna, it's hard to believe that there are no differences in microhabitat use among species.

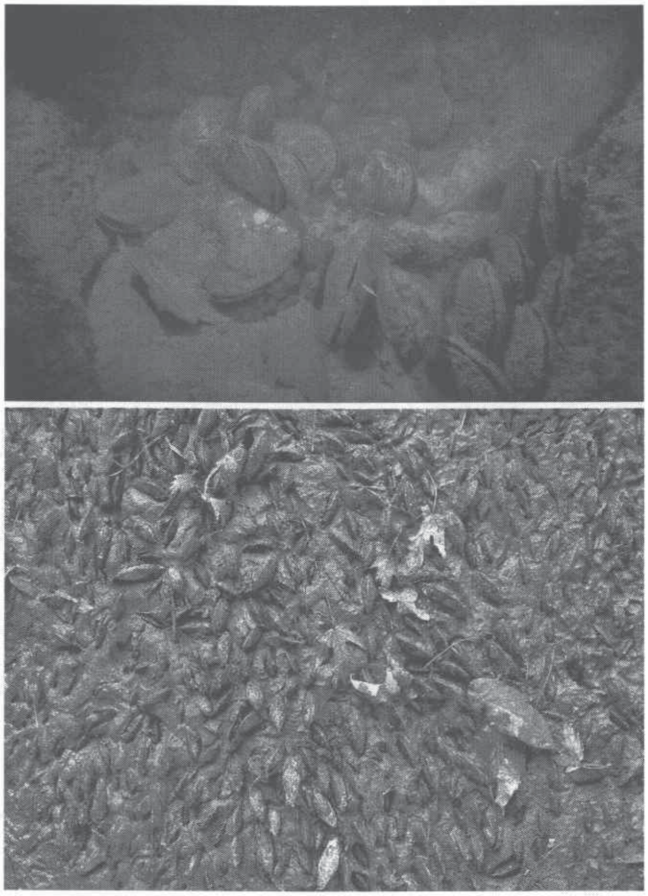

Figure 4.8. Dense aggregations of freshwater mussels. (top) The spectaclecase, *Cumberlandia monodonta*, under a large slab rock (William Roston, photo). (bottom) Bed of the eastern elliptio, *Elliptio complanata*, exposed by low water (Ethan Nedeau, photo).

There are several potential reasons for our failure to find strong patterns of microhabitat segregation in mussels. First, most studies of microhabitat use were conducted in small streams (but see Strayer et al. 1994). Small streams may provide a lower diversity of habitats and typically support lower mussel richness than large rivers (Section 8.2); therefore it is perhaps not surprising that few consistent patterns have emerged from these studies. Second, studies of mussel microhabitats often focus on areas that support high mussel densities because it is difficult to obtain statistically useful samples from habitats with low mussel density. However, focus on specific microhabitats has likely obscured important patterns of assemblage structure. Finally, our inability to detect strong habitat differences among species could be because either we are not measuring habitat in the right way or because strong differences truly do not exist. Both of these latter explanations are likely true to some extent.

Although traditional characterizations of mussel habitats are often vague, the literature also is replete with remarkably consistent observations of species habitat use, many of which ring true to field biologists despite the lack of quantitative supporting data. In this section, I attempt to step back and examine microhabitat use through a wider lens. After doing so, several patterns of microhabitat specialization become apparent.

4.2.A. Striking examples of microhabitat specialists

A few species consistently occur in specific microhabitats. A well-known specialization is occurrence under large, nonembedded slab rocks. Many small mussel species are found frequently and often at higher abundance under rocks but also commonly occur in other habitats (e.g., *Elliptio dilatata*, *Epioblasma* spp., *Villosa iris*, *V. trabalis*; Layzer and Madison 1995; Sietman et al. 1999; W. R. Haag, observation). However, a few species are nearly always found under rocks. The specialization of the salamander mussel, *Simpsonaias ambigua*, for this habitat has been known for more than 100 years: "The habits are somewhat peculiar; it is sometimes found in mud and on gravel bars, but in greatest numbers and perfection hidden in the mud under flat stones; more than two hundred have been taken from under a single flat rock of about one square foot area" (Call 1900, 527), and "all of the adult individuals were found under flat stones of the flag-stone type" (Howard 1915, 8). Shells of this species are found frequently, but live specimens usually are not encountered until spaces under large, flat rocks are examined (Clarke 1985; W. R. Haag, observation). The diminutive little-wing pearlymussel, *Pegias fabula*, also is found primarily under rocks (Ahlstedt and Saylor 1998). In the Mobile Basin and Eastern Gulf regions, the delicate spike, *Elliptio arctata*, is usually "crowded together and packed vertically under large rocks in swift water. . . . The occurrence of subfossil shells along with mature and juvenile specimens attests to their specificity of habitat" (Hurd 1974, 74; see also Williams et al. 2008). The spectaclecase, *Cumberlandia monodonta*, is a large species that is often found at high abundance under slab rocks (Call 1900; Stansbery 1966; Buchanan 1980; Baird 2000; Figure 4.8). At Muscle Shoals, on the Tennessee River, *C. monodonta* "was plentiful under rocks in the shallow water, as many as two hundred found under one slab" (Hinkley 1906, 54). *Cumberlandia*, *Margaritifera margaritifera*, and *M. falcata* also are found at high abundance wedged between boulders (Stansbery 1966; Buchanan 1980; Vannote and Minshall 1982; Hastie et al. 2001).

Beds of aquatic vegetation also provide specialized habitats for some species. Another small species, the rayed bean, *Villosa fabalis*, is found most commonly among the roots of aquatic plants, especially water willow, *Justicia americana*; "by pulling up the plants it sometimes was brought to light in goodly numbers" (Ortmann 1919, 264). Ortmann (1919) suggested that the apparent rarity of this species was an artifact of not searching in its specialized habitat. Similarly, I have found dense aggregations of *Villosa lienosa* and *V. nebulosa* in *Justicia* beds, but these species also are found in other habitats at the same sites. Species that are found primarily under flat rocks also sometimes occur within aquatic plant beds, including *C. monodonta*, *E. arctata*, and *S. ambigua* (Stansbery 1966; Williams et al. 2008; W. R. Haag, observation), or alongside submerged logs (*C. monodonta*; Call 1900).

The rabbitsfoot, *Quadrula cylindrica*, and Cumberland monkeyface, *Q. intermedia*, occur predominantly in slow current immediately adjacent to swift riffles where they lie exposed on the surface of the substrate (Ortmann 1919; Williams et al. 2008). The foot is reduced in these species, suggesting that they are poorly adapted for burrowing (P. Johnson, personal communication). In the pistolgrip, *Q. verrucosa*, nearly all females exhibit this habitat preference and behavior, but males are often found in a variety of other habitats where they may be deeply buried (W. R. Haag, observation; see also Ortmann 1919; Williams et al. 2008). Lying on the surface of the substrate is suggested to have an unspecified reproductive function (Williams et al. 2008), but this behavior can be observed throughout much of the year (W. R. Haag, observation).

4.2.B. Lentic microhabitats in streams

The most widespread pattern of microhabitat specialization in streams is the predominant occurrence of many species in slack water depositional areas in pools, sloughs, behind sand or gravel bars, or along stream margins. I refer to these areas as *lentic microhabitats* because they provide localized patches of lentic habitat in an otherwise lotic context (Figure 4.9). Lentic microhabitats are most prevalent and extensive in lowland streams and large rivers, but they occur to a lesser extent even in small, upland streams.

The preference of many species for lentic microhabitats has long been noted in North America and elsewhere. Say (1830–1838) described the habitat of the flat floater, *Anodonta suborbiculata*: “It is found in ponds near the Wabash River, but rarely, if ever, in the river itself, as it prefers still water and a muddy bottom.” Similarly, Coker et al. (1919) describe the habitat of the giant floater, *Pyganodon grandis*, in streams as in “the slack waters along river shores or in sloughs” (35) and report that the fatmucket, *Lampsilis siliquoidea*, is found “usually close along shore, perhaps well up on the banks and out of the main current” (29). In laboratory experiments, *Elliptio complanata* and *Pyganodon grandis* actively selected mud over sand substrates (Downing et al. 2000). In the Atlantic region, the northern lance, *Elliptio fisheriana*, occurred only in areas of slow current and small particle size near the bank, while *E. complanata* and the yellow lampmussel, *Lampsilis cariosa*, were more generally distributed (Villella et al. 2004). In Swedish streams, *Anodonta piscinalis* occurred most commonly in depositional areas on stream margins, while *Unio pictorum* dominated in mid-channel habitats (Brönmark and Malmqvist 1982), and Australian mussel assemblages showed marked differences among depositional

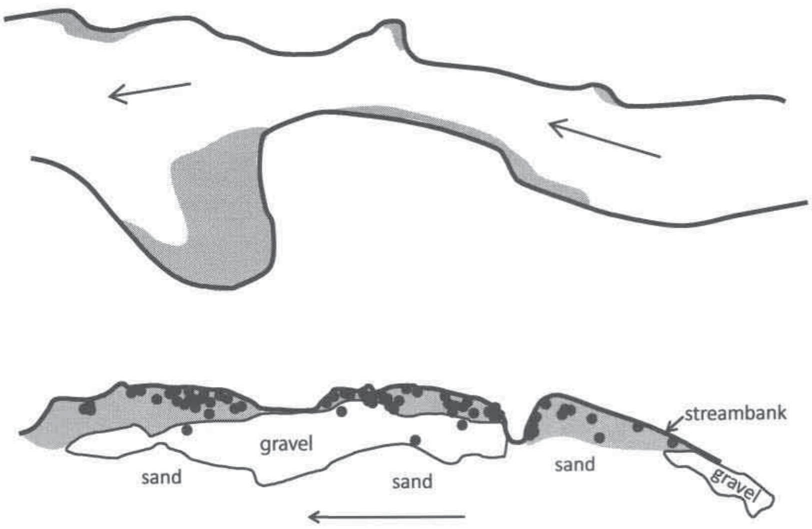

Figure 4.9. Lentic microhabitats in streams. (top) Occurrence of slack water, depositional areas (gray shading) along stream margins; arrows indicate direction of flow (after Carling 1992). (bottom) Distribution of the little spectaclecase, *Villosa lienosa* (dots), along the right shore of Chewacla Creek, Alabama. Shaded areas are lentic microhabitats with low flow and silt substrate; other indicated substrate types are in current; arrow shows direction of flow (J. Stoeckel, unpublished data).

and main-channel microhabitats (Brainwood et al. 2008). These observations show that the occurrence of a distinctive lentic microhabitat guild is widespread, but the nature of this association has not been discussed at length.

In North America, the lentic microhabitat guild is best developed in lowland streams and large rivers, commensurate with the greater extent of lentic microhabitats in these stream types. In these streams, assemblages in lentic microhabitats are strikingly different from those in adjacent lotic, main-channel habitats. Furthermore, the occurrence of these assemblages often corresponds remarkably well and on a fine scale to the distribution of lentic microhabitats (Figure 4.9). The guild includes species that exhibit one of three types of habitat affinity: (1) species characteristic of isolated lentic habitats, (2) species that are largely restricted to streams but occur mainly in lentic microhabitats (riverine lentic microhabitat specialists), and (3) riverine species that appear to be generalists with regard to lentic versus lotic microhabitats (riverine habitat generalists). Phylogenetic representation differs among these three categories. The first category is composed of Anodontini and a few Lampsilini (Section 4.1.D.2), riverine lentic microhabitat specialists are composed primarily of Lampsilini, and riverine generalists include a wider taxonomic array. Assemblages in lentic microhabitats also are distinguished by having consistently lower density than in nearby lotic habitats.

In lowland portions of the Mobile Basin, the lentic microhabitat guild includes a distinctive group of species that are rare in main-channel habitats as well as a

Table 4.6. *Differences in mussel assemblages in the main channel and adjacent lentic microhabitats in the Sipsey River, Alabama*

Main channel lotic microhabitat	Proportion	Lentic microhabitat	Proportion
Pleurobema decisum[1]	0.322	*Quadrula asperata*[2]	0.314
Fusconaia cerina[1]	0.222	*Lampsilis straminea*[3]	0.255
Quadrula asperata[2]	0.167	*Villosa lienosa*[3]	0.118
Elliptio arca[1]	0.109	*Obovaria jacksoniana*[3]	0.078
Q. verrucosa[1]	0.071	*Pleurobema perovatum*[3]	0.059
Q. rumphiana[1]	0.059	*Q. verrucosa*[1]	0.059
Lampsilis ornata[1]	0.008	*Potamilus purpuratus*[3]	0.059
Medionidus acutissimus[1]	0.008	*Pleurobema decisum*[1]	0.020
Obovaria unicolor[2]	0.008	*Villosa vibex*[3]	0.020
Obliquaria reflexa[2]	0.008	*Leptodea fragilis*[3]	0.020
Pleurobema perovatum[3]	0.004		
Lampsilis straminea[3]	0.004		
Elliptio crassidens[1]	0.004		
Megalonaias nervosa[1]	0.004		
Total individuals	259		51

Note: Main channel microhabitat was a gravel point bar and deep gravel run in the channel thalweg; lentic microhabitat was along a silt–sand bank with no current. The two microhabitat types were immediately adjacent and separated by less than 10 m. Table entries are results of 50-min timed searches in each microhabitat (W. R. Haag, unpublished data). Superscripted numbers give habitat affinity of each species: 1, riverine species occurring primarily in main channel microhabitats; 2, riverine habitat generalists; 3, riverine lentic microhabitat specialists (see text). Habitat affinities were determined by principal component analysis of habitat use at a nearby site (Haag 2002).

few generalists. In contrast to main-channel habitats, which are dominated by Pleurobemini and Quadrulini, lentic microhabitats are composed primarily of lampsilines and the generalist *Quadrula asperata* (Table 4.6). In addition, these assemblages are characterized by the presence of *Pleurobema perovatum*, which rarely occurs in main-channel habitats, unlike the related *P. decisum*. Other genera have similar species pairs that occur primarily in one or the other microhabitat (e.g., *Lampsilis*, *Obovaria*). Lentic microhabitats in this region also include *Lampsilis teres* and characteristic lentic species such as *Anodonta suborbiculata*, *Pyganodon grandis*, *Toxolasma parva*, *Uniomerus tetralasmus*, and *Utterbackia imbecillis* (Haag and Warren 2010). These assemblages typically occur at low density, unlike main-channel habitats, which support mussel densities of more than 10/m^2 (Table 4.6; Haag and Warren 2010).

Lentic microhabitat assemblages are similar in other lowland and large rivers in the Mississippian region. These lentic microhabitats support overall mussel densities 5–30 times less than densities in main-channel habitats, and assemblage composition differs markedly (Holland-Bartels 1990; Ahlstedt and McDonough 1993; Haag and Warren 2007; Zigler et al. 2008). Lentic microhabitat assemblages include characteristic lentic species (*A. suborbiculata*, *P. grandis*, *Toxolasma* spp., *Utterbackia imbecillis*), riverine lentic microhabitat specialists (*Lasmigona complanata*, *Lampsilis teres*, *Leptodea fragilis*, *Potamilus* spp.), and riverine generalists (*Amblema plicata*, *Obliquaria reflexa*, *Megalonaias nervosa*, *Quadrula quadrula*, *Q. pustulosa*). Despite this diverse array of species, lentic microhabitats typically support much lower species richness than main-channel habitats, and they conspicuously lack many riverine specialists (e.g., *Actinonaias*, *Cyclonaias*, *Cyprogenia*, *Ellipsaria*, *Pleurobema*, *Ptychobranchus*).

In low-gradient streams of the Southern Atlantic province and the Eastern Gulf region, a high proportion of species are associated with lentic microhabitats, and these habitats often support the highest species richness in the stream (Sickel 1980; Brim Box and Williams 2000; Brim Box et al. 2002). Only a few species are typically confined to main-channel habitats with current (e.g., *Elliptio angustata*, *E. arctata*, *E. congarea*, *E. crassidens*, *E. roanokensis*, *Elliptoideus sloatianus*) (Brim Box and Williams 2000; Savidge 2006). However, similar to the Mississippian region, high-density mussel aggregations are typically limited to main-channel habitats (Savidge 2006).

Lentic microhabitat assemblages are poorly developed in small, upland streams. In upland streams of the Mississippian region, lentic microhabitats often are inhabited by *Hamiota*, *Lampsilis siliquoidea*, *Potamilus alatus*, *Toxolasma lividus*, and several *Villosa* as well as by characteristic lentic species. These species may be most abundant in lentic microhabitats, but they occur frequently in lotic habitats as well (Strayer 1981; Haag and Warren 1998; Williams et al. 2008). In the Northern Atlantic province, assemblage differences between lentic and lotic microhabitats are obscured further by the apparently broad microhabitat requirements of most species (Section 4.1.D.2). Only two species appear to show strong affinity for lotic microhabitats (*Alasmidonta varicosa* and *Margaritifera margaritifera*; Nedeau et al. 2000). Conversely, only *Pyganodon cataracta* shows a strong affinity for lentic microhabitats in streams (Nedeau et al. 2000). Among riverine specialists, *Alasmidonta heterodon* shows some affinity for depositional areas (Strayer and Ralley 1993; Michaelson and Neves 1995; Nedeau 2008).

4.2.C. Generalists and less obvious specialists: The remaining 90 percent

Although a number of North American species occur in rather specific microhabitats, remarkably little specialization is apparent for the vast majority of species. Even at small scales, lotic habitats present a broad range of conditions along gradients of substrate, current, and depth (e.g., Bain and Stephenson 1999). Numerous attempts to find patterns of microhabitat segregation among species along these gradients have largely failed, with the exception that some have identified elements of lentic microhabitat or large-river guilds (Strayer and Ralley 1993; Strayer et al. 1994; Haag

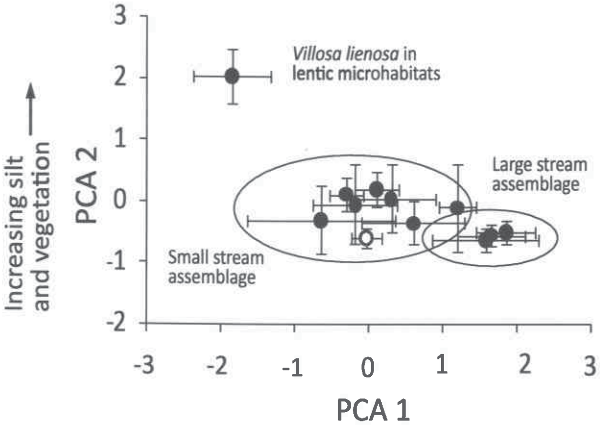

Figure 4.10. Principal component analysis of mussel species ordinated by microhabitat variables in upland tributaries of the Black Warrior River system, Alabama (error bars are ±2 SE of mean PC scores). The analysis separates one species occurring primarily in lentic microhabitats and separates large-stream from small-stream assemblages. Otherwise, microhabitat use overlaps broadly among species and among samples with no mussels (open circle) (adapted from Haag and Warren 1998).

and Warren 1998; Brim Box et al. 2002; Figure 4.10). For example, in a small-stream assemblage in Michigan, 21 of 22 species showed no difference in microhabitat use based on substrate, current, depth, proximity to the stream bank, and presence of aquatic vegetation; the only detectable pattern was a tendency for the rainbow, *Villosa iris*, to occur near shore, presumably in lentic microhabitats (Strayer 1981). A similar approach in the Mississippi River identified a lentic microhabitat guild occurring in low flow and fine sediment (e.g., *Lasmigona complanata, Potamilus* spp., *Pyganodon grandis, Toxolasma parva*) but was otherwise unable to discriminate among habitat use for more than 20 additional species (Holland-Bartels 1990).

In addition to providing little evidence of habitat partitioning, traditional microhabitat variables have shown little utility in predicting the occurrence of mussel aggregations within stream reaches (reviewed in Strayer 2008). For example, in small streams, quadrats with and without mussels were not readily distinguishable based on depth, current, substrate, and vegetative cover (Figure 4.10). Furthermore, microhabitat variables associated with mussel aggregations vary greatly among rivers. Although gravel-bottomed riffles and runs are typically associated with high mussel abundance and richness, mussel assemblages in the South Fork Eel River, California, occurred almost exclusively in pools (Howard and Cuffey 2003), and in lowland streams, highest abundance and richness often occur in sand or silt substrates (Manning 1989; Miller et al. 1992a; Kesler et al. 2001).

Certainly not all mussel species are strictly equivalent in their habitat requirements, and traditional microhabitat gradients are useful for predicting mussel occurrence in some situations. In lakes, mussel abundance is related to depth, substrate, and wind exposure, and mussel species may differ in their occurrence along these gradients (Ghent et al. 1978; Cyr 2008). Similarly, some stream species show subtle differences in microhabitat use, particularly in larger streams with a greater diversity of habitats. For example, *Epioblasma, Hemistena*, and *Medionidus* nearly always occur in swift, shallow riffles, but *Megalonaias nervosa* and *Quadrula rumphiana* are more prevalent in slower, deeper runs (e.g., Haag 2002). Additional research, particularly in mid-sized and large streams, will doubtless show other subtle patterns of microhabitat specialization. Nevertheless, it is clear that many species overlap widely in habitat use. In mid-sized and large streams of the Mississippian region, more than 20 species often can be found in a single, 0.25 m^2 quadrat (Holland-Bartel 1990; C. Davidson and S. Ahlstedt, personal communication), illustrating the similar habitat requirements of many species.

4.2.D. Stability and disturbance at the microhabitat scale

Because they typically live more than 5 years and have limited mobility, the one habitat requirement that nearly all mussel species share is a stable environment. In Section 4.1.D.1, I discussed the important role of habitat stability in determining mussel occurrence at large scales. An emerging theme in mussel ecology is that habitat stability is a primary factor determining mussel occurrence even at small scales. Unlike traditional measures of microhabitat, measures of substrate stability, particularly shear stress at high flow, are strongly correlated with and predictive of mussel occurrence in habitats from small streams to the Mississippi River (Vannote and Minshall 1982; Layzer and Madison 1995; Strayer 1999a; Johnson and Brown 2000; Hastie et al. 2000a; Howard and Cuffey 2003; Gangloff and Feminella 2007; Zigler et al. 2008; Allen and Vaughn 2010). The importance of stable substrate was noticed, if not articulated specifically, by early workers: "On one side [of the river] the bottom was composed of a very soft gravel, in which no mussels were found. About 50 feet from the bank, however, the gravel was firmer and there were mussels" (Boepple and Coker 1912, 11).

Substrate stability and other hydraulic variables are important for potentially two reasons. Most obviously, areas of stable habitat represent refugia from scour during floods (Strayer 1999a; Hastie et al. 2001). In a flashy desert stream, the Texas hornshell, *Popenaias popei*, occurred only under rock shelves and undercut banks, which acted as flow refuges at high flows (Levine 2009). In large rivers, the occurrence of stable flow refuges successfully predicted the occurrence of dense mussel beds (Morales et al. 2006a). These beds may persist for many years, allowing large numbers of individuals to accumulate over time. In the Ohio River, 64 percent of mussel beds surveyed in 1967 were still in existence in 1982 (Williams and Schuster 1989). Similarly, the large size and advanced age of western pearlshells (*Margaritifera falcata*) in flow refuges suggest that these habitats are stable for many decades (Vannote and Minshall 1982).

Mussel beds may be self-perpetuating to an extent if dense mussel aggregations further stabilize the substrate (Vaughn and Spooner 2006a). Flow characteristics also may be important in determining habitats in which juveniles can settle and successfully colonize. Juveniles may be transported long distances and unable to settle in habitats with high flow but may be concentrated and better able to settle in flow refuges (Morales et al. 2006a). This mechanism provides one possible explanation for the higher recruitment seen for some species during low-flow years (Chapter 7). However, settlement time varies seasonally among species and occurs under varying flow conditions, and many low-flow habitats in streams do not support dense mussel aggregations. Consequently, juvenile transport seems a less compelling explanation than substrate stability for small-scale patterns of mussel distribution (Strayer 2008).

Substrate stability provides a likely mechanism for several patterns of microhabitat use. Microhabitats under slab rocks, in beds of aquatic plants, or near other structure are likely stable at high flows and may provide important refuges in otherwise inhospitable stream reaches (Sietman et al. 1999). Species that characteristically use these microhabitats are either small or do not bury deeply (e.g., *Cumberlandia*) and may be particularly susceptible to dislodgement by currents. Habitat stability also helps explain the lack of consistency in microhabitat associations across stream types. Stability of stream substrates differs according to local hydraulic conditions (Strayer 2008). For example, silt and sand substrates that are easily transported during floods in upland streams may be stable in lowland streams, allowing colonization by dense mussel assemblages. Lentic microhabitats also may represent flow refuges across a range of streamflow conditions. In sand-bottomed Gulf Coast streams, lentic microhabitats may be the only available stable habitats, explaining why they have higher diversity than main-channel habitats in this region. However, the consistently low mussel density in lentic microhabitats suggests that they are only transient refuges that are periodically disturbed by high flows, drought, and a variety of other factors (Zigler et al. 2008).

4.3. There must be something missing

Mussels show several strong patterns of habitat specialization at both large and small scales. Nevertheless, the apparent similarity in habitat use among many species creates a vexing problem for ecologists given the great diversity of the North American fauna: how can so many species coexist if their habitat requirements are the same? This is also a problem for conservationists tasked with delineating and protecting mussel habitats. Clearly there must be other aspects of mussel ecology that play a strong role in structuring assemblages and reducing overlap in resource use among species.

Traditionally, differences in mussel assemblages among habitats have been explained by vague ideas about "habitat preferences" of species. For many other organisms, specific mechanisms governing habitat requirements have been elucidated (e.g., physiological requirements for germination of plant seeds, availability of specific food resources for animals). Habitat stability appears to play a large role in determining mussel occurrence at all scales. Similarly, a few species appear physiologically adapted to specific water chemistries (Section 4.1.C). Otherwise, the basis of habitat requirements for mussels has rarely been proposed or tested, and few morphological or other adaptations provide plausible mechanisms for the presence or absence of species in certain habitats. For example, some species that occur often in silt have winged or greatly inflated and thin shells that are thought to buoy them in these substrates (Section 1.3.C). However, this mechanism does not explain why these species typically do not dominate in other habitats or why other species lacking these adaptations also live in silt substrates. Similarly, the distinctive large-river habitat guild of the Mississippian region has been recognized for more than 100 years, but few have asked *why* these species are restricted to large rivers.

In the following chapters, I explore the many ways – apart from habitat use – in which mussel species show strong ecological differences. Then, in Chapter 8, I attempt to show how these ecological differences can explain patterns of habitat specialization and how they interact to structure mussel assemblages at multiple scales.

Chapter 5

Host use and host infection strategies

The seemingly well-mannered and unobtrusive demeanor of freshwater mussels belies the fact that they are aggressive parasites. Although all benthic life history stages are free living, glochidia larvae (Figure 5.1) of nearly all species require a brief period as parasites on fishes or, rarely, amphibians. Adult females employ a fascinating array of insidious strategies to transmit glochidia to hosts, including spectacular mimicry that is among the best developed in the natural world. The host–parasite relationship of mussels is unique among bivalves and has important ramifications for many aspects of mussel ecology and conservation.

Glochidia were first identified as larval mussels in the late 1600s by Antonie van Leeuwenhoek, the Dutch scientist who developed one of the first microscopes (Watters 1994a). However, 100 years later, scientists concluded that glochidia were a separate species that were parasites of the mussel gill and gave them the name *Glochidium parasiticum* (Heard and Dinesen 1999; *Glochidium* is from the Greek word meaning "barb of an arrow" and probably refers to the apical hooks of anodontine glochidia). Although van Leeuwenhoek's earlier diagnosis as larval mussels was confirmed in 1832, the name glochidia stuck. Thirty more years transpired before the parasitic relationship between glochidia and fishes was elucidated in Germany by Franz Leydig (Watters 1994a; Heard 1999). By the early 1900s, biologists began to recognize the importance of the host relationship in the distribution, ecology, and conservation of mussels (e.g., Simpson 1899; Lefevre and Curtis 1910).

After release from the female mussel, glochidia can attach to nearly any fish species, other aquatic organisms, and even inanimate objects (Lefevre and Curtis 1910; Watters and O'Dee 1998). However, mussel species differ greatly in the number and species of hosts on which their glochidia can survive and metamorphose into juveniles. Within about 6 hours after attachment to a potential host, glochidia are encapsulated by migration of the host epithelial tissue, forming a cyst (Rogers-Lowery and Dimock 2006; Figure 5.2). Glochidia that encyst on nonsuitable hosts are rejected by the fish immune system and die. Those that attach to suitable hosts are able to survive the host

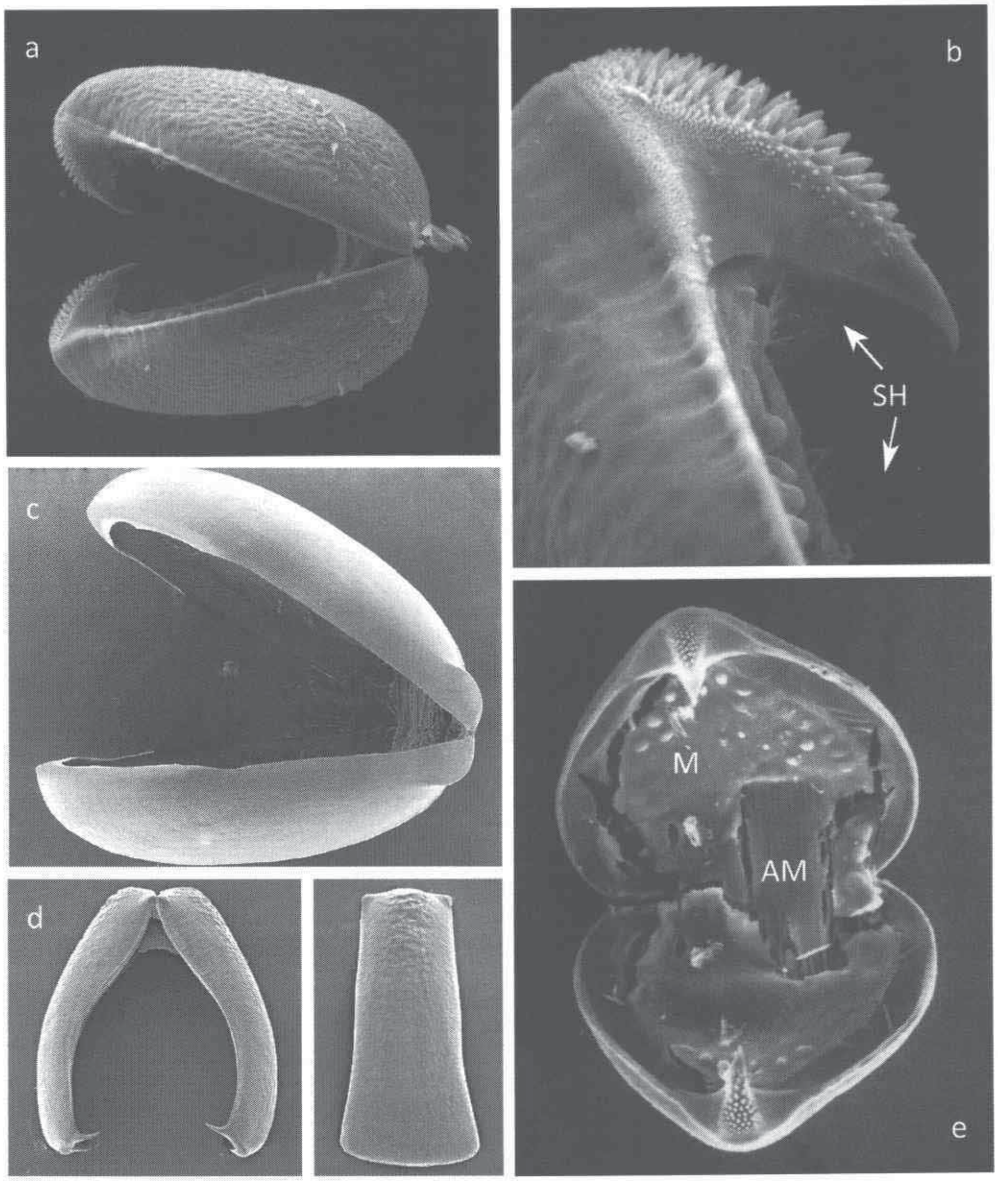

Figure 5.1. Freshwater mussel glochidia. (a) Hooked glochidium of the brook floater, *Alasmidonta varicosa* (Anodontini; total length ~350 μm). (b) Detail of apical hook of *A. varicosa* showing microstylets on hook and sensory hairs (SH). (c) Unhooked glochidium of the southern rainbow, *Villosa vibex* (Lampsilini; total length ~240 μm). (d) Hooked, "axe-head" or *ligulate* glochidia of the pink heelsplitter, *Potamilus alatus* (Lampsilini; total length ~218 μm). (e) Glochidium of *A. varicosa* showing mantle tissue (M) and single adductor muscle (AM). (a,b,e, Barry Wicklow, photos; c,d, Christine O'Brien, photos).

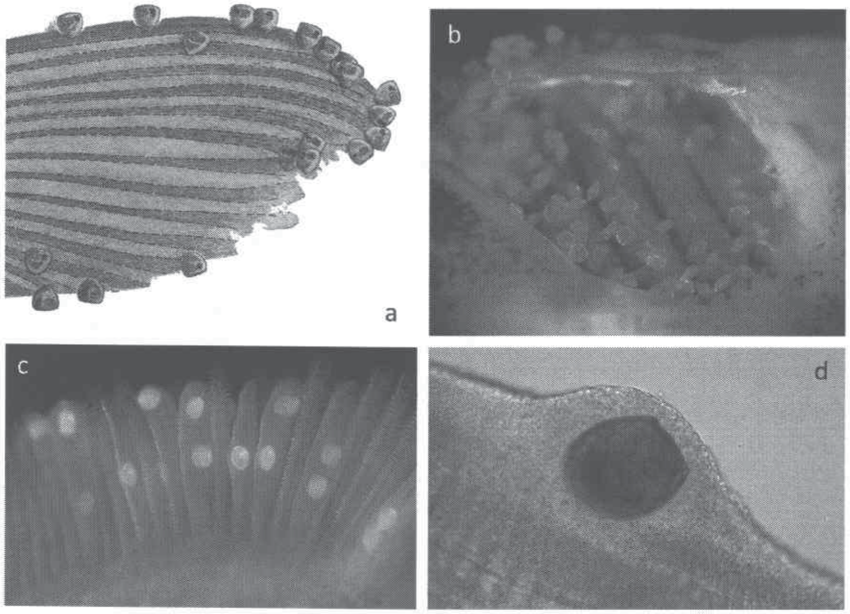

Figure 5.2. (a) Hooked anodontine glochidia attached to fish fin (from Lefevre and Curtis 1912). (b) Heavy infestation of unhooked lampsiline glochidia on the gills of a darter; gill cover (operculum) is raised to show gills within. (c,d) Unhooked glochidia encysted on fish gill filament (b,c,d, Chris Barnhart, photos).

immune response and complete metamorphosis to juvenile mussels, after which they emerge from the cyst to begin a free-living existence (Meyers et al. 1980; Waller and Mitchell 1989; Kirk and Layzer 1997; O'Connell and Neves 1999).

Although they undergo a complete anatomical metamorphosis (Section 1.4.C.4), glochidia of most species do not grow while encysted on hosts (Lefevre and Curtis 1912). Notable exceptions include the miniature glochidia (<100 μm) of the Margaritiferidae, *Leptodea*, *Truncilla*, the *Quadrula quadrula* group (including *Q. apiculata*, *Q. fragosa*, *Q. quadrula*, and *Q. rumphiana*), *Q. verrucosa*, and the axe-head or *ligulate* glochidia of *Potamilus*, all of which grow substantially (more than 2 times glochidial size) before excysting from hosts (reviewed in Barnhart et al. 2008). Howard (1913) reported growth of encysted *Q. pustulosa* (a species without miniature glochidia) on catfish, but this has not been substantiated (Barnhart et al. 2008). With the exception of the *Q. quadrula* group, species with miniature glochidia have among the highest fecundities of any mussel species, which may be possible because of the lower energetic investment in individual glochidia (Section 6.2.C). Many species with miniature glochidia also share the trait of an extended period of encystment, often overwintering on hosts (Howard and Anson 1922; Young and Williams 1984a, 1984b; Steingraeber et al. 2007). Overwintering is typically associated with fall release of glochidia and suppression of glochidial growth in cold temperatures (see subsequent discussion), but a lengthy parasitic period including overwintering also is reported for

Leptodea, *Potamilus*, and *Truncilla*, all of which release glochidia in spring or summer (Howard and Anson 1922). However, glochidia of these three genera also can complete metamorphosis, grow, and excyst from hosts rapidly (in about 2–4 weeks), similar to species without miniature glochidia that do not grow on hosts (B. Sietman, personal communication). Other than water temperature, the factors that determine the encystment period are poorly known, but it appears that compensatory growth of miniature glochidia may be necessary for juvenile survival in some cases, perhaps because miniature juveniles would have difficulty settling and maintaining position in flowing water (Barnhart et al. 2008). Excystment of larger juveniles also may allow attainment of reproductive maturity in the first year for short-lived species such as *Leptodea*, *Potamilus*, and *Truncilla* (Chapter 6).

Mussel species are often classified with regard to host use as either generalists or specialists. In reality, host breadth is a continuum ranging from species that can metamorphose on only a single species to those that can use nearly any fish species. Nevertheless, this dichotomy is useful from an ecological perspective, and I will use it with the following definitions. Generalists have broad immunological compatibility with hosts, and glochidia are able to metamorphose on a taxonomically wide array of fishes, usually including multiple fish families (Section 5.2.A). Specialists can metamorphose on only a few fish species, usually within a single family and sometimes on only a single species (Section 5.2.B).

The taxonomic breadth of host use is determined by innate, species-level immune responses (Barnhart et al. 2008). However, individual fishes of suitable host species may acquire temporary resistance to glochidia after repeated exposures (Reuling 1919; Arey 1923; Bauer and Vogel 1987; Watters and O'Dee 1996; Rogers and Dimock 2003). Acquired resistance can result in rejection, poor encystment, or decreased metamorphosis success of both specialists and generalists (Dodd et al. 2005; Rogers-Lowery and Dimock 2006). Acquired resistance can reduce metamorphosis success for at least 12 months (Dodd et al. 2006) and is not species specific; fishes that acquire resistance to glochidia of one mussel species also can be resistant to other, unrelated species (Dodd et al. 2005). Within suitable host fish species, younger and smaller individuals are often parasitized more heavily, perhaps because the incidence of acquired resistance is higher in older fishes (e.g., Bauer and Vogel 1987). Consequently, acquired resistance is an important feature of the host relationship because it further reduces the availability of suitable hosts, especially in streams with large mussel populations.

Most species release glochidia and infect hosts from early spring to summer (Section 1.4.C). At warm temperatures, metamorphosis and excystment of glochidia on suitable hosts occurs rapidly, usually from 2–6 weeks (e.g., Zale and Neves 1982b; Haag and Warren 1997), but glochidial development is strongly temperature dependent. At least two species in the Quadrulini, the washboard, *Megalonaias nervosa*, and winged mapleleaf, *Quadrula fragosa*, release glochidia exclusively in the fall;

Q. fragosa releases in September and October when water temperatures decline to 15–21°C (Woody and Holland-Bartels 1993; Heath et al. 2000; Haggerty et al. 2005; Hove et al. 2012). Development of encysted *Q. fragosa* glochidia slows with decreasing water temperature and ceases at less than 9.6°C, suggesting that glochidia overwinter on hosts and complete metamorphosis after water temperatures rise in the spring (Steingraeber et al. 2007). Fall release and overwintering of glochidia also is reported for *Margaritifera margaritifera* (Young and Williams 1984a, 1984b), *Simpsonaias ambigua*, and *Obovaria olivaria* (Howard and Anson 1922); however, *O. olivaria* also releases in spring (B. Sietman, personal communication). Although *Lampsilis, Ligumia*, and *Villosa* release glochidia primarily in the spring, they may begin to display lures to attract hosts (Section 5.3.C) soon after maturation of glochidia in the fall (W. R. Haag, observations; B. Sietman, personal communication). Development of glochidia that infect hosts during this time also may be slowed by decreasing water temperature, causing glochidia to overwinter on hosts (Howard and Anson 1922; Watters and O'Dee 1999). A proposed benefit of overwintering is that juveniles can excyst earlier in the following year, thus having a longer growing season (Howard and Anson 1922; Steingraeber et al. 2007). Another potential advantage is that because few species release glochidia in the fall, host fishes may have a lower incidence of acquired resistance from previous or existing glochidial infections.

5.1. The accidental parasite

Like most riverine organisms with limited mobility, ancestral freshwater mussels were faced with the major problem of upstream dispersal. For riverine organisms, individuals that enter the drift (e.g., bivalve or insect larvae) are swept downstream, depleting upstream populations. Aquatic insects solve this problem mainly by aerial dispersal of adults. Freshwater mussels solve the problem in part by brooding their larvae within the female (Section 1.4.C) – a trait shared by most freshwater bivalve groups worldwide – instead of having free-floating, planktonic larvae like many marine bivalves. This trait reduces downstream transport, but it does not aid in upstream dispersal. The invasive Asian clam, *Corbicula fluminea*, is capable of rapid upstream dispersal potentially because the byssal threads of juveniles become entangled with fishes (Section 10.6.C.2).

Glochidia of several mussel species produce adhesive larval threads, similar to the byssal threads of juveniles (Section 5.3.A). These threads become entangled with or adhere to fishes, facilitating encystment of parasitic glochidia (Lefevre and Curtis 1910; Wood 1974; Woody and Holland-Bartels 1993; O'Brien and Williams 2002). Even without parasitism, entanglement of free-living mussel larvae on fishes could have conferred the strong selective advantage of upstream transport (Watters 2001; Barnhart et al. 2008). Within the Unionidae, larval threads are present in most Anodontini but also occur sporadically in all other tribes, except the Lampsilini (reviewed in Barnhart et al. 2008), suggesting that larval threads are a primitive character that has been lost in groups that developed more specialized host infection strategies. Consequently, the association between mussel larvae and fishes may have begun primarily in response to the problem of upstream dispersal, with the parasitic relationship arising as a secondary, accidental development.

After mussel larvae were routinely associated with fishes via larval threads, they may have begun to clamp onto fish tissues to gain firmer attachment, leading to the additional selective advantage of obtaining nutrition from fishes. Because larvae that attached to fish tissues would have been subjected to antiectoparasite immune responses, a critical step in the evolution of parasitic glochidia was development of resistance to these responses. Although heavy glochidial infections can cause significant stress and even death of fishes (Kaiser 2005; Howerth and Keller 2006), most natural infections are of low intensity (fewer than 10 glochidia per fish; Neves and Widlak 1988) and are assumed to be relatively benign. For example, gill damage to fishes after successful encystment and metamorphosis of compatible glochidia was similar to that sustained by rejection of incompatible glochidia (Barnhart et al. 2008, citing C. Barnhart, unpublished data). However, darters exposed to glochidial infestations similar to those seen in the wild experienced higher ventilation rates, lower activity and antipredator responses, and reduction of body mass compared to noninfected individuals, suggesting that even low infestations incur costs for fishes (Crane et al. 2011).

Nevertheless, selection pressure for fishes to resist glochidial infection may be lower than the strong selection on larvae to acquire resistance to host defenses (Barnhart et al. 2008). Because of this imbalance in selective pressures between hosts and parasites, the ability of glochidia to circumvent host immune responses may have arisen quickly. Once glochidia developed compatibility with a particular fish species sufficient to allow successful metamorphosis, there would have been a strong selective disadvantage to further diversification of these traits, leading to stabilization of the host relationship. These relationships likely developed according to the abundance and behavioral characteristics of fishes that, in turn, dictated which species were routinely encountered by larvae. For example, the specialized host relationships of the alewife floater, *Anodonta implicata*; ebonyshell, *Reginaia ebena*; and eastern pearlshell, *Margaritifera margaritifera*, may have developed in response to the overwhelming seasonal abundance of their migratory host fishes (Barnhart et al. 2008). Consequently, variation in fish assemblages across large scales resulted in a diverse array of host relationships.

It is unknown when the parasitic relationship arose. Fossil unionoids appear in North America by the Triassic (250–200 mya), but fossil glochidia are known only from the Quaternary (before 2.6 mya) (Watters 2001, citing Brodniewicz 1968). However, fossil impressions of unionoid gills from the Jurassic (200–146 mya) show apparent calcium concretions similar to those that serve as sources for glochidial shell formation in modern mussels (Richard et al. 1991), suggesting that glochidia may have been present at a much earlier date. North American mussels in the Triassic co-occurred with many freshwater fish groups that are now extinct; if specific host relationships had developed by that time, a sizable portion of the mussel fauna may have also gone extinct due to loss of their fish hosts (Watters 2001). Conversely, the appearance of a diverse unionoid fauna by the Cretaceous (145–65 mya) may have been facilitated by a broadening of the host resource coincident with the great radiation in freshwater teleost fishes (Watters 2001).

5.2. Patterns of host use

Because of the critical importance of the parasitic stage, identification of host fishes has been the focus of extensive historical and recent research. Work at the Fairport Biological Station and associated researchers in the early 1900s (Section 2.2.B) provided the first body of data on North American host fish relationships, primarily with the goal of identifying hosts that could be used in artificial propagation of commercially important mussel species. These data remain invaluable and represented the bulk of host fish information available until the 1980s. However, many of the proposed hosts were inferred from natural or laboratory infections without confirmation that glochidia metamorphosed into juvenile mussels, and some of these relationships have turned out to be incorrect (e.g., Fritts et al., in press). Furthermore, these studies often did not report fish species that were unsuitable hosts, or they tested the suitability of only a small number of species. Consequently, many of these relationships are of limited ecological use because the degree of host specialization is unknown. In the 1980s, host studies accelerated and remain a focus of many research programs. Modern studies typically use metamorphosis of glochidia into juveniles in laboratory trials and the robustness of metamorphosis as measures of host suitability. However, results of modern host studies also need to be scrutinized carefully to evaluate whether a reported host species is likely to be a primary host that is important in nature, a marginal host of limited compatibility (see Section 5.2.B), or even an artifact of laboratory technique. The best modern studies assess host use across a comprehensive cross section of the co-occurring fish assemblage, providing a clearer picture of ecological breadth of host use (e.g., Hove et al. 2011, 2012; Fritts et al., in press).

Although laboratory host trials are a powerful tool to assess the physiological compatibility of mussel–fish pairings, the frequency with which potential hosts encounter glochidia in the wild remains poorly known. The few existing field studies show high concordance between patterns of infestation on wild fishes and host suitability demonstrated in laboratory trials (Neves and Widlak 1988; Hove and Neves 1994; Boyer et al. 2011; Hove et al. 2012). Recent development of DNA bar coding for identification of newly metamorphosed juveniles from wild fishes will allow a better understanding of host use in the wild (Boyer et al. 2011).

Host use remains poorly known for several widespread species, particularly *Actinonaias*, *Alasmidonta* spp., *Elliptio complanata, Obliquaria reflexa*, *Plectomerus dombeyanus*, *Uniomerus* spp., and most species of the Southern Atlantic province. The host relationship of *Cumberlandia monodonta* has posed an unusually intractable problem: more than 50 fish species have been tested for suitability, but none so far have resulted in metamorphosis of glochidia (M. Hove, personal communication). Nevertheless, host use is now known reasonably well for about 130 North American mussel species, or about one-third of the fauna, and these species represent a broad phylogenetic cross section of mussel diversity. On the basis of this body of data, a number of consistent patterns of host use have emerged.

Nearly all North American species use fishes as hosts. The single known exception is the salamander mussel, *Simpsonaias ambigua*, which appears to be a specialist on the mudpuppy (*Necturus maculosus*), a large aquatic salamander (Section 5.2.B). The plain pocketbook, *Lampsilis cardium*; creeper, *Strophitus undulatus*; and paper pondshell, *Utterbackia imbecillis*, have metamorphosed in the laboratory on other salamanders and frogs (Watters and O'Dee 1998; van Snik Gray et al. 2002). However, most amphibians do not occur in permanent water bodies inhabited by fishes (and mussels), or they are restricted to shallow margins of streams or lakes (e.g., Petranka 1998), and it is doubtful that species other than *Necturus* commonly serve as hosts in nature. Of the approximately 130 North American mussel species with host information, about 20 percent are generalists and most (80%) are host specialists (summarized from Cummings and Watters 2010).

Mussel hosts encompass a broad cross section of North American fish diversity. Of native freshwater fish families, only the paddlefish (Polyodontidae), smelts (Osmeridae), trout–perch (Percopsidae), cavefishes (Amblyopsidae), and pygmy sunfishes (Elassomatidae) have not been reported to carry or serve as hosts for mussel glochidia (Weiss and Layzer 1995; Cummings and Watters 2010). In addition, lampreys (Petromyzontidae) rarely carry natural glochidial infections but have not been confirmed as suitable hosts. Most widespread and common fish families are used widely (Figure 5.3). Sunfishes and black basses (Centrarchidae), minnows (Cyprinidae), darters and other perches (Percidae), catfishes (Ictaluridae), sculpins (Cottidae), and drum (Sciaenidae) are hosts for a large number of species, but gars (Lepisosteidae), sturgeons (Acipenseridae), herrings (Clupeidae), and trout (Salmonidae) also serve as primary hosts for several species. A notable exception is the suckers (Catostomidae), a diverse and abundant family across North America. Only five mussel species (mostly Anodontini) are known to metamorphose on suckers, but only one, the Cumberland elktoe, *Alasmidonta atropurpurea*, appears to be a specialist on suckers (Gordon and Layzer 1993). Suckers also may be a primary host for *A. marginata*, although a wide variety of other fishes are marginally suitable (B. Sietman, personal communication; Section 5.2.B). The benthic habits of suckers would seem to put them in frequent contact with glochidia, and their conspicuous

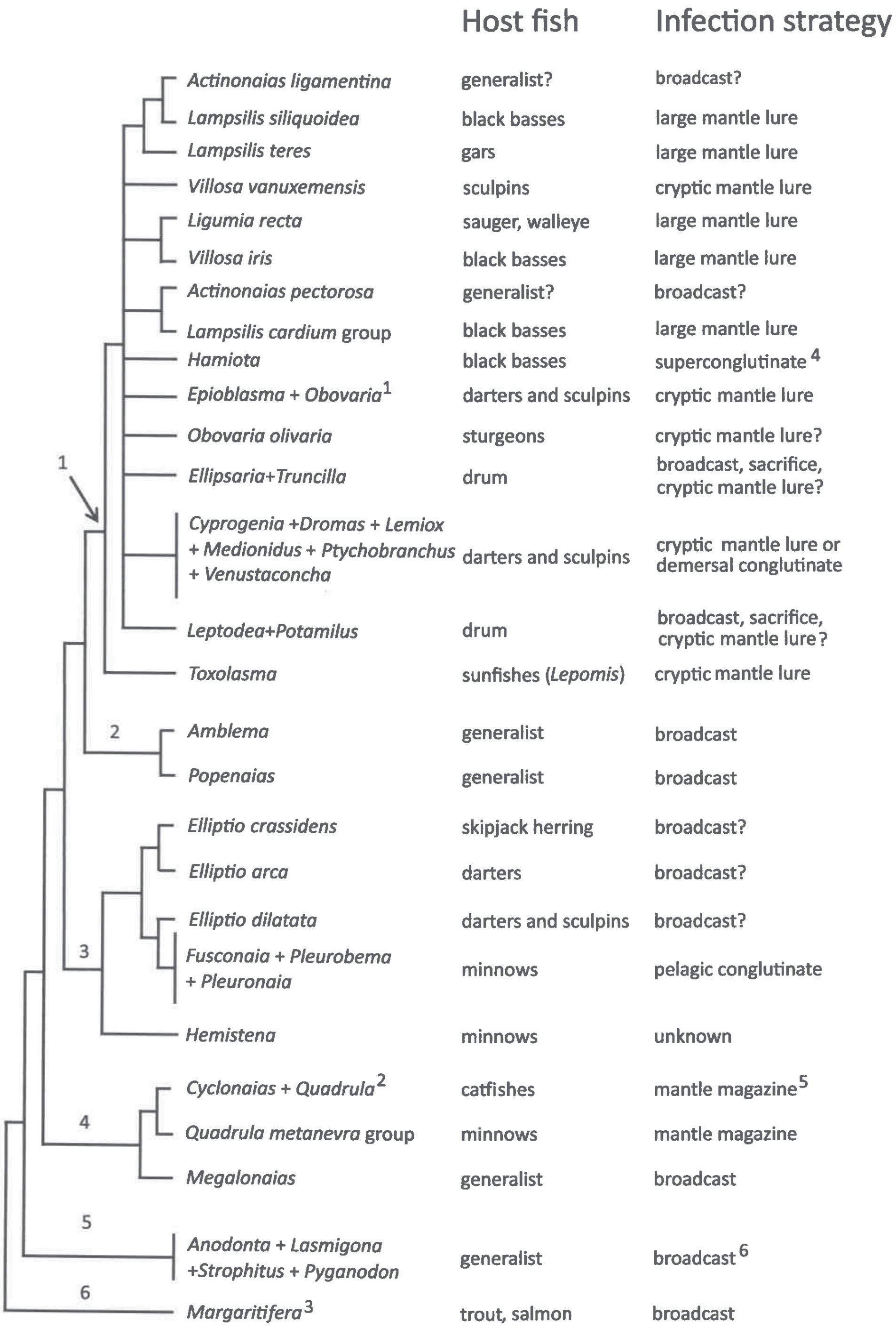

Figure 5.3. Phylogenetic distribution of primary host use and host infection strategies in North American mussels. Major lineages are as follows: 1, Lampsilini; 2, Amblemini; 3, Pleurobemini; 4, Quadrulini; 5, Anodontini; 6, Margaritiferidae. Species and genera are grouped based on monophyly and common host use. Note that polyphyly exists for several genera (e.g., *Actinonaias, Lampsilis, Villosa, Elliptio, Quadrula*).

underrepresentation as hosts is puzzling and unexplained. Similarly, although many mussel species parasitize larger catfishes (*Ictalurus* and *Pylodictis*), the widespread and diverse madtoms (*Noturus*) have not been identified as a primary host for any mussel species (Section 5.2.B).

Mussels show striking variation in host use and host use has a strong phylogenetic component (Figure 5.3). For example, specialization on sunfishes occurs only in the Lampsilini, and specialization on catfishes occurs only in the Quadrulini, despite the abundance and wide distribution of these fishes. Generalists are restricted primarily to the Anodontini and occur rarely in other groups (Section 5.2.A). Within tribes, host use can vary greatly among closely related lineages. Host use of the *Cyclonaias* + *Quadrula* group is restricted to catfishes, but the sister *Q. metanevra* group uses minnows exclusively (Figure 5.3). Divergence in host use is especially apparent within the large tribe Lampsilini, whose members specialize on at least six fish families (Figure 5.3). In contrast, host use is highly conserved within most lineages, especially at the genus level. For specialists, nearly all cases of apparent use of multiple fish families by a single mussel genus are the result of polyphyly in former generic classifications (e.g., *Lampsilis, Fusconaia, Obovaria, Quadrula, Villosa*). One of the few possible exceptions is among the Alabama spike, *Elliptio arca*, and the elephant-ear, *E. crassidens*, which use darters and skipjack herring, respectively, and other *Elliptio*, which may be generalists (Keller and Ruessler 1997; Nedeau et al. 2000); however, phylogenetic relationships among *Elliptio* are unresolved and host use for most species is poorly known.

The great differences in host use among lineages, but its conserved nature within lineages, suggests that mechanisms to overcome the host immune system are canalized traits that are not easily modified. Consequently, shifts in host use may have been primary drivers of speciation events. The Margaritiferidae is the basal group within the order Unionoida suggesting that host specialization was a primitive trait (Figure 5.3). In addition to northern species that specialize on salmonids, other margaritiferids appear to have extremely narrow host use (Johnson and Brown 1998; see previous discussion of *Cumberlandia*), which may in part explain the currently restricted distribution of the family (Section 1.2). Within the Unionidae, the prevalence of generalists in the basal group Anodontini suggests that broadening of host use may have initially led to divergence of the family by allowing expanded geographic distribution, but

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Figure 5.3 (*continued*) Species without robust host data or of uncertain phylogenetic placement (e.g., *Reginaia ebena*) are omitted. Notes: [1]excludes *O. olivaria*; [2]includes the *Q. pustulosa* and *Q. quadrula* groups and *Q. verrucosa* (Serb et al. 2003); [3]excludes *M. hembeli* and *M. marrianae* for which host use is unknown; [4]also display large mantle lures (*H. altilis*); [5]also produce mucoid conglutinates; [6]conglutinates in *S. undulatus* only. (Phylogeny based on Campbell et al. 2005; host use and attraction strategies summarized from Zanatta and Murphy 2006; Barnhart et al. 2008; Cummings and Watters 2010).

subsequent specialization resulted in great taxonomic diversification. Although this history is conjectural, it is clear that extensive coevolution with the diverse North American fish fauna has been an integral factor in the development of the rich North American mussel fauna.

At least two species have apparently developed secondarily the ability to bypass the parasitic stage. Female green floaters, *Lasmigona subviridis*, are often found brooding fully developed juvenile mussels (Barfield and Watters 1998; Lellis and King 1998). Juveniles in the gills show active pedal feeding and may grow prior to release. Direct development appears to occur consistently within individuals and populations, but other populations produce glochidia that can metamorphose on a wide taxonomic array of fishes similarly to generalists, including other *Lasmigona*. All *L. subviridis* ($n = 8$) examined in a Virginia stream in April contained fully metamorphosed, active juveniles and no glochidia. At the same time in another Virginia stream, all individuals ($n = 8$) contained only glochidia, which metamorphosed on five fish species in four families (J. Jones, personal communication). The use of only one strategy at a given time within individuals and populations suggests that direct development is facultative and triggered by some cue. However, whether this developmental mode varies among years within individuals or populations and the phylogenetic relationships between parasitic and nonparasitic populations are unknown. Interestingly, Ortmann (1919) observed gravid individuals of *L. subviridis* on at least 11 dates over 4 years but apparently never observed juvenile mussels in the gills; however, it is unclear whether he examined gill contents of these individuals. *Lasmigona subviridis* is typically hermaphroditic (Ortmann 1919; van der Schalie 1970), which, together with direct development, apparently allows this species to occur in very small streams with low mussel and fish abundance (Chapter 8). Glochidia of two other generalists, *Strophitus undulatus* and *Utterbackia imbecillis*, were reported convincingly to undergo direct development in female gills (Lefevre and Curtis 1911; Howard 1915). This phenomenon has been substantiated recently only for *U. imbecillis* (Dickenson and Sietman 2008), and both species can metamorphose parasitically on a wide range of fishes (Tucker 1928; van Snik Gray et al. 2002; Cummings and Watters 2010).

5.2.A. Generalists

Generalist host use is distributed unevenly across the North American fauna. Most generalists are members of the Anodontini, and this trait characterizes the tribe to a large extent, even though several anodontines are specialists (Section 5.2.B). Apart from the Anodontini, generalists are rare but may occur in all major phylogenetic groups, except perhaps the Margaritiferidae. Generalist host use is documented or suggested in the Amblemini (*Amblema* and *Popenaias*; O'Brien and Williams 2002; Carman 2007) and the Quadrulini (*Megalonaias*; Coker et al. 1921; Weiss and Layzer 1995; but see Woody and Holland-Bartels 1993). In addition, *Actinonaias* (Lampsilini) and some *Elliptio* (Pleurobemini) may be generalists to some extent (Keller and Ruessler 1997; Nedeau et al. 2000; Layzer and Khym 2003–2004); otherwise all species in these tribes whose host use is known are specialists.

Breadth of host use varies among generalists, and some species do not appear to be entirely catholic in their host use. For example, the southern creekmussel, *Strophitus subvexus*, metamorphosed on 10 fish species in five families, but metamorphosis success varied among fish species (Haag and Warren 1997). The Carolina heelsplitter, *Lasmigona decorata*, metamorphosed on 21 fish species in five families, but metamorphosis success was highest and most consistent on minnows (Eads et al. 2010). Similar inconsistent results across fish species are reported for other generalists (O'Brien and Williams 2002; van Snik Gray et al. 2002). Other generalists appear able to metamorphose on virtually any fish species. *Utterbackia imbecillis* metamorphoses robustly on a wide range of native and exotic fishes as well as amphibians (Watters and O'Dee 1998). Glochidia of the giant floater, *Pyganodon grandis*, metamorphosed in the laboratory on 21 of 24 fish species tested and were present as natural infestations on 16 of 21 species examined (Trdan and Hoeh 1982).

Variation in host breadth among generalists may be due to at least two factors. First, fishes used in laboratory studies may have had varying degrees of acquired resistance from previous infections in the wild. This explanation is unsatisfactory because it contrasts with the largely consistent results of host studies of specialists (Section 5.2.B). Second, some results may be artifacts of laboratory conditions. At 21°C, the flat floater, *Anodonta suborbiculata*, metamorphosed on only one of eight species tested, but at 10°C, glochidia metamorphosed on a wider array of fishes and metamorphosis success was higher, suggesting that low temperatures suppress host immune responses (Barnhart and Roberts 1997; Roberts and Barnhart 1999). Results from some studies may be biased by experimental conditions that were not reflective of conditions at which infection occurs naturally (e.g., Haag and Warren 1997). However, other trials conducted closer to ambient conditions produced similar inconsistent results among species (Eads et al. 2010), suggesting that a wide variety of unknown factors influence host compatibility for generalists.

Glochidia of the Anodontini are well adapted for parasitizing a wide array of fishes. Glochidia of all species in the tribe have large, depressed shells with large adductor muscles and stout apical hooks that are adorned with rows of small teeth or *microstylets* (Wood 1974; Hoggarth and Gaunt 1988; Hoggarth 1999; Figure 5.1). These features increase the gripping strength of glochidia and allow them to penetrate tough external fish tissues such as fins and skin. Shell closure of hooked glochidia also is triggered to a greater extent by mechanical stimulation than unhooked glochidia, which are more sensitive to chemical stimuli (Lefevre and Curtis 1910; Shadoan and Dimock 2000). Presumably, these traits, along with adhesive larval threads (Section 5.3.A), allow anodontine glochidia to attach readily to a wide array of fishes in a variety of situations. Anodontine glochidia are considered primarily external parasites occurring especially on the fin margins (Lefevre and Curtis 1910; Howard and Anson 1922; Wood 1974; Figure 5.2). However, these glochidia may occur on both fins and gills (d'Eliscu 1972; Dartnall and Walkey 1979; Threlfall 1986) or primarily on gills (Weiss and Layzer 1995).

Glochidia of generalists in other groups lack the adaptations of the Anodontini and are similar to the glochidia of specialists, further supporting that generalist host use arose secondarily in these groups. With the exception of the Anodontini and *Potamilus* (Section 5.2.B), glochidia of all North American species are unhooked but vary widely in size (Barnhart et al. 2008; Figure 5.1). Hookless glochidia of specialists attach primarily to host gills and rarely to fins or other external surfaces (Lefevre and Curtis 1910; Neves and Widlak 1988; Figure 5.2). In contrast, hookless glochidia of the generalists *Amblema*, *Megalonaias*, and *Popenaias* attach frequently to gills and external surfaces or exclusively to the fins (Surber 1915; Weiss and Layzer 1995; O'Brien and Williams 2002; Carman 2007). Bauer (1994) proposed an increase in host breadth with increasing glochidial size. However, this relationship was an artifact of the small number of species in that study combined with the uniformly large size of anodontine glochidia (all of which were generalists in his study). Across the fauna as a whole, glochidial size is not a consistent predictor of host breadth for North American species and may largely be a phylogenetic artifact. For example, a specialist, the little-wing pearlymussel, *Pegias fabula* (Anodontini), has among the largest glochidia of any species, and a generalist, the threeridge, *Amblema plicata*, has glochidia that are smaller than many specialists (see Barnhart et al. 2008).

5.2.B. Specialists

In contrast to the restricted occurrence of generalists, specialist host use characterizes most North American mussel groups and most species. Even several Anodontini appear to be specialists (e.g., *Alasmidonta atropurpurea, A. heterodon, A. viridis, Pegias fabula, Simpsonaias ambigua*; Cummings and Watters 2010). Patterns of specialization have a strong phylogenetic basis (Figure 5.3). For example, all species in the *Fusconaia* + *Pleurobema* + *Pleuronaia* group use minnows almost exclusively, the *Cyclonaias* + *Quadrula* group use only catfishes, and *Simpsonaias ambigua* appears to use only mudpuppies (*Necturus*) and is not able to metamorphose on fishes (Howard 1915). However, the degree of specialization varies widely among species. Many species that specialize on darters use a wide array of darter species (e.g., Jones and Neves 2002; Haag and Warren 2003; Jones et al. 2004). Other species use only a subset of fishes within a particular family. Catfish specialists within the *Cyclonaias* + *Quadrula* group metamorphose robustly only on *Ictalurus* or *Pylodictis* but poorly or not at all on madtoms (*Noturus*) and bullheads (*Ameiurus*) (e.g., Hove et al. 1997; Haag and Warren 2003; Hove et al. 2011, 2012). The degree of specialization also can vary within mussel lineages. Although host use of the sister genera *Fusconaia* and *Pleurobema* is restricted to minnows, the gulf pigtoe, *F. cerina*, metamorphosed on 12 minnow species in nine genera, but the southern clubshell, *P. decisum*, metamorphosed consistently on only a single species (Haag and Warren 2003). Similarly, the Cumberland monkeyface, *Quadrula intermedia*, metamorphosed on only two minnow species in a single genus, but its sister species *Q. metanevra* metamorphosed on 21 minnow species in 11 genera (Yeager and Saylor 1995; Fritts et al., in press).

In an ecological sense, host use may be even more specific than indicated by laboratory host studies. The proportion of glochidia that metamorphose in laboratory trials often varies widely among fish species. Glochidia of *Fusconaia cerina* metamorphosed on 12 fish species, but metamorphosis was robust and consistent on only 6 species, suggesting that immunological compatibility of glochidia with the other 6 fishes is only marginal (Haag and Warren 2003). This type of variation in metamorphosis success among closely related host species is seen for many mussels, both specialists and generalists (e.g., Haag and Warren 1997; Rogers et al. 2001; Jones et al. 2004, 2010), indicating a gradient of immunological compatibility ranging from primary to marginal hosts. Host compatibility also shows coadaptation with local fish stocks such that metamorphosis success can be higher compared with individuals of the same fish species from more distant populations (Riusech and Barnhart 2000; Rogers et al. 2001; Eckert 2003). Within co-occurring populations of a mussel species and its primary host, metamorphosis is generally consistent and robust among individuals (Haag and Warren 2003). However, there can also be variation in metamorphosis success among individual fishes of a host species at a single site (Riusech and Barnhart 2000). In addition to immunological compatibility, some host relationships established in the laboratory may not be ecologically relevant if host species rarely encounter glochidia in the wild because of host habitat use or the type of glochidial release strategy used by a particular mussel species (Section 5.3).

There is one important exception to the phylogenetic basis of host use. Specialization of several species follows patterns of fish feeding behavior in addition to, or instead of, phylogenetic relationships among hosts. Nearly all mussel species that parasitize darters also use sculpins (*Cottus*), small benthic fishes that occupy a similar feeding niche as darters. One of the few exceptions is the birdwing pearlymussel, *Lemiox rimosus*, which appears to use only darters (Jones et al. 2010). The relative compatibility of darters versus sculpins varies. In some species, compatibility of darters and sculpins is similar (Yeager and Saylor 1995), but in others, either darters or sculpins appear to be marginal hosts (Michaelson and Neves 1995; Jones and Neves 2002; Jones et al. 2004), and a few species appear to specialize on sculpins (Zale and Neves 1982b, 1982c). It is curious that none of these species also use madtom catfishes (*Noturus*), which occupy a similar feeding niche as darters and sculpins. Some species of *Lampsilis* that specialize on black basses (*Micropterus*) also can metamorphose on other unrelated large, sight-feeding predators such as yellow perch (*Perca flavescens*), walleye and sauger (*Sander*), gar (*Lepisosteus*), and pikes (*Esox*) (Waller et al. 1985; Waller and Holland-Bartels 1988; Keller and Ruessler 1997). Similar to host use of darters and sculpins, the relative compatibility of these fishes compared to black basses varies. Northern pike (*Esox lucius*) was a marginal host for *L. higginsi* (Waller and Holland-Bartels 1988), and *L. ornata*, *Hamiota altilis*, and *Villosa vibex* (other specialists on black basses) did not metamorphose on pikes (Haag et al. 1999; Haag and Warren 2003). In contrast, the black sandshell, *Ligumia recta*, metamorphosed robustly only on sauger (*S. canadense*) and marginally on black basses and crappie (*Pomoxis*) (Khym and Layzer 2000), and the yellow sandshell, *Lampsilis teres*, metamorphosed more robustly on gar compared to black bass (Howard 1914; Keller and Ruessler 1997). Sunfishes (*Lepomis*), which are closely related to black basses but have different feeding behaviors, typically are unsuitable or marginal hosts for *Lampsilis* (Zale and Neves 1982b; Waller and Holland-Bartels 1988; Haag and Warren 2003). These patterns suggest that mechanisms of glochidial release and host attraction oriented toward specific fish feeding guilds (Section 5.3) have been important in the evolution of host specificity by influencing the frequency with which mussel glochidia encounter fishes (Section 5.1).

Another widespread but perhaps ecologically less important exception is the ability of glochidia of many specialists to metamorphose on topminnows (Fundulidae), livebearers (Poeciliidae), and sticklebacks (Gasterosteidae) in addition to their primary host fishes in other families. This pattern is evident for a large number of species, including at least the Anodontini, Lampsilini, and Pleurobemini (Young 1911; Neves et al. 1985; Haag and Warren 1997; O'Brien and Williams 2002; Allen et al. 2007), suggesting that these fishes are "universal hosts" for many otherwise specialist mussel species. However, topminnows, livebearers, and sticklebacks are nearly always marginal hosts that produce low and inconsistent glochidial metamorphosis. Furthermore, the surface-feeding habits of these fishes and their typical absence in open waters of streams may render them less vulnerable to infection by glochidia in the wild (Haag and Warren 1997).

Glochidia of specialists occur primarily on the gills of their hosts (Coker et al. 1921; Howard and Anson 1922). The hookless glochidia (Figure 5.1) of most specialists are considered adapted for attachment to soft gill tissue and poorly adapted for penetrating tougher fin and external tissues (Lefevre and Curtis 1910). These glochidia may have microscopic stylets or rows of micropoints along the shell margin that evidently aid in attachment to gills, but most species lack the prominent hooks of the Anodontini (Hoggarth 1999). In rare cases, glochidia of the Lampsilini occur on fish opercula or fins, but this occurs only on fishes that are heavily infected (Neves and Widlak 1988); however, glochidia that encyst on external surfaces may develop normally (Lefevre and Curtis 1910). The hooked glochidia of some specialists in the Anodontini also occur primarily on gills (e.g., *Alasmidonta viridis*, Zale and Neves 1982c; *Simpsonias* *ambigua* on *Necturus*, Howard 1915), but others occur in equal prevalence on external surfaces and gills (Gordon and Layzer 1993).

Apart from the Anodontini, glochidia with prominent hooks are found only in *Potamilus* (Lampsilini) (Figure 5.1), but these hooks are nonhomologous to those of anodontines and apparently arose independently (Hoggarth 1988; Roe and Lydeard 1998b). Despite the presence of hooks, glochidia of *Potamilus* attach only to gills (Coker and Surber 1911; Surber 1915; Roe et al. 1997). The prevalence of specialists on host gills is unexplained but may be related to mechanisms of resistance to host immune responses or the method by which females transmit glochidia to hosts.

5.3. Host infection strategies

Because glochidia are incapable of locomotion and survive only a few days after release (Section 1.4.C), mussels are faced with the problem of efficiently transferring glochidia to hosts. Specialists face the additional challenges of transmitting glochidia to a particular species and reducing the number of glochidia that encounter incompatible fishes. Apparent adaptations for host infection, including mantle lures and glochidial packets, have been noted for many years (e.g., Coker et al. 1921; Chamberlain 1934), but host infection formerly was thought to be largely a matter of chance (Arey 1932a; Chamberlain 1934). However, extensive research in the last 20 years has revealed a startling array of anatomical and behavioral adaptations for host infection. These strategies are highly concordant with patterns of host fish use and in many cases appear to target specific fish species or feeding guilds (Figure 5.3). Far from being left to chance, host infection is a highly developed, active process that has coevolved closely with patterns of host use. In the remainder of this chapter, I provide a description and functional classification of the diversity of host infection strategies of North American mussels (Table 5.1).

5.3.A. Broadcasting

Broadcasting involves release of glochidia into the water where they encounter hosts largely by chance. Broadcasters have no apparent adaptations to attract hosts to the gravid female mussel (Section 5.3.C), nor do they release glochidia in packets that resemble fish food items (Section 5.3.B). Broadcasting was formerly thought to be the primary mode of host infection (e.g., Arey 1932a; Chamberlain 1934). In reality, it appears that few species rely on this rather haphazard strategy (Figure 5.3). Because broadcasting infects hosts indiscriminately, many broadcasters are generalists, and indeed, nearly all Anodontini appear to be broadcasters. However, specialists in the Margaritiferidae also are broadcasters, and the prevalence of this strategy in these two basal groups suggests that broadcasting is a primitive trait (Figure 5.3). Broadcasting appears to have been retained or to have arisen secondarily in a limited number of

Table 5.1. *Summary of host infection strategies of North American freshwater mussels*

Strategy	Targeted fishes	Mussels known or suspected to use strategy
Broadcasting		
Passive entanglement	nonselective	*Alasmidonta, Amblema, Anodonta, Anodontoides, Elliptio, Lasmigona, Megalonaias, Popenaias, Pygandon, Strophitus,*[a] *Utterbackia*
Free glochidia	nonselective	*Anodonta implicata, Leptodea* (?), *Margaritifera, Pegias, Potamilus* (?), *Simpsonaias, Truncilla* (?)
Female sacrifice	molluscivores	*Leptodea leptodon (L. fragilis, Potamilus, Truncilla, Quadrula?)*
Conglutinates[b]		
Pelagic conglutinates	drift-feeding minnows	*Fusconaia, Plethobasus, Pleurobema, Pleuronaia*
Demersal conglutinates	benthic invertivores	*Cyprogenia, Dromus, Obliquaria, Ptychobranchus*
Mucoid conglutinates	catfishes	*Cyclonaias, Quadrula pustulosa* group
Superconglutinates	top predators	*Hamiota*
Mantle lures		
Large lures	top predators	*Hamiota, Lampsilis, Ligumia recta, Villosa*[c]
Cryptic lures	benthic invertivores	*Epioblasma, Lemiox, Ligumia nasuta, L. subrostrata, Medionidus, Obovaria, Toxolasma, Venustaconcha, Villosa*[d] *(Ellipsaria, Truncilla?)*
Mantle magazines	catfishes or minnows	*Cyclonaias, Quadrula*

[a] *Strophitus subvexus* and possibly *S. undulatus*.

[b] The unique conglutinates of *Strophitus undulatus* are not included in this classification (see text).

[c] *Villosa iris, V. nebulosa, V. vibex*, and probably *V. taeniata*.

[d] *Villosa lienosa, V. umbrans, V. vanuxemensis*; lures of other *Villosa* are unknown, but species such as *V. fabalis, V. perpurpurea*, and *V. trabalis* may have cryptic mantle lures.

species in all other major North American groups (Figure 5.3), but future research will likely reveal additional host attraction mechanisms in species currently considered by default to be broadcasters. Although I have described this strategy as haphazard, even broadcasters have adaptations to increase the likelihood of glochidia encountering hosts. For example, most broadcasters produce large numbers of glochidia; this strategy includes species with the highest fecundities known for North American mussels (Chapter 6). Other adaptations are reflected in two major types of broadcasting: passive entanglement and broadcast of free glochidia.

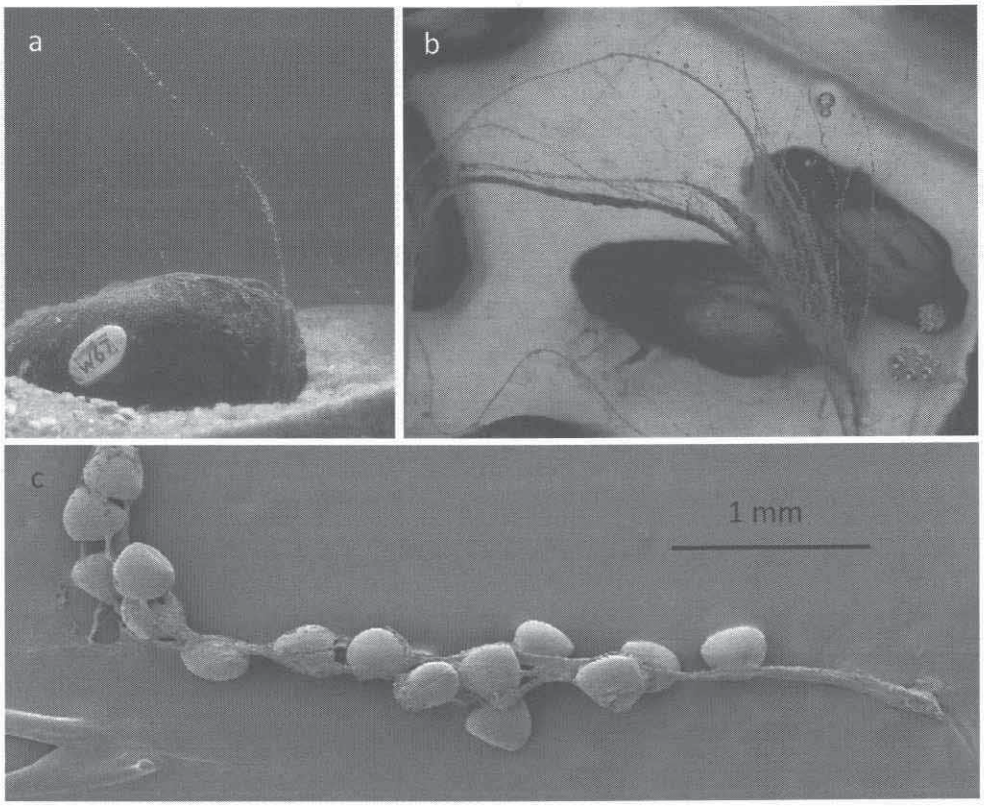

Figure 5.4. Mucus webs. (a) Single mucus strand with embedded glochidia released from a giant floater, *Pygandon grandis*; other strands are visible in the background (James Stoeckel, photo). (b) Mucus web of European *Unio pictorum*. (c) Scanning electron micrograph of mucus strand of *U. pictorum* showing embedded glochidia (b,c from Aldridge and McIvor 2003).

5.3.A.1. Passive entanglement

In most broadcasters, the probability of infection is increased either by releasing glochidia in mucus webs or strings or by larval threads produced by glochidia. These structures entangle fishes, bringing glochidia into proximity with the host (Lefevre and Curtis 1912; Wood 1974; Woody and Holland-Bartels 1993; O'Brien and Williams 2002; Aldridge and McIvor 2003). A proposed additional function is to provide drag to maintain glochidia in the water column; however, glochidia in webs or with larval threads sink readily to the bottom, but larval threads may allow them to be resuspended by passing fishes (Wood 1974). Mucus webs are released from the female mussel's exhalent aperture along with large numbers of glochidia entrained in the web. Webs are frequently seen streaming from the female mussel, and they may later snag on other objects (Matteson 1948; Aldridge and McIvor 2003; Figure 5.4). Prior to release, glochidia are associated with copious mucus in the female gills. The larval thread is extruded from a gland in the glochidial mantle and is adhesive and up to 2 mm long but can stretch approximately 9 times its length (Wood 1974). The thread disappears before metamorphosis and is not homologous to the byssus found in juvenile mussels (Arey 1921; Section 1.4.B.1). Threads often become entangled during release from the female, resulting in weblike masses of glochidia similar to mucus webs (Wood 1974; Roberts and Barnhart 1999; O'Brien and Williams 2002). Individual glochidia also may lie on the bottom with the valves agape and the larval thread floating up into the water, facilitating attachment to passing fishes (Wood 1974).

Larval threads are known in *Alasmidonta marginata*, *Amblema*, *Anodonta*, *Elliptio complanata*, *Lasmigona holstonia*, *Megalonaias*, *Popenaias*, *Pyganodon*, *Strophitus*, and *Utterbackia* (Coker et al. 1921; Wood 1974; Clarke 1985; Woody and Holland-Bartels 1993; Hoggarth 1999; Roberts and Barnhart 1999; O'Brien and Williams 2002; Carman 2007), all of which are considered both broadcasters and generalists. Larval threads are absent in most specialists that use other infection strategies. Release of glochidia entrained in mucus is reported for *Alasmidonta*, *Amblema*, *Anodontoides*, *Cumberlandia*, *Elliptio*, *Lasmigona*, *Popenaias*, *Pyganodon*, *Quadrula*, and *Strophitus* (Lefevre and Curtis 1910, 1912; Matteson 1948; Raulerson 1960; Haag and Warren 1997, 2003; Carman 2007; M. Hove and J. Stoeckel, personal communication). Again, most of these species are generalists, for which passive, indiscriminant infection of fishes seems an appropriate strategy. For some specialists, release of glochidia in mucus is associated with more complex behaviors targeting specific fish groups (e.g., *Quadrula*; Sections 5.3.B and 5.3.C). For other specialists, releases have been observed only in captivity and may be artifacts of laboratory conditions (e.g., *Elliptio arca*; Haag and Warren 2003); similar to *Quadrula*, the mode of release in the wild likely includes more complex behaviors that result in preferential infection of specific fishes.

Infection of fishes via entanglement by webs or larval threads has been observed primarily in the laboratory, but the distribution of glochidia on naturally infected fishes supports passive entanglement as a primary mode of infection in the wild. Glochidia of most generalists – including both hooked and unhooked glochidia – that appear to use passive entanglement attach primarily to external surfaces of fishes or, with equal frequency, to external surfaces and gills (Section 5.2.A). Furthermore, fishes that feed near the bottom are infected more frequently and carry greater glochidial loads than pelagic-feeding fishes (Martel and Lauzon-Guay 2005). Periods of highest infection of yellow perch (*Perca flavescens*) with glochidia of *Pyganodon grandis* coincided with springtime movement of perch from deep water to the littoral zone and subsequent shifts to suction feeding on benthic invertebrates in the substrate; fishes became heavily infected on the gills, fins, head, and gill covers (Jansen 1991), suggesting haphazard but frequent encounters with glochidia. In contrast, glochidia of most specialists that are proposed to broadcast webs based on laboratory observations (e.g., *Elliptio arca*; see previous discussion) occur exclusively on fish gills, suggesting that host infection is an active but as yet undocumented process targeting fish feeding behaviors.

5.3.A.2. Broadcast of free glochidia

Some broadcasters release free glochidia that have no apparent physical adaptations to increase chances of encounters with hosts. Broadcast of free glochidia is documented conclusively for few species, but these species share a common suite of adaptations that apparently help them overcome the long odds of glochidia encountering a host. The low probability of host encounters is compounded further because most of these species are host specialists. One solution to this problem is release of prodigious numbers of glochidia during a short time period; indeed, the highest fecundities recorded among freshwater mussels are produced by species that broadcast free glochidia (Chapter 6). Glochidial release by *Margaritifera margaritifera* is highly synchronous with nearly all individuals in a population releasing glochidia within 1–2 days (Hastie and Young 2003). In one population, glochidial abundance in the drift peaked at 27,654 glochidia/m^3 (Young and Williams 1984a), which is more than 3 orders of magnitude higher than peak densities reported for nonbroadcasting species (less than 20/m^3), which release glochidia over more protracted periods (Neves and Widlak 1988; Culp et al. 2011). Similarly, individual *M. falcata* released their entire complement of glochidia within about 50 s as a mass that disintegrated rapidly, resulting in large numbers of free glochidia drifting in the current (Murphy 1942). In the laboratory, the alewife floater, *Anodonta implicata*, rapidly expelled "clouds of glochidia" likened to "shotgun blasts" within 48 hours after water temperature reached 20°C (Davenport and Warmuth 1965). In *A. implicata* and European *A. anatina*, release of glochidia occurred simultaneously with spawning runs of their anadromous host fishes (alewife, *Pomolobus psuedoharengus*, and European smelt, *Osmerus eperlanus*, respectively; Davenport and Warmuth 1965; Anders and Wiese 1993), indicating that broadcast of free glochidia is timed to coincide with periods of high host density.

Two other specialists, the little-wing pearlymussel, *Pegias fabula*, and salamander mussel, *Simpsonaias ambigua*, have no known physical adaptations to facilitate glochidial transmission but have among the lowest fecundities of any freshwater mussel species (see Chapter 6). Both species are small (less than 40 mm) and occur typically under flat rocks (Section 4.2.A). In these confined habitats, they coexist closely with their hosts (*P. fabula*, darters and sculpins; *S. ambigua*, mudpuppy, *Necturus maculosus*). Many darters and sculpins reside under rocks (Greenburg and Holtzman 1987; Greenburg 1991), and sculpins spawn on the underside of rocks in early spring (Jenkins and Burkhead 1994), coinciding with the period of glochidial release for *P. fabula* (J. Layzer, personal communication). *Necturus maculosus* also lives under rocks (Petranka 1998) and may be collected simultaneously with *S. ambigua* (Howard 1915). In an October sample from the Mississippi River, 80 percent of *N. maculosus*

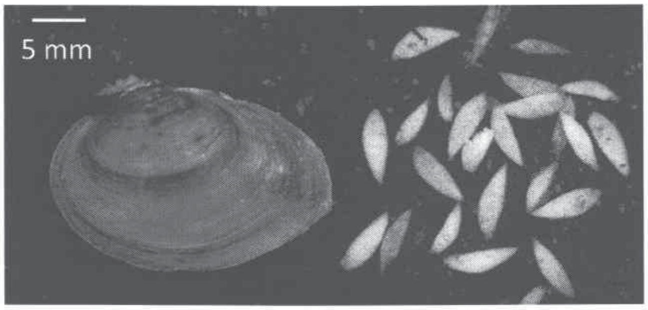

Figure 5.5. Conglutinates released by a female ovate clubshell, *Pleurobema perovatum* (W. R. Haag, photo).

were infected with glochidia of *S. ambigua* (Howard 1915). Living in close proximity to and in confinement with their hosts appears to make broadcasting a small number of free glochidia an effective host infection strategy for these species (but see Section 5.3.D).

Host infection strategies are poorly known for several important components of mid-sized- and large-stream mussel assemblages, including *Actinonaias, Ellipsaria, Leptodea, Potamilus*, and *Truncilla*. All of these species, except *Actinonaias*, are specialists on freshwater drum, and recent evidence suggests that they employ both active and passive strategies to target these fishes (Section 5.3.D). Host use and infection strategies of *Actinonaias* remain poorly known. Glochidia can metamorphose on black basses and sauger but also on sculpins (Layzer and Khym 2003–2004; J. Jones, personal communication), suggesting that they may be generalists. Although closely related to *Lampsilis* (Campbell et al. 2005), *Actinonaias* apparently have no modified mantle lure (Section 5.3.C); very rarely, females may show slight modification of the mantle margin, but this is absent in most individuals (B. Sietman, personal communication). Furthermore, *Actinonaias* have high fecundity (Chapter 6), and mature glochidia brooded in female gills are not associated with mucus (B. Sietman, personal communication; W. R. Haag, observations). These traits are suggestive of broadcast of free glochidia, but this behavior has not been observed. *Actinonaias* is a dominant and perhaps keystone member of many mussel assemblages (Chapter 8), and a better understanding of its reproductive biology is sorely needed.

5.3.B. Conglutinates

Many mussel species release glochidia in discrete clusters called conglutinates. Conglutinates have been referred to also as *placentae* or *ovisacs* (see Barnhart et al. 2008). In general, conglutinates are molded in the water tubes of the female gill during brooding, and they retain the shape of the tubes after release (Lefevre and Curtis 1910; Figure 5.5). However, a wide variety of nonhomologous conglutinate structures exists, and functional conglutinates occur in all major mussel lineages, except the Margaritiferidae, suggesting that conglutinate production carries a strong selective advantage and arose multiple times (Figure 5.3; Barnhart et al. 2008; Watters 2008b). Functional conglutinates mimic food items of host fishes – often to a remarkable degree – thereby facilitating host infection. Furthermore, by exploiting specific predator–prey relationships of hosts, many conglutinates appear to reduce the probability of glochidia infecting incompatible fishes.

In addition to functional conglutinates, many species abort conglutinate-like structures in response to stress or disturbance, but these apparently have little or no role in host infection. These structures are referred to as *puerile conglutinates* because they are often composed of eggs or developing embryos; adhesion between egg membranes provides structure (Barnhart et al. 2008). Puerile conglutinates are released by many species, including those that also produce functional conglutinates, but are especially prevalent in the Pleurobemini and Quadrulini (Lefevre and Curtis 1910, 1912; Yeager and Neves 1986; Haag and Warren 2003). The adaptive significance of this behavior is unclear, but it may be a stress response to alleviate reduced respiratory efficiency in brooding females (Aldridge and McIvor 2003). This idea is supported by the absence or rarity of such behavior in the Anodontini, in which brooding females develop secondary water tubes, and in the Lampsilini, which brood glochidia in only a portion of the gills (Section 1.4.C.3). Because they often contain no mature glochidia capable of attaching to fish, puerile conglutinates clearly do not serve to infect hosts.

Some Lampsilini that infect hosts primarily by mantle lures (Section 5.3.C) also may release loose conglutinates composed of mature glochidia. These conglutinates usually disassociate readily because egg membranes weaken or dissolve when glochidia mature. These aggregates are typically released late in the brooding season, apparently to make room for the next brood, but also may represent a secondary strategy for host infection (Barnhart et al. 2008). In laboratory experiments, pondmussels, *Ligumia subrostrata*, released conglutinates only after a lengthy period of lure display and when display frequency decreased to less than 30 percent of peak levels (Gascho-Landis et al., in press). Conglutinates produced by lure-displaying species are simple, unadorned structures that appear to represent little, if any, additional cost to female mussels. In contrast, functional conglutinates of other species that represent a primary strategy for host infection may incur a substantial cost to females either by encasing glochidia in elaborate, pigmented membranes or by the presence of nondeveloping structural eggs, which decrease fecundity by up to 50 percent (see subsequent discussion). Consequently, conglutinate release in lure-displaying species appears to be a secondary, bet-hedging strategy to reduce wastage of glochidia that ultimately must be released to make room for the subsequent brood and perhaps also to minimize oxygen stress associated with brooding or lure display in summer (Gascho-Landis et al., in press).

Other species that produce functional conglutinates have no other apparent adaptations for host attraction, suggesting that conglutinates are a primary infection strategy. Conglutinates are essentially broadcast from the female mussel (except for mucoid conglutinates; Section 5.3.B.3) but unlike broadcasting (sensu Section 5.2.A), conglutinates appear to be a highly effective and targeted strategy for infecting hosts. Accordingly, species that produce functional conglutinates produce far fewer glochidia than broadcasters (Chapter 6). Only *Hamiota* and some Quadrulini use functional conglutinates in conjunction with mantle lures (Sections 5.3.B.4 and 5.3.B.5). Functional conglutinates encompass four distinct host attraction strategies that target specific fish feeding guilds and include one notable outlier.

5.3.B.1. Pelagic conglutinates

Pelagic conglutinates are small, simple structures that drift in the current. These conglutinates are generalized mimics of small aquatic or terrestrial invertebrates such as flatworms, small leeches, or oligochaetes (Figure 5.5; Plate 13). Pelagic conglutinates are known only in *Fusconaia*, *Pleurobema*, *Pleuronaia*, and potentially *Plethobasus* (all Pleurobemini), occurring in all species that have been studied, and their structure is similar in most species. Pelagic conglutinates are composed of the contents of a single female gill water tube and are either lance shaped or oval; average 5–9 mm long and 1–4 mm wide; and are composed of one or two layers of eggs, resulting in a flattened or subcylindrical cross section (Bruenderman and Neves 1993; Haag and Warren 1997; O'Brien and Williams 2002; Layzer et al. 2003; White et al. 2008). Conglutinate color varies among species and can be red, orange, pink, gray, tan, or white, but conglutinates are usually uniformly colored and have no additional ornamentation. Within a species, conglutinate color may be polymorphic, varying among but not within individuals (Haag and Warren 2003). Individual females produce an average of 84–135 conglutinates, each containing 101–420 mature glochidia (Bruenderman and Neves 1993; Hove and Neves 1994; Haag and Staton 2003).

A characteristic of pelagic conglutinates in nearly all species is the presence of a high percentage of undeveloped eggs. In conglutinates of *Fusconaia cerina* and *Pleurobema decisum*, about 50 percent (range = 18–66) of eggs never develop (Haag and Staton 2003). Earlier workers attributed this to sperm limitation and poor fertilization success (Lefevre and Curtis 1912). It is now apparent that undeveloped eggs are necessary to maintain the structural integrity of the conglutinate, providing a matrix formed by adhesion among the egg membranes (Haag and Warren 2003; Barnhart et al. 2008; Watters 2008b). The mechanism preventing structural eggs from developing is unknown. Normally developing eggs are scattered throughout this matrix, but their egg membranes degenerate on maturity, allowing glochidia to be liberated easily from the conglutinate (Plate 13). Mature glochidia are colorless, but pigment within undeveloped eggs imparts the color to these conglutinates (Lefevre and

Curtis 1910, 1912). A single exception to the prevalence of undeveloped eggs is reported for the fine-rayed pigtoe, *F. cuneolus* (Bruenderman and Neves 1993). With the exception of *Cyprogenia* and *Dromas* (Section 5.3.B.2), undeveloped eggs are rare in species that do not produce pelagic conglutinates (Haag and Staton 2003).

Nearly all species that produce pelagic conglutinates are specialists on drift-feeding minnows, especially *Cyprinella* and *Notropis* (Bruenderman and Neves 1993; Haag and Warren 1997, 2003; Layzer et al. 2003; White et al. 2008), and this release strategy is strongly oriented for selective infection of these fishes. Within a population, glochidial release is loosely synchronous, occurring over 2–3 months from late spring to summer, but is punctuated by one or two brief periods of mass conglutinate release (Neves and Widlak 1988; Weaver et al. 1991; Bruenderman and Neves 1993; Hove and Neves 1994; Culp et al. 2011). In the wild, female *Fusconaia cerina* and *Pleurobema decisum* forcibly and rapidly eject conglutinates approximately 15–20 cm into the water, where they drift with the current well above the bottom; during release periods, large numbers of drifting conglutinates are present in the mid-water column in deep riffles and runs (Haag and Warren 2003). Drift-feeding minnows, such as *Cyprinella*, are sight feeders that forage predominantly in the middle to upper water column on small, drifting invertebrates (Baker and Ross 1981; Ross 2001). In confined laboratory settings, a wide variety of host and nonhost fish species, including minnows, darters, and sunfishes, will ingest pelagic conglutinates (Haag and Warren 2003; Layzer et al. 2003). However, in the wild, only *Cyprinella* have been observed attacking these conglutinates (Haag and Warren 2003). Similarly, naturally occurring glochidial infestations of *Fusconaia, Pleurobema*, and *Pleuronaia* are found most commonly on drift-feeding minnows but are uncommon or absent on benthic minnows (e.g., *Campostoma anomalum, Erimystax* spp., *Hybopsis amblops, Phenacobius uranops*), sculpins, sunfishes, and darters (Neves and Widlak 1988; Weaver et al. 1991; Bruenderman and Neves 1993; Hove and Neves 1994). These observations support pelagic conglutinates as a highly targeted strategy that decreases encounters with incompatible fish species.

5.3.B.2. Demersal conglutinates

Demersal conglutinates are often complex structures that remain in close proximity to the stream bottom. These conglutinates resemble a variety of food items of benthic fishes and include some of the most elaborate mimicry seen in host infection strategies. Demersal conglutinates occur only in *Cyprogenia, Dromus, Obliquaria*, and *Ptychobranchus* (all Lampsilini). They are composed of the entire contents of a single female gill water tube, but other aspects of their structure vary widely among genera, suggesting that this release strategy arose independently in different lineages. With the likely exception of the threehorn wartyback, *Obliquaria reflexa*, species that produce these conglutinates are specialists on benthic feeding darters or sculpins.

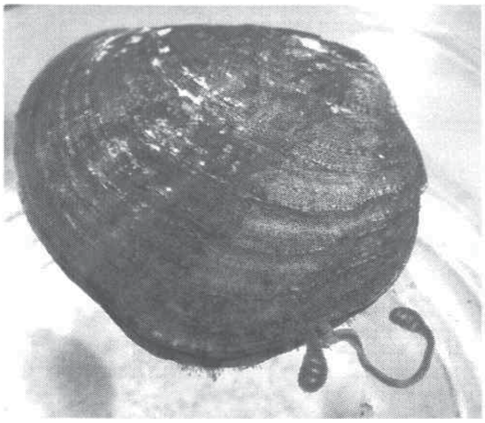

Figure 5.6. Wormlike conglutinates being released from female western fanshell, *Cyprogenia aberti* (Chris Barnhart, photo).

Cyprogenia and *Dromus* produce large conglutinates similar in structure to pelagic conglutinates (Lefevre and Curtis 1912; Chamberlain 1934; Jones and Neves 2002; Eckert 2003; Jones et al. 2004). Structure and color are imparted by undeveloped eggs, which constitute about 50 percent of the conglutinate. Unlike pelagic conglutinates, the undeveloped eggs form a central structural core surrounded by mature glochidia on the outer surface. Conglutinates of the dromedary mussel, *Dromus dromas*, are flattened; 20–50 mm in length; 4–7 mm wide; red, pink, or white; and resemble leeches. Individual females produce 33–151 conglutinates, each containing 519–1,892 glochidia. Conglutinates of *Cyprogenia* are wormlike; 20–80 mm in length; 1–4 mm wide; and brick red, pink, brown, or white (Plate 14), but conglutinate size and color vary within and among populations. The basal end of *Cyprogenia* conglutinates is expanded into a slotted, ribbed head composed mostly of undeveloped eggs; the percentage of mature glochidia increases toward the proximal end and is nearly 100 percent at the tip. Individual females produce 1–33 conglutinates, each containing 2,800–5,272 glochidia. Release of demersal conglutinates by *Cyprogenia* and *Dromus* differs in important ways from release of pelagic conglutinates. Conglutinates are released singly from the exhalent aperture, each requiring 3–12 hours; during this time, conglutinates protrude from the aperture and wave in the current, resembling tubificid worms (in *Cyprogenia*; Figure 5.6), and then they fall to the bottom after release is complete. Both in the wild and in captivity, fishes have been observed seizing partially extruded conglutinates and pulling them from the mussel and also feeding on released conglutinates that were lying on the bottom (Chamberlain 1934; M. C. Barnhart, personal communication).

Ptychobranchus produces small, elaborate conglutinates that mimic food items of darters and sculpins to an astonishing degree (Luo 1993; Hartfield and Hartfield 1996; Barnhart and Roberts 1997; Haag and Warren 1997; Watters 1999; Plate 14).

A high percentage of eggs develop into mature glochidia; therefore adhesion among undeveloped eggs does not provide structure. Instead, glochidia are encased in a pigmented sac made up of three layers of membranes, which contains the entire glochidial contents of a single gill water tube. Shape and pigmentation vary among and within species, but all *Ptychobranchus* conglutinate types share two features: (1) the adhesive proximal end of the conglutinate, which acts as a holdfast to anchor conglutinates to the substrate after release, and (2) the presence of eyespots or dark lateral stripes, which represent zones of weakness in the sac membranes. When pressure is exerted on the conglutinate, the membranes rupture in these zones, ejecting glochidia from the sac. In the kidneyshells, *P. fasciolaris* and *P. occidentalis*, conglutinates are cylindrical, 7–15 mm in length, and strongly resemble larval fishes. Mimicry is heightened by eyespots on the swollen distal "head," dark lateral bands suggesting myomeres (parallel bundles of muscles visible on the flanks of small fishes), and the tapered proximal end. Within a population of *P. fasciolaris*, smaller individuals may produce a smaller conglutinate form that differs in coloration from the form produced by larger individuals. Conglutinates of the triangular kidneyshell, *P. greeni*, also occur in two forms within a single population, but an individual produces only a single form. One form resembles the elongate conglutinates of *P. fasciolaris* and *P. occidentalis*, but the other form is round and pearl colored with two distinct eyespots and strongly resembles a developing fish egg. The relationship of these conglutinate forms to female body size or other variables, or whether they represent two distinct species, is unknown. Conglutinates of the fluted kidneyshell, *P. subtentum*, represent perhaps the most detailed mimicry of any species. Pigmentation patterns bear an uncanny resemblance to a blackfly pupa. In all species, conglutinates fall quickly to the bottom after release, where they stick to pebbles or other substrata, and predation of *P. occidentalis* conglutinates by darters (*Etheostoma* spp.) has been observed in the laboratory.

Obliquaria reflexa produces large, distinctive conglutinates that combine features of other demersal conglutinates (Lefevre and Curtis 1912; Haag and Staton 2003; Watters 2008b). A high percentage of eggs develop into mature glochidia, but unlike other species with this trait, eggs membranes of even mature glochidia remain intact and are bound tightly to each other. The strong adhesion between egg membranes imparts an elastic rigidity to these conglutinates and makes it difficult to disassociate glochidia even with a sharp probe. Conglutinates are tubular and slightly curved, about 20–40 mm in length and 3 mm in diameter, and uniformly white. Females produce an average of only eight conglutinates, each containing about 3,000–5,000 glochidia. Conglutinates are released singly and, during release, often protrude partially from the exhalent aperture, similar to *Cyprogenia*. Conglutinates are strongly negatively buoyant and sink rapidly to the bottom after release (W. R. Haag, observation). Within a population, release occurs fairly synchronously over several weeks, during which time conglutinates may be seen strewn over the stream bottom.

Release of demersal conglutinates is a strategy oriented strongly toward parasitization of benthic fishes. *Cyprogenia, Dromus*, and *Ptychobranchus* occur primarily in riffles with coarse sand and gravel substrates in close proximity to their darter and sculpin hosts. In such habitats, presentation of partially extruded conglutinates from the exhalent aperture or release of adhesive conglutinates ensures that glochidia remain among bottom substrates, where they are vulnerable to predation by small benthic fishes but less vulnerable to drift-feeding minnows. Furthermore, the small size of *Ptychobranchus* conglutinates coupled with their detailed mimicry of common darter and sculpin food items reinforces their appeal to these fishes, while reducing their attractiveness to large predators. In addition to their well-known insectivory, many darters and sculpins prey heavily on fish eggs and newly hatched fry (Boschung and Mayden 2004), and spawning of many fish species coincides closely with release of *Ptychobranchus* conglutinates (W. R. Haag, observation).

Hosts for *Obliquaria reflexa* are unknown, but the similarity of the species' distribution and habitat preference to *Leptodea, Potamilus*, and *Truncilla* suggests that *O. reflexa* also parasitize freshwater drum (Section 5.3.D). However, nearly metamorphosed glochidia of *O. reflexa* were found on the gills of goldeye (*Hiodon alosoides*) (Barnhart and Baird 2000), a predaceous fish with well-developed teeth on the tongue and jaws. Use of either fish species could explain the puzzling difficulty with which glochidia are liberated from the conglutinates of *O. reflexa*. These large, demersal conglutinates could be preyed on by a wide variety of fishes, but crushing (drum) or tearing (goldeye) may be required to liberate glochidia; this adaptation would reduce the potential for attachment to incompatible hosts. Regardless, the small number of conglutinates produced and low fecundity suggest that the infection strategy of *O. reflexa* is highly efficient.

5.3.B.3. Mucoid conglutinates

Mucoid conglutinates also are strongly associated with the stream or lake bottom, but all other aspects of their construction and release differ from demersal conglutinates. Mucoid conglutinates are large, unpigmented, poorly consolidated conglomerations of glochidia and mucus that appear to be generalized mimics of caterpillars, large aquatic insect larvae, or large worms (Plate 20). Mucoid conglutinates also differ from other conglutinate types in that they are extruded from the gills and stored in a "mantle magazine" just prior to release (Section 5.3.C.3). These conglutinates are known only in the Quadrulini in *Cyclonaias* and the *Quadrula pustulosa* group; mucoid conglutinates have not been observed in the *Q. quadrula* group or *Q. verrucosa*, and the *Q. metanevra* group appears to release free glochidia, but all of these species also have mantle magazines. Species that produce mucoid conglutinates have comparatively low fecundity, generally producing fewer than 50,000 glochidia (Chapter 6).

Conglutinate structure is provided by the loose mucus matrix within which glochidia are contained, but unfertilized, structural eggs are absent, and conglutinates have no encasing membrane (Haag and Staton 2003). Mucoid conglutinates contain the contents of multiple gill water tubes and possibly the entire gill contents, similar to superconglutinates of *Hamiota* (Section 5.3.B.4). Mucoid conglutinates produced by pimplebacks, *Quadrula pustulosa*, in the Little Tallahatchie River, Mississippi, were about 35–70 mm long, 20 mm wide, and 10 mm thick (W. R. Haag, observations). The mucus matrix was clear to milky with discrete white masses of glochidia embedded within. Glochidial masses were widely spaced and arranged in two diffuse, parallel rows separated by a central region without glochidia. Each mass apparently represents the contents of a single gill water tube, and each row represents a series of adjacent gravid water tubes from a single gill. A single conglutinate released from a 37.8 mm female contained an estimated 19,750 glochidia (95% confidence interval = 8,492–31,008); the confidence interval around this estimate contains the predicted total fecundity for a 37.8 mm female (9,285 glochidia) based on a length–fecundity relationship for the same population (Haag and Staton 2003). The gills of this female were empty when collected after release of the conglutinate, further suggesting that the entire gill contents were deposited. Mucoid conglutinates of *Cyclonaias* are similar in structure but can be up to 200 mm long, and they also appear to contain the entire contents of the gravid gills (Sietman et al., 2012; Plate 20).

All species that produce mucoid conglutinates are specialists on catfishes, and the large size and benthic nature of these conglutinates are likely efficient for targeting these fishes. Conglutinate release can be triggered by touching the displayed mantle magazine or by attacks on the magazine by host fishes (Barnhart et al. 2008; Sietman et al., 2012; Section 5.3.C.3). Release occurs rapidly (less than 2 s), during which conglutinates swell as they emerge from the exhalent aperture, likely due to an osmotic gradient between the internal environment and the surrounding water (W. R. Haag, observations; see Section 5.3.B.5). Mucoid conglutinates also were observed streaming from the exhalent aperture of *Cyclonaias* (Sietman et al., 2012; Plate 20), bearing further similarity to superconglutinates of *Hamiota*. After release, conglutinates are extremely pliant, and they quiver in response to slight currents or touch. Conglutinates are negatively buoyant but are suspended readily by currents and settle to the bottom in a darting and undulating manner resembling a large, swimming alderfly or mayfly larvae. Release of conglutinates by *Q. pustulosa* in Mississippi in late June to early July coincided with a large hatch of burrowing mayflies (*Hexagenia* sp.), and free conglutinates were found lying on the stream bottom among shed mayfly exuvia during this time (W. R. Haag, observation).

5.3.B.4. Superconglutinates

Superconglutinates are large conglutinates produced only by the genus *Hamiota* (Lampsilini) (Haag et al. 1995, 1999; Hartfield and Butler 1997; O'Brien and Brim Box 1999; Blalock-Herod et al. 2002; Plate 15). This remarkable strategy was unknown to the scientific community until its discovery in 1988 by Robert S. Butler.

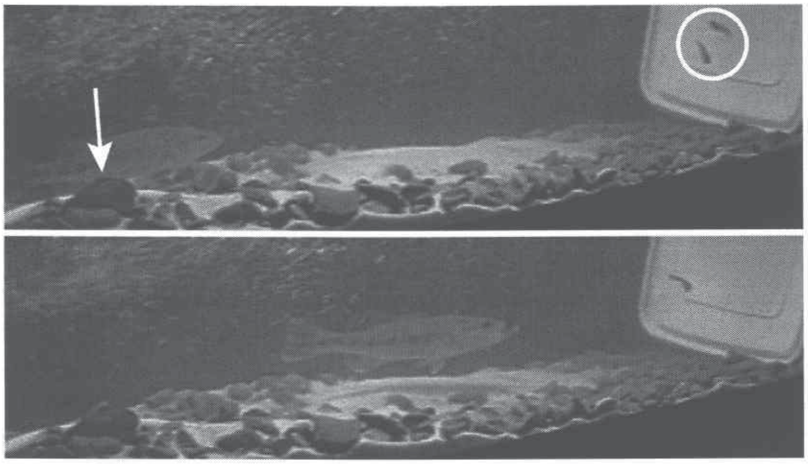

Figure 5.7. Superconglutinates of the orange-nacre mucket, *Hamiota perovalis*. (top) Female mussel (arrow) in aquarium with dissociated superconglutinates (circle) trailing by mucus tether (not visible). (bottom) Redeye bass (*Micropterus coosae*) attacking superconglutinate (W. R. Haag, photos).

Superconglutinates are about 30–50 mm long and contain the entire glochidial contents of a single gill. They are released simultaneously in pairs such that nearly the entire reproductive complement of a female mussel is released at one time. Glochidia are contained within a pigmented membrane that often includes an eyespot and lateral stripe invoking a strong resemblance to a small fish. Glochidia are arranged in a series of closely spaced parallel segments each representing the contents of an individual gill water tube. This arrangement imparts a resemblance to the myomeres of a small fish. After release from the gills, each superconglutinate is deposited at the end of a clear mucus tube 10–15 mm in diameter and up to 2.5 m in length, which is tethered to the female mussel through the exhalent aperture. The two tubes are joined initially but disassociate later, resulting in two tubes emanating from the female (Figure 5.7). Release usually begins in the morning and requires about 1.5–4 hours to deploy the superconglutinates fully. The tethered lures dart erratically in stream currents, creating a remarkable resemblance to a distressed fish. In contrast to the protracted release period of other lampsilines (Section 5.3.C), superconglutinate release occurs somewhat synchronously within populations, over 5–6 weeks in spring or early summer. All four species that produce superconglutinates are host specialists on black basses (*Micropterus* spp.).

Release of superconglutinates is oriented strongly toward transmission of glochidia to large piscivorous fishes such as black basses. Attacks by bass on superconglutinates of the orange-nacre mucket, *H. perovalis*, were observed in the laboratory, and infection occurs after fishes briefly ingest the conglutinate (Haag and Warren 1999; Figure 5.7). This mode of transmission reduces infection of smaller or nonpiscivorous fish species that are incompatible hosts. Superconglutinates are durable and remain intact after fish attacks, and multiple fishes may be infected by a single superconglutinate. Superconglutinates and their mucoid tether can become detached from the female but later snag on woody debris, where they continue to display fishlike motion and presumably remain attractive to hosts for several days (Haag et al. 1995, 1999). The tether persists for several weeks, but glochidial packets disintegrate in about 3 days, and glochidia are viable for only 4–5 days at water temperatures of about 20°C (O'Brien and Brim Box 1999). The fine-lined pocketbook, *Hamiota altilis*, also has a well-developed, large mantle lure similar to *Lampsilis* (Section 5.3.C.1) that is displayed prior to release of superconglutinates; therefore this species appears to attract and infect hosts using both lure and superconglutinate strategies (Haag et al. 1999). Mantle lures are absent or greatly reduced in other *Hamiota* (Hartfield and Butler 1997), indicating increased specialization for infecting hosts solely via superconglutinates.

5.3.B.5. Strophitus undulatus

The odd conglutinates of the creeper, *Strophitus undulatus*, have been known for more than 150 years, but they are not easily classified with regard to their function (Watters 2002; Barnhart 2010; Plate 16). These are the only conglutinates known to be produced within the Anodontini (but see subsequent discussion), and their structure differs from all other conglutinate types. Conglutinates of *S. undulatus* are milky, translucent, and rod shaped; 3–7 mm long by 0.3–0.4 mm wide; and composed of a homogeneous, adhesive mucoid matrix within which are embedded 1–15 glochidia. After release from the hypertonic gill fluid, conglutinates swell in the hypotonic ambient environment, causing them to writhe and quiver for several minutes until osmotic equilibrium is reached. Osmotic pressure also forces glochidia through pores to the external surface of the conglutinate, at which time they open their valves widely, but they remain tethered to the conglutinate by a larval thread. Other *Strophitus* do not produce conglutinates, but phylogenetic relationships of these species are poorly known.

Unlike other conglutinate producers, *S. undulatus* is a host generalist (van Snik Gray et al. 2002), and their unusual conglutinates may infect hosts in two different ways, combining active and passive infection strategies. First, they may mimic maggots or other insect larvae, and the writing motion could elicit attacks from many fish species (Watters 2002). Second, the hooked glochidia of *S. undulatus* attach readily to fish fins, and the adhesive nature of these conglutinates combined with the external placement of glochidia may facilitate passive infection of hosts (Barnhart 2010). Similar conglutinates are reported for the generalists, *Lasmigona*, in which glochidia are tethered to a core of undeveloped eggs rather than a mucoid matrix (Watters 2008b). However, release of these conglutinates has not been observed, and gravid *Lasmigona* typically have a low percentage of undeveloped eggs (Lefevre and Curtis 1910, 1912).

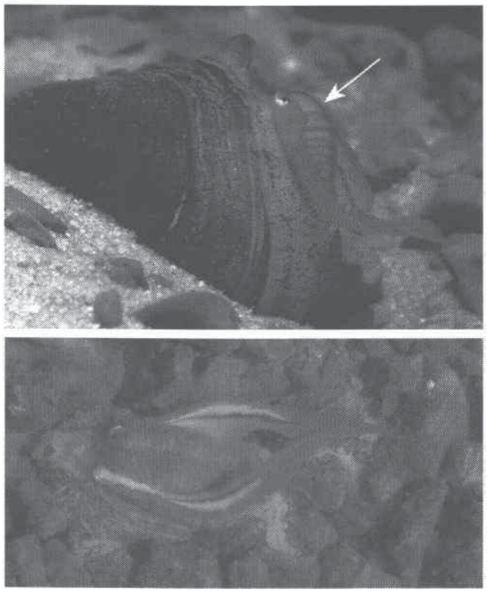

Figure 5.8. (top) Mantle lure display of the plain pocketbook, *Lampsilis cardium*, in an aquarium; note conspicuous eyespot and gravid gill (arrow; from Haag and Warren 1999). (bottom) Display of the pocketbook, *L. ovata*, in the wild; large pads between the flaps are the gravid gills (Paul Freeman, photo).

5.3.C. Mantle lures

Mantle lures include the most spectacular, varied, and widely known mussel host infection strategies. These lures are displayed by gravid female mussels and mimic an array of fish prey items. Fishes attack the lures, resulting in release of glochidia and infection of hosts. Mantle lures are known only in the Lampsilini and Quadrulini. In the Lampsilini, the lure is a permanently modified portion of the inner lobe of the female mantle margin located anterior to the inhalent aperture and elaborated into pigmented flaps or papillae (Kraemer 1970; Figure 5.8); in some species, the gravid gills also constitute part of the lure. In the Quadrulini, the exhalent aperture is modified into a lure (Section 5.3.C.3). Lures are displayed only when females are gravid and lie retracted within the shell during nongravid periods; mantle margins or apertures of males are not modified or displayed (Kraemer 1970).

Mantle lures are predominant and have diversified most widely in the Lampsilini and are diagnostic of several genera (Figure 5.3). Mantle lures are proposed to have appeared early in the evolution of the Lampsilini and were lost subsequently in several clades (e.g., *Actinonaias*, *Cyprogenia* + *Dromas*, *Leptodea* + *Potamilus*) (Zanatta and Murphy 2006). The structure and function of Quadrulini mantle lures differ fundamentally from lampsiline lures, suggesting that they arose independently. All species that use mantle lures are host specialists, and lure morphology targets specific fish feeding guilds, reducing transmission of glochidia to incompatible species. With the exception of some Quadrulini, lure displayers produce moderate to large numbers of glochidia (Chapter 6). Mantle lures can be classified into three groups based on their structure and the types of fishes they attract.

5.3.C.1. Large lures

The largest and most conspicuous mantle lures are produced by species that parasitize top predators such as black basses (*Micropterus*), rock basses (*Ambloplites*), and walleye and sauger (*Sander*). Large mantle lures occur only in the Lampsilini in *Hamiota altilis*, *Lampsilis*, *Ligumia recta*, *Villosa iris*, *V. nebulosa*, *V. vibex*, and probably other *Villosa* such as *V. taeniata*. These lures mimic fish prey items, such as small fishes, crayfish, or large insect larvae such as hellgrammites, or consist of generalized, large arrays of flaps and papillae (Plate 17). Lures can be more than 75 mm in length and usually are elaborately pigmented, often with a distinctive eyespot and lateral stripe. Lures are generally similar within species, but the wavy-rayed lampmussel, *Lampsilis fasciola*, can have at least four distinct lure morphologies within a single population (Zanatta et al. 2007b). Similarly, *Hamiota altilis* may exhibit two radically different lures (P. Johnson, personal communication; Plate 17). Lures often are partially amputated or torn, suggesting damage from past fish attacks (Figure 5.9).

In captivity, displaying *Lampsilis* often assume a headstand pose, with one-third to one-half of the shell exposed above the substrate surface (Kraemer 1970; Barnhart and Roberts 1997; Haag et al. 1999). In the wild, females usually remain fully buried with only the lure visible above the substrate (Zanatta et al. 2007b; Figure 5.8). In *Villosa* and *Ligumia recta*, displaying females are usually completely exposed, lying on top of the substrate or under the edge of large, flat rocks (Haag et al. 1999; C. Barnhart, personal communication). During full display, the gravid gills protrude conspicuously beyond the shell margin between the mantle lobes, and the lobes are flapped or pulsated in intermittent, rhythmic bursts (Kraemer 1970; Haag and Warren 1999). In the rainbow, *Villosa iris*, lure display is accompanied by a rocking motion of the entire animal; this behavior, along with the pigment pattern of the lure and the fluttering of long, tentacle-like papillae, bears a striking resemblance to a live crayfish (Plate 17; Barnhart 2010). Periods of full display and lure movement are punctuated by periods of relative inactivity, during which the lures may be retracted completely or only partially displayed (Haag and Warren 2000).

Daily rhythms of lure display vary among species. Displays of two sympatric species of *Villosa* overlapped little in the laboratory and in the wild; Alabama rainbows, *V. nebulosa*, displayed only at night, while southern rainbows, *V. vibex*, displayed mostly by day (Haag and Warren 2000). In the laboratory, display frequency of the plain pocketbook, *Lampsilis cardium*, decreased with decreased light intensity, but sympatric *L. reeviana* and *L. siliquoidea* displayed vigorously in the dark (Kraemer 1970). Segregation of display time may be a mechanism to avoid host competition among species with similar host use (Section 8.3.B).

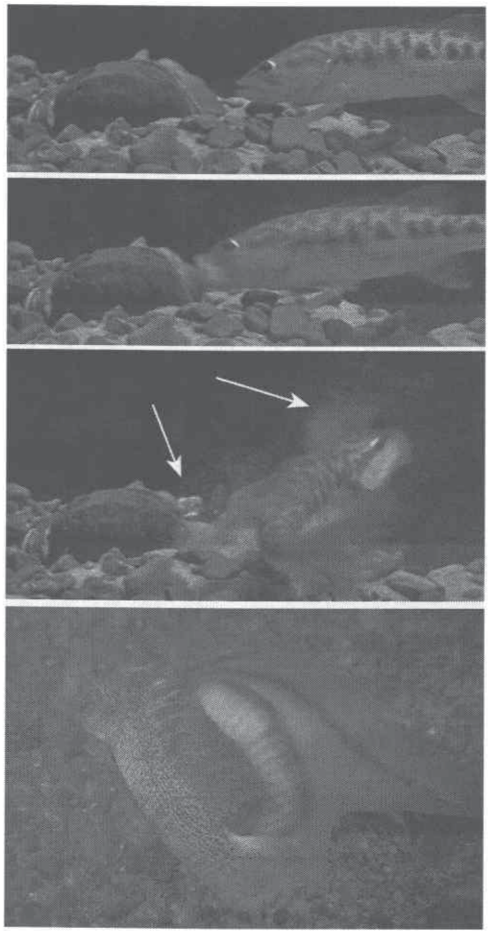

Figure 5.9. Redeye bass (*Micropterus coosae*) attacking mantle lure of a plain pocketbook, *Lampsilis cardium*. Arrows show glochidia liberated from gill during attack (from Haag and Warren 1999). (bottom) Lure of *L. cardium* showing amputation of distal portion of left mantle flap from previous fish attack (Bernard Sietman, photo).

Large lures have been reported in the scientific literature for over a century, but their role in host infection remained controversial despite their remarkable resemblance to fish prey items. Some early workers recognized their function as a lure for host fishes (Wilson and Clark 1912; Coker et al. 1921; Howard and Anson 1922), but other functional explanations included aeration of glochidia within the gills (Ortmann 1911), fanning sperm into the female apertures (Utterback 1931), and suspending glochidia in the water column (Kraemer 1970). These other functions have been refuted, and recent studies have confirmed that lures elicit attacks from fishes, resulting in host infection (Haag and Warren 1999, 2000; Barnhart et al. 2008; Figure 5.9). Transmission of glochidia occurs only when fishes rupture the gravid gill during attacks, explaining the conspicuous placement of the gills between the mantle lobes. Unlike mantle magazines (Section 5.3.C.3), simply touching the lure causes it to retract and does not cause glochidial release, and chemical or other cues associated with fish presence similarly do not appear to stimulate release. In a laboratory experiment, *Villosa vibex* released large numbers of glochidia only when fish had physical access to displaying mussels and not when physical access was denied, even though water flow between fish and mussels was unimpeded (Haag and Warren 2000). Consequently, gravid females confined in the laboratory in the absence of host fishes display lures for months without releasing glochidia (Howells 2000; W. R. Haag, observations).

Large lures reduce transmission of glochidia to incompatible fish species in two ways. First, because large lures mimic prey items of top predators, they likely are less attractive to other species. Second, although incompatible fish species occasionally may be attracted to and even attack large lures (Coker et al. 1921; Haag and Warren 1999), the necessity of rupturing the gravid gill likely reduces glochidial transmission. *Villosa vibex* released fewer glochidia in the presence of nonhost minnows (*Cyprinella camura*) than with a host species, largemouth bass (*Micropterus salmoides*), suggesting that attacks from smaller fishes do not generate the force necessary to liberate large numbers of glochidia (Haag and Warren 2000).

Host infection occurs over a protracted time period, and many species are gravid and display lures for much of the year (Kraemer 1970; Howells 2000; Haag and Warren 2003). Peak periods of glochidia release often are in spring, but glochidia of *Lampsilis* and *Villosa* are found in the drift or on fishes year-round (Tedla and Fernando 1969; Zale and Neves 1982a, 1982b; Neves and Widlak 1988; Watters and O'Dee 1999). *Villosa nebulosa* and *V. vibex* released on average only about 10 percent of their total glochidial complement during individual encounters with host fishes (average $\approx$ 5,000 glochidia per encounter), suggesting that multiple hosts may be infected by a single female over a protracted period (Haag and Warren 2000). An exception to the typical protracted release was reported for a population of fatmuckets, *L. siliquoidea*, in Minnesota, in which glochidial release occurred synchronously over 3 weeks (Trdan 1981). Long periods of lure display may allow infection of hosts even in headwater streams or other habitats where hosts occur at low densities (Section 8.3.B).

Large lures are clearly a primary strategy for host infection in most species, but secondary strategies may exist. Displaying *Villosa nebulosa* and *V. vibex* released small numbers of glochidia (fewer than 50) daily, even in the absence of host fishes (Haag and Warren 2000). These small releases were explained as either "leakage" from gravid gills or a secondary strategy for passive host infection. Many species release loose conglutinates after a lengthy period of lure display, suggesting a secondary infection strategy associated with the need to empty the gills for deposition of the subsequent brood (Section 5.3.B). Lure display appears to be a secondary strategy only in *Hamiota*. In these species, production of superconglutinates appears to be the primary strategy, but their release is preceded by a short period of lure display (Haag et al. 1999). In *Hamiota*, elaborate mantle lures occur only in *H. altilis*, and lures are greatly reduced in the other three species (Hartfield and Butler 1997; Haag et al. 1999), supporting the secondary role of these lures in host infection.

5.3.C.2. Cryptic lures

Cryptic lures are smaller and less conspicuous but can involve mimicry and behaviors equally extravagant to large lures. These lures are structurally and functionally homologous to large lures (Zanatta and Murphy 2006), but they target distinctly different groups of fishes. Species with cryptic lures are host specialists on darters, sculpins, or small sunfishes such as *Lepomis* (Centrarchidae). Cryptic lures consist of small arrays of pigmented mantle flaps, papillae, or caruncles, but their morphology varies widely among genera. Many cryptic lures resemble small benthic invertebrates such as insect larvae, but others seem to rely mostly on motion to entice attacks from fishes. Cryptic lures are known only in the Lampsilini, including *Epioblasma*, *Lemiox*, *Ligumia subrostrata* and *L. nasuta*, *Medionidus*, *Obovaria*, *Toxolasma*, *Venustaconcha*, and several *Villosa*.

Cryptic lures target small, benthic predators while limiting their attractiveness to other fishes. In contrast to the conspicuous displays of large lures, cryptic lures usually involve only subtle movements and may be displayed from within interstices in the substrate (Plate 18). In the Alabama moccasinshell, *Medionidus acutissimus*, the modified portion of the mantle is up to 20 mm long, but movement is restricted to a 2 mm white patch that flickers rapidly (Haag and Warren 2003). Lure displays of *Ligumia nasuta*, *L. subrostrata*, and *Venustaconcha* consist of a 5–10 mm portion of the mantle that is fluttered rhythmically or flipped open rapidly to briefly reveal the gravid gills within (Corey et al. 2006; Allen et al. 2007; Barnhart 2010; Plate 18; Gascho-Landis et al., in press).

Some cryptic lures obviously mimic specific fish prey items. The lure of the birdwing pearlymussel, *Lemiox rimosus*, bears a remarkable resemblance to a small snail of the genus *Leptoxis*, which is heightened by a subtle, side-to-side motion mimicking snail movements (Jones et al. 2010; Plate 18). Several darter species, including the greenside darter (*Etheostoma blennioides*), a primary host for *L. rimosus*, feed heavily on *Leptoxis* in some streams (Starnes and Starnes 1985; Haag and Warren 2006). The lure of *Toxolasma* consists of a pair of thin flaps that terminate in fleshy, thumblike white, pink, or orange caruncles up to 10 mm in length that resemble a small worm (Plate 18). The caruncles rotate in opposite directions resembling twiddling thumbs but periodically and simultaneously reverse directions. This behavior is accompanied by a rapid rippling of the mantle margin to reveal the gills within (Kraemer 1984); hosts for *Toxolasma* are sunfishes (*Lepomis*; Stern and Felder 1978; Hill 1986). The lure of the Cumberland moccasinshell, *Medionidus conradicus*, includes two thin, elongated papillae that resemble the paired cerci of a mayfly or stonefly larva (Plate 18), similar to cryptic lures of *Epioblasma* (see subsequent discussion).

In several species, cryptic lures appear to exploit the egg-feeding habits of fishes such as sculpins and small sunfishes (*Lepomis*) (Plate 18). In the pondmussel, *Ligumia subrostrata*, and *Toxolasma*, the distal ends of the gravid water tubes are white and beadlike and strongly resemble fish eggs (Kraemer 1970); in the little spectaclecase, *Villosa lienosa*, and Coosa creekshell, *V. umbrans*, glochidial masses may be extruded slightly from the gills, furthering the resemblance to an egg cluster (W. R. Haag, observations). In these species, the mantle lure may serve primarily as a source of motion to attract fishes to the egg mimic lure of the gills. In some species of *Epioblasma*, the mantle lure itself resembles a cluster of fish eggs (see subsequent discussion).

Without doubt, the most insidious host infection strategy involves the cryptic lures and host-trapping behavior of the riffleshells, *Epioblasma*. Although aspects of these lures were noted by Ortmann (1911, 1924a), this remarkable behavior was not documented fully until after 2003 (Barnhart et al. 2008). All *Epioblasma* appear to be specialists on darters or sculpins (Cummings and Watters 2010). When females are gravid, they emerge from the substrate and gape widely to expose the modified mantle (Plate 19). The modified portion of the mantle is dominated by a large region of spongy tissue called the *cymapallium*, which may be mottled gray, black, white, or blue (Jones et al. 2006a; Barnhart et al. 2008). Within the cymapallium are two small papillae about 5 mm in length (termed *microlures*) that possibly mimic the paired cerci of aquatic insect larvae or a series of small vesicles resembling fish eggs; both types of structures rotate or move from side to side. Displaying females are unresponsive to disturbance unless the mantle is touched, which prompts the shell to snap shut within 0.1 s (Barnhart et al. 2008). Darters are attracted to these microlures, and when they attack them, the fish become trapped between the shell valves, usually by the head (Plate 19), but small fish can be completely enclosed by the shell; these host captures have been observed repeatedly in the laboratory and in the field (Mulcrone 2004; Jones et al. 2006a; Barnhart et al. 2008). The shells of female *Epioblasma* also are modified for host capture, having either recurved denticles or a recurved edge that helps to hold the fish (Figure 5.10).

After capture, the cymapallium swells to form a gasketlike seal around the head of the captured fish, which is held for up to 30 min (Plate 19). Free glochidia are then expelled from the mussel gills into the mantle cavity, and with both inhalant and exhalant apertures closed, rhythmic contractions of the adductor muscles cause glochidia to be pumped directly through the fish's mouth and over the gills. Smaller fishes may die from asphyxia or crushing of the skull, and dead *Etheostoma* with crimp marks on their heads have been observed in the field during release periods

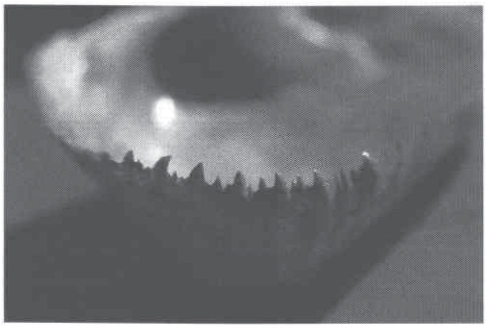

Figure 5.10. Shell margin denticles of female snuffbox, *Epioblasma triquetra* (Chris Barnhart, photo).

of *Epioblasma*. However, larger darters like logperch (*Percina caprodes*), a primary host for many *Epioblasma*, are more likely to survive, suggesting a high degree of specificity in this infection strategy (Barnhart et al. 2008).

Similar to other host attraction strategies employed by specialists, cryptic lures appear remarkably adapted to attract and infect only a specific set of fishes. In addition to the lures of *Epioblasma*, attacks by fishes on other cryptic lures and subsequent release of glochidia have been observed both in the field and the laboratory (Corey et al. 2006; Allen et al. 2007), but these interactions are less well studied than those involving large lures. Like large lures, glochidial release is dependent on encounters with fishes during attacks and cannot be stimulated by simply touching the lure with an inanimate object (Corey et al. 2006; W. R. Haag, observation). However, cryptic lures differ from large lures in several important ways. In cryptic lures, gravid gills typically do not protrude beyond the shell margin; rather, gravid gills are partially hidden by the mantle lure or only exposed during movement of the lure. This creates the illusion of a hidden prey item and may entice small fishes to investigate these lures while excluding larger fishes. In *Epioblasma*, glochidia are actively released by the female during host capture rather than glochidial release being dependent on the force of a fish rupturing the gravid gill, as in large lures. For other types of cryptic lures, the mode of glochidial release during fish attacks is unknown. Because of their small size, inconspicuous appearance, and the types of prey items they mimic, cryptic lures are highly evolved to target small fishes that feed closely among benthic substrates such as darters, sculpins, and small sunfishes and appear to be unlikely to attract larger predators or drift-feeding fishes.

5.3.C.3. Mantle magazines

Apart from the Lampsilini, mantle lures are known only in the Quadrulini, including *Cyclonaias* and possibly all species of *Quadrula* (Barnhart et al. 2008; Hove et al. 2011; Sietman et al., 2012). Like superconglutinates and host trapping, these remarkable lures and their associated mucoid conglutinates were apparently unknown until recently. Mantle magazines attract host fishes to the gravid female mussel, but they differ markedly from lampsiline lures in all other anatomical and functional aspects. The mantle magazine is an expansion of the mantle surrounding the exhalent aperture and is found only in gravid females (Plate 20). The mantle magazine serves two related purposes. First, glochidia or mucoid conglutinates are released from the female gills and stored in the magazine for a period of minutes to hours. Second, mantle tissue in this region is pigmented and elaborated into a lure that elicits attacks from fishes. Storage of glochidia in the magazine allows them to be released abruptly by reflexive contraction of the shell when the lure is attacked by a host fish (Barnhart et al. 2008).

The fish food items mimicked by mantle magazines are not obvious to the human eye, but construction of the magazine and release of glochidia vary among species in accordance with host use (Plate 20). Specialists on catfishes, including the *Quadrula quadrula* group and the pistolgrip, *Q. verrucosa*, have large, highly elaborated and pigmented lures associated with the mantle magazine. These species apparently do not release glochidia or mucoid conglutinates in response to touch; instead, release may rely on suction generated during a fish attack (Hove et al. 2011; Sietman et al., 2012). The lures of *Cyclonaias* and the *Quadrula pustulosa* group (also catfish specialists) are smaller, but these species release large mucoid conglutinates (Section 5.3.B.3). The larger lures may be generalized mimics of caterpillars or grubs, but it is proposed that all involve chemical attractants that capitalize on the keen olfactory sense of catfishes (Barnhart et al. 2008; Hove et al. 2011). These lures also are displayed most conspicuously at night, corresponding to the nocturnal feeding habits of catfishes (Hove et al. 2011). In contrast, species in the *Q. metanevra* group that specialize on minnows have diminutive, brightly colored lures that are displayed by day and may attract these small, sight-feeding predators; these species release quick bursts of free glochidia on stimulation of the lure (Barnhart et al. 2008; Sietman et al., 2012).

5.3.D. Drum specialists and female sacrifice

Host infection strategies are poorly known for a group of species prominent in large-river mussel assemblages in the central United States, including *Ellipsaria*, *Leptodea*, *Potamilus*, and *Truncilla*. These species apparently lack conspicuous lures, conglutinates, mucus webs, or other structures for transmitting glochidia to hosts. All are specialists on freshwater drum (*Aplodinotus grunniens*; Figure 5.3), which forage by suction feeding in the substrate and prey heavily on mollusks (Section 7.2.A). Except for the butterfly, *Ellipsaria lineolata*, these species have very high fecundities (Chapter 6), suggesting that they broadcast large numbers of free glochidia onto adjacent sediments, where they are encountered incidentally by feeding drum. Patterns of natural glochidial infections on drum support this hypothesis in part. Glochidia of the fragile papershell, *Leptodea fragilis*, *Potamilus*, and *Truncilla*, are found exclusively on the gills of drum (Surber 1915; Coker et al. 1921), indicating that glochidia are encountered during feeding rather than entangling on fins and external surfaces like other broadcasters. However, drum are consistently infected by glochidia of these species, and infestations are often higher than on hosts for other mussel species. Coker et al. (1921, 156) observed that drum "are almost invariably heavily loaded with glochidia." In the Wabash River, Indiana, up to 68 percent of drum were infected with glochidia of *Leptodea fragilis*, *Potamilus*, or *Truncilla* (Cummings and Mayer 1993). Five drum from the St. Francis River, Arkansas, carried an average of 289 *P. purpuratus* glochidia per fish (Surber 1915), and in the Barren River, Kentucky, a single drum carried 232 *P. alatus* glochidia, while other fish species carried only 1–5 glochidia of other mussel species (Weiss and Layzer 1995). The prevalence and intensity of glochidia infestation indicate that drum are exposed frequently to large numbers of glochidia of these mussels and suggest that encounters are not a random process.

In all of these genera, recent observations documented subtle behaviors in gravid females that are absent in nongravid females or males (B. Sietman, personal communication). Although these species do not have obvious mantle lures, gravid females emerge slightly or fully from the substrate, the valves gape widely, and the mantle margin may show subtle pulsations or contractions. In *Ellipsaria* and *Truncilla*, the mantle margins flip back suddenly when touched to reveal the gravid gills within (Plate 18), but this behavior was not observed in *Leptodea* or *Potamilus*. The significance of these behaviors is unknown, but they may be a type of cryptic lure that attracts foraging drum, which extract glochidia from the gravid gills by suction. Interestingly, gravid female hickorynuts, *Obovaria olivaria*, a specialist on benthic, suction-feeding sturgeon, exhibit similar behaviors (B. Sietman, personal communication).

An alternative explanation for the prevalence of *Leptodea*, *Potamilus*, and *Truncilla* glochidia on drum is that these fishes become infected by consuming gravid female mussels (Coker et al. 1921; Howard and Anson 1922). This strategy has not been confirmed, but the specialization of drum for molluscivory is well known (Chapter 7), and other observations support this mode of infection. All of these species are thin shelled, and *Truncilla* and female scaleshells, *L. leptodon*, are diminutive (rarely more than 50 mm), likely never exceeding the gape size of large drum. *Truncilla* and small *Leptodea fragilis* and *Potamilus* are preyed on by fishes to a much greater extent than other, co-occurring mussel species (Chapter 7). In *L. leptodon*, sex ratios are highly skewed against females, and small males (less than 50 mm) also are rare (Barnhart 2001), further suggesting that small individuals (including all females) suffer inordinately high mortality. Female *L. leptodon* also have highly elaborated, uncalcified posterior shell margins (Plate 5) that may function in attracting fish predators, suggesting that this species is particularly adapted for female sacrifice (Barnhart 2001).

For small species like *Leptodea leptodon* and *Truncilla*, female sacrifice through predation by drum may be a primary strategy for transmission of glochidia to hosts.

Although large adults of *L. fragilis* and *Potamilus* likely exceed the gape size of drum, they can produce glochidia as early as their first year (Chapter 6) and may remain accessible as prey to drum for 1–2 years. Consequently, female sacrifice may be an important secondary strategy even for larger species. After these species grow beyond the gape limitations of drum, broadcast of free glochidia or display of cryptic lures (see previous discussion) may become the primary mode of glochidial transmission.

In addition to drum, other large fishes may become infected with mussel glochidia incidentally while feeding on gravid mussels. Large catfishes often feed on mussels, including adult mussels of reproductive size (Section 7.2.B). Middens of crushed mussel shells likely attributable to flathead catfish (*Pylodictis olivaris*) contain several mussel species, including those for which catfishes are suitable hosts (*Quadrula asperata, Q. rumphiana, Q. verrucosa*), but also species that cannot metamorphose on catfishes (*Elliptio arca, Lampsilis* spp., *Pleurobema decisum*). For the former group, predation by large catfish may represent a secondary mode of transmitting glochidia to hosts. It also has been proposed that mudpuppies (*Necturus*) eat salamander mussels, *Simpsonaias ambigua*, and become infected with glochidia in the process (Howard 1951). However, this seems unlikely because the gills of mudpuppies are external and may not be exposed to glochidia during feeding on mussels. In contrast, fish gills are within the buccal cavity and would be exposed directly to large numbers of glochidia when a gravid mussel is crushed in a fish's mouth.

Perhaps more than any other feature of their natural history, the diversity of host relationships illustrates the great ecological differences among North American mussel species. The degree to which infection strategies are specialized to target a diverse cross section of the North American fish fauna is a compelling example of host–parasite coevolution and indicates extensive partitioning of the host resource. Much remains to be learned about mussel host use and host infection strategies. The recent discovery of many remarkable adaptations for host infection suggests that more surprises await us, and these strategies will surely turn out to be more specialized and intricate than we now know. As we shall see in subsequent chapters, host use and infection strategies have a major influence on many other aspects of mussel ecology and conservation.

Chapter 6

These are very different animals

Life history variation in mussels

Apart from the striking differences in host use among species, other life history traits of mussels were poorly known until recently. In the absence of information about growth and longevity, fecundity, and age of maturity, mussels were treated as a rather ecologically homogeneous group of animals. Generalized depictions of mussel life history included variations on the following theme: slow growing, long-lived, high fecundity, and late maturity (e.g., McMahon and Bogan 2001; Strayer et al. 2004). This characterization appears derived largely from European studies of *Margaritifera margaritifera*, which is probably the best studied mussel in the world. This homogeneous depiction of mussel life history – in addition to being not very interesting – is problematic from an evolutionary perspective: how can so many ecologically equivalent species coexist?

Not surprisingly, recent research shows that mussel life history diversity is much greater than previously assumed. Most species depart widely from the generalized depiction of life history based on *M. margaritifera*, and in fact, its life history is unusual relative to most species. Some mussel species indeed have much greater life spans than most invertebrates, but others are quite short-lived, and in general, the range of longevity for mussels is similar to that seen for marine bivalves, crustaceans, and echinoderms and even vertebrates (e.g., Hurlbert et al. 2007). Similarly, the range of fecundity in mussels is comparable to that seen in other aquatic invertebrate groups (e.g., Menge 1974). Clearly the prevalent generalized depiction of mussel life histories is not useful. The great variation among species shows that freshwater mussels encompass a range of very different animals.

6.1. Growth and longevity

Freshwater mussels and other bivalves have become quite famous for their longevity. The annual rings deposited in bivalve shells are similar to tree rings and can provide lengthy and detailed growth histories (Section 1.3.A). The life span of *Margaritifera*

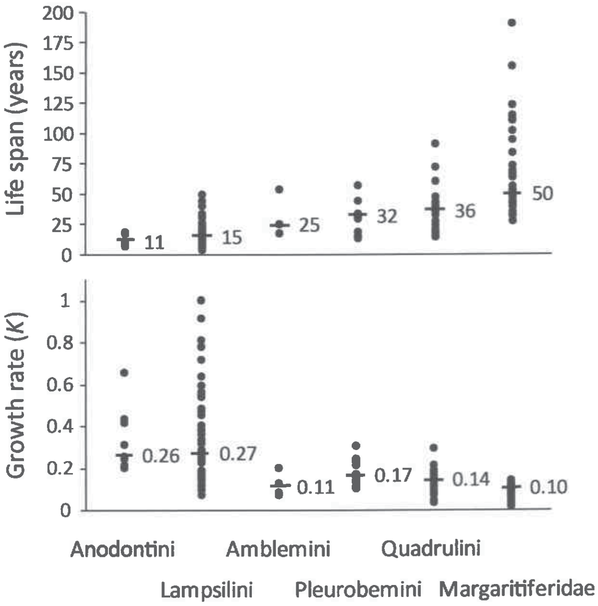

Figure 6.1. Variation in life span and growth rate among mussel groups. Dashes and numbers represent median values for each phylogenetic group (from Haag and Rypel 2011).

margaritifera, which may approach 200 years (Bauer 1992; Ziuganov et al. 2000), is one of the longest reported for any noncolonial animal (Hurlbert et al. 2007), but it falls short of the ocean quahog (*Arctica islandica*), a bivalve of cold waters in the North Atlantic that lives more than 400 years (Schöne et al. 2005c; Wanamaker et al. 2008). However, freshwater mussel life spans vary widely among and within species. Even *M. margaritifera* may live only 30–40 years in some places (see subsequent discussion). Several other species commonly live more than 50 years, but the life span of most ranges from 15 to 40 years, and some rarely live more than 5 years (Figure 6.1).

Like most organisms, mussel growth is rapid during the first few years of life but slows with increasing age, as resources are diverted to reproduction and maintenance (Figure 6.2). The amount of energy allocated to growth versus other functions and the timing of this allocation are fundamental life history characteristics of any organism. Patterns of energy investment in growth differ greatly among mussel species (Figure 6.3). Species such as the fragile papershell, *Leptodea fragilis*, and giant floater, *Pyganodon grandis*, grow rapidly in a few years, but others, such as the elephant-ear, *Elliptio crassidens*; southern clubshell, *Pleurobema decisum*; and pimpleback, *Quadrula pustulosa*, grow slowly over a long time period. Figure 6.3 suggests that there is little relationship between size and life span: short-lived species range widely in size, and small to medium-sized species can reach advanced ages. What is evident from this graph, however, is a relationship between life span and the rate at which

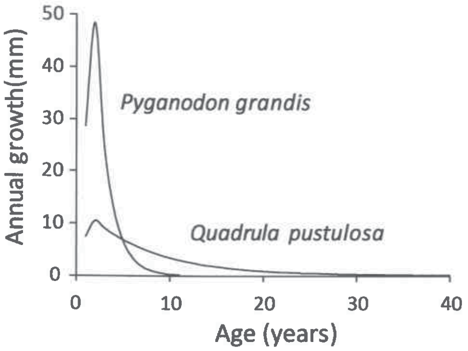

Figure 6.2. Lifetime growth for two mussel species. Growth is lower in the first year because animals may not settle to the substrate until well into the growing season and may exhibit compensatory growth in the second year (the first full year of life) (data from Haag and Rypel 2011).

species approach their growth asymptote (the point at which growth declines such that size increases little with age): species that approach the asymptote rapidly have short lives, and vice versa. The rate at which species approach their growth asymptote is described by the parameter *K* in the von Bertalanffy growth equation (e.g., Ricker 1975; Haag 2009a). Higher values of *K* indicate more rapid attainment of the growth asymptote and can be interpreted as representing earlier and greater investment in growth and a generally higher growth rate.

Mussel life span is strongly negatively correlated with *K*, and this relationship explains a high percentage of the variation in life span (Figure 6.4). Correlations between life history variables can be artifacts of shared, inherited traits within phylogenetic lineages that do not necessarily have adaptive significance, but this relationship remains strong even when phylogenetic relationships are accounted for (Haag and Rypel 2011). In contrast, life span is positively correlated with shell size and mass, but these relationships explain little of the variation in life span (Figure 6.4). Species with maximum length less than 50 mm are uniformly short-lived (less than 20 years), but otherwise, there is little relationship between size and life span. Shell mass is only broadly related to longevity. In many long-lived species, continual deposition of nacre over time results in thick, massive shells, but other longest-lived species have comparatively thin shells (e.g., *Cumberlandia monodonta, Margaritifera*).

Life span and patterns of investment in growth have a strong phylogenetic component (Figure 6.1). Short-lived species (less than 15 years) are restricted to the Anodontini and Lampsilini. The median life span for these two groups is similar, but the Anodontini is characterized by uniformly short life spans rarely exceeding 20 years. In contrast, the Lampsilini includes species with the shortest known life spans (*Leptodea fragilis, Medionidus acutissimus*, and *Toxolasma parva*; all 5 years or less) as well as species that reach advanced ages (e.g., *Actinonaias ligamentina, Obovaria unicolor*; more than 40 years). Most species in the Amblemini, Pleurobemini, and

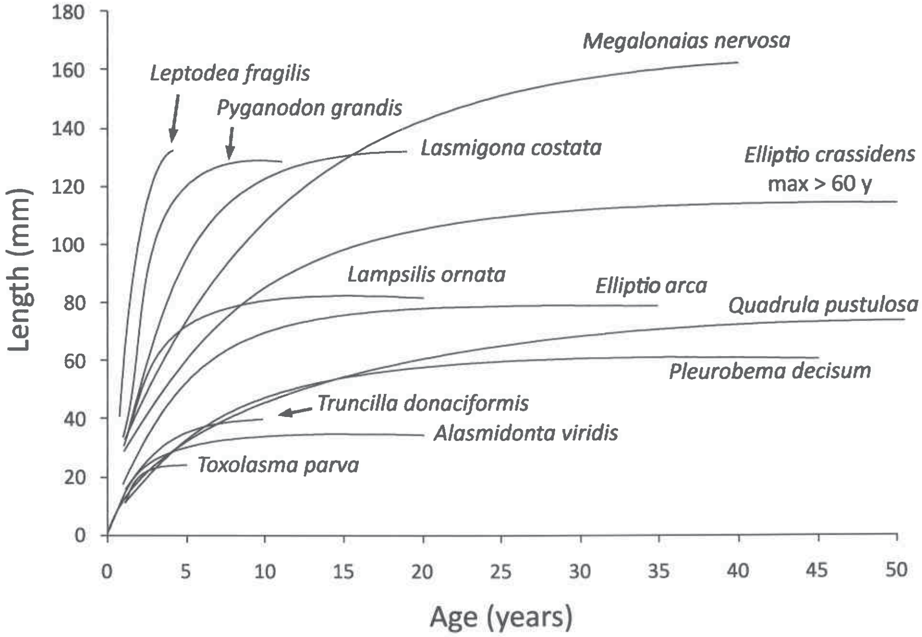

Figure 6.3. (top) Growth trajectories of representative North American freshwater mussels based on von Bertalanffy growth curves (data from Haag and Rypel 2011). (bottom) Disparity between size and age among mussel species. The individual on the left (Alabama hickorynut, *Obovaria unicolor*, 39 mm) is 21 years old, but the much larger bleufer, *Potamilus purpuratus* (right, 132 mm), is only 8 years old (W. R. Haag, photo).

Quadrulini have life spans more than 20 years, and all three tribes include species that live more than 50 years. The Margaritiferidae is the longest-lived group, but life span varies widely among populations (see subsequent discussion). As expected, variation in the growth rate, *K*, shows an opposite pattern to longevity, being uniformly high in the Anodontini, highly variable in the Lampsilini, and uniformly low in the other groups (Figure 6.1).

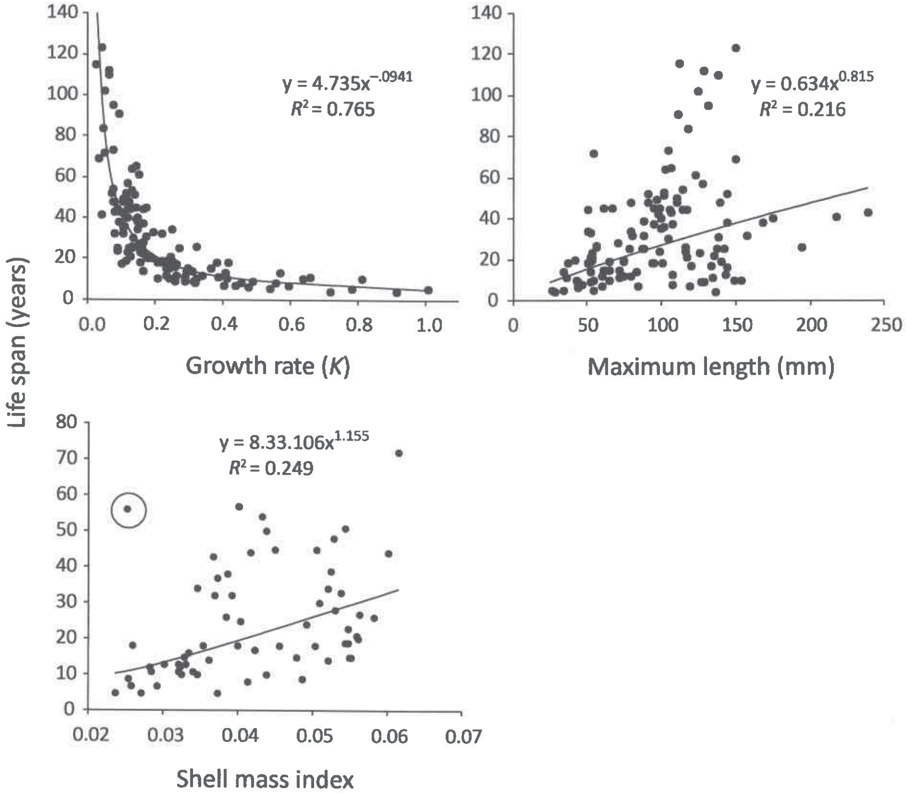

Figure 6.4. Relationships between life span and growth variables among 52 mussel species from 126 populations; the shell mass data set (bottom) includes 42 species from 70 populations. Shell mass index is the cube root of shell mass/length used to remove allometric effects. Circled point on shell mass graph is the spectaclecase, *Cumberlandia monodonta* (see text) (data from Haag and Rypel 2011).

Life span and growth rate appear constrained to some extent by phylogeny, but these traits show considerable plasticity in response to environmental variables. In transplant experiments, mussel growth showed little influence of site of origin, and in some cases, growth quickly assumed characteristics of resident individuals at the transplant site (Jokela and Mutikainen 1995a; Kesler and van Tol 2000; Kesler et al. 2007). Growth rate and life span can vary along latitudinal gradients apparently because of lower water temperatures and shorter growing seasons in northern latitudes (Dunca and Mutvei 2001; Schöne et al. 2004). Northern populations of *Margaritifera margaritifera* grow slowly and reach ages of more than 100 years, but southern populations grow up to 7 times faster and may live fewer than 30 years (Figure 6.5; see also Ziuganov et al. 2000; Helama and Valovirta 2008). Less dramatic latitudinal effects on growth and life span are evident for other North American and European species (Hochwald 2001; Haag and Rypel 2011), but these effects have not been

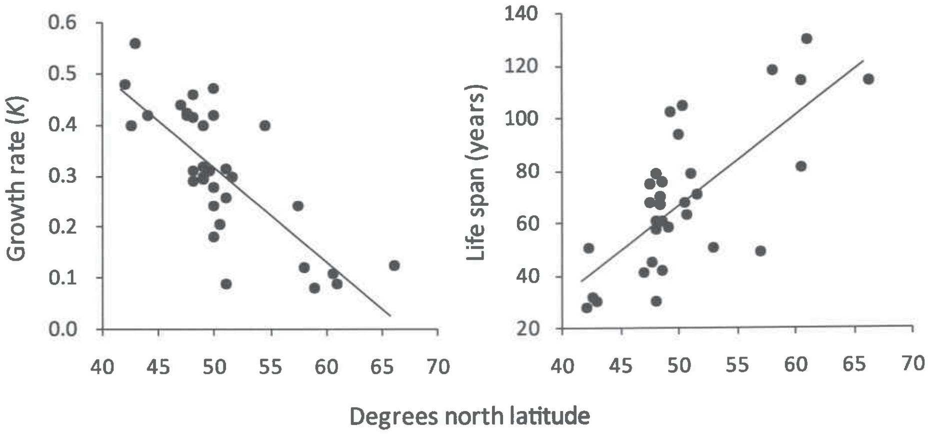

Figure 6.5. Latitudinal gradients in growth rate and life span among populations of the eastern pearlshell, *Margaritifera margaritifera* (redrawn from Bauer 1992).

studied at large geographic scales. Human modification of stream temperature may have similar effects. Streams affected by cold, hypolimnetic discharge from reservoirs often have relict mussel assemblages that predate dam construction (Section 10.3.C). Mussels from these streams have unusually massive shells (Parmalee et al. 1980), and the persistence of individuals for many years after dam construction suggests that depressed growth rates facilitate greatly increased life span beyond the normal range for a species. Conversely, increased temperatures associated with global warming may increase mussel growth rates (Kendall et al. 2010) and would be expected to decrease life span.

Other environmental variables influence growth and life span and may supersede effects of water temperature or climate. Growth rate and shell size or thickness are often lower in regions with low calcium and bicarbonate concentrations necessary for shell production (Section 1.3.B). The Sipsey and Buttahatchee rivers, Alabama and Mississippi, flow through Cretaceous sands and clays and have low bicarbonate concentrations (7–13 mg/L). Mussels in these rivers had lower growth rates but greater life spans than populations of the same species at similar or more northerly latitudes (Haag and Rypel 2011). Biological productivity and eutrophication also influence growth rate. Mussels in enriched waters grow more rapidly than in less productive waters (Morris and Corkum 1999; Valdovinos and Pedreros 2007), in some cases resulting in decreased life spans (Arter 1989; Bauer 1992). Extremely low growth rates potentially associated with food limitation may allow mussels to reach advanced ages (Kesler et al. 2007), similar to the effects of chronically depressed water temperature. Sediment type and exposure to wind and current also may influence growth rate and shell size (Hinch et al. 1986; Bailey and Green 1988; Griffiths and Cyr 2006).

Environmental factors can also result in substantial but predictable annual variation in growth within a population. In several southeastern U.S. rivers, patterns of annual growth variation were similar among species, and growth was negatively correlated with stream discharge; in some cases, growth in low-flow years was more than 2 times higher than in high-flow years (Rypel et al. 2008, 2009). Similarly, annual growth of western pearlshells, *Margaritifera falcata*, in Oregon was strongly negatively related with stream discharge and positively but more weakly correlated with water temperature (Black et al. 2010). A negative relationship between streamflow and growth may be due to (1) greater energy requirements needed to maintain position during high flows, (2) decreased filtering efficiency in turbid conditions after rainfall events, and (3) increased food concentration in the form of microbial and algal biomass during low flows (Rypel et al. 2009).

Growth and life span can differ among individuals in a population due to nonenvironmental factors. In species with shell sexual dimorphism, males are typically larger than females (except for the pistolgrip, *Quadrula verrucosa*), and growth rate (*K*) can differ significantly between sexes (Haag and Rypel 2011). In some species, males live longer than females suggesting that the costs of brooding glochidia and attracting hosts may reduce life span or incur higher mortality (Jones and Neves 2011). In species without sexual dimorphism, sexes have similar growth trajectories and life spans (Haag and Rypel 2011). Parasitism by trematodes can reduce mussel growth but primarily affects older individuals (Taskinen and Valtonen 1995; Taskinen 1998). An unusual example of within-population variation is the apparent growth polymorphism seen in the Alabama orb, *Quadrula asperata*. In the Sipsey River, Alabama, a small percentage of individuals had growth rates approximately one-third those of the remainder of the population, mean length at age was about 60% of other individuals, and the maximum life span of slow-growing individuals was more than 2 times higher (Haag and Rypel 2011). These stunted individuals occurred in the same habitat as normal individuals and showed no evidence of past injuries that reduced growth, suggesting that slow growth is a canalized, alternate energy allocation strategy. Similar growth polymorphisms also are present in the threeridge, *Amblema plicata*, and pimpleback, *Q. pustulosa* (W. R. Haag and A. Rypel, unpublished data). The significance of this alternate growth form is unknown, but one possibility is that it is an adaptation to avoid muskrat predation, which is of lower intensity on small individuals (Jokela and Mutikainen 1995b; Section 7.2.A).

Life span and growth rate in mussels vary across nearly 2 orders of magnitude, and as a group, mussels cannot be accurately characterized as slow growing and long-lived. Species that invest heavily and early in growth have reduced life spans compared with species that grow more slowly and reach maximum size later in life. This relationship is a general phenomenon in animals and is explained by the rate of living hypothesis and its molecular mechanism, the free radical theory of aging, which state that faster growth or energy expenditure results in shorter life span due to increased oxidative stress and other cellular damage (Beckman and Ames 1998; Bonsall 2005). This trade-off is indicative of fundamentally different energy allocation strategies and suggests that mussel life histories have been shaped by divergent selective forces.

6.2. Reproductive traits

6.2.A. Sex ratios and mating systems

Most mussel species are gonochoristic (Section 1.4.C), but population sex ratios vary widely. Across 45 populations (37 species), half had sex ratios significantly different than 1:1; 14 were male biased and 8 were female biased (Table 6.1). Sex ratios show little or no concordance with phylogeny. Most tribes had populations that were male biased, female biased, and with equal sex ratios. Sex ratios also vary within genera (e.g., *Epioblasma, Lampsilis, Quadrula*) and even among populations (e.g., *Actinonaias ligamentina, Quadrula asperata, Utterbackia peggyae*).

The ecological significance of variable sex ratios in mussels is poorly understood. In gonochoristic animals, frequency-dependent selection favoring the rarer sex tends to produce and maintain equal sex ratios (Fisher 1930). Unequal sex ratios can result from competition among males for matings, variation in breeding condition of females, and local resource competition (Rickleffs and Miller 2000), but these mechanisms are difficult to imagine for broadcast spawners. Local resource competition could occur for food or host resources, but this mechanism normally requires greater natal dispersal of males relative to females (Charnov 1982), an unlikely scenario for mussels. Differential mortality of males and females also can cause unequal sex ratios. Strongly skewed sex ratios (greater than 2:1) appear to occur primarily in lampsiline species that display lures to attract hosts (Section 5.3.C), and these populations are often male biased (Table 6.1). Lure display may incur higher female mortality, and in some cases, female sacrifice may be an adaptation to infect hosts (e.g., scaleshell, *Leptodea leptodon*; Section 5.3.D). However, female-biased populations of these species also exist (Table 6.1), and some apparently male-biased populations may be artifacts of sample bias (see subsequent discussion). Differential mortality among sexes has not been investigated in mussels, nor have mechanisms been proposed that could lead to differential survival in species without mantle lures.

In most other mussel species, sex ratios are equal or only slightly biased toward one sex (less than 2:1; Table 6.1). Freshwater mussels, along with a few marine bivalves, have an unusual system of sex determination called *doubly uniparental inheritance* (Hoeh et al. 1996; Liu et al. 1996). Two types of mitochondrial DNA exist, a male and a female type, which are transmitted paternally and maternally, respectively, but sex ratio of the brood is controlled primarily by the female nuclear genotype (Kenchington et al. 2002). Interestingly, the male mitotype evolves at a faster rate than the female type, perhaps because of relaxed selection on the male type (Stewart et al. 1996). Because of this system, broods of individual females may be strongly biased in favor

Table 6.1. *Sex ratios for North American mussel populations given as the proportion of males in the population*

Family or tribe Species	Site	Sex ratio[a]	*N*	Source
Margaritiferidae				
Cumberlandia monodonta	Meramec River, MO	0.47^{ns}	100	Baird (2000)
Unionidae				
Amblemini				
Amblema plicata	Little Tallahatchie River, MS	0.46^{ns}	41	Haag and Staton (2003)
Amblema plicata	Sipsey River, AL	0.43^{ns}	30	Haag and Staton (2003)
Anodontini				
Anodonta heardi	Myakka River, FL	0.37^{*}	60	Heard (1975)
Arcidens confragosus	Tennessee River, AL	0.54^{ns}	35	Haggerty et al. (2011)
Pyganodon gibbosa	Holmes Creek, FL	0.66^{*}	53	Heard (1975)
Utterbackia imbecillis	Lake Talquin, FL	0.00^{***} (0.49)	70	Heard (1975)
Utterbackia peggyae	Lake Talquin, FL	0.65^{***} (0.01)	123	Heard (1975)
Utterbackia peggyae	Holmes Creek, FL	0.44^{ns} (0.10)	102	Heard (1975)
Lampsilini				
Actinonaias ligamentina	Green River, KY	0.62^{***}	430	Moles and Layzer (2008)
Actinonaias ligamentina	Green River, KY	0.47^{ns}	88	Moles and Layzer (2008)
Epioblasma torulosa rangiana	Clinton River, MI	0.59^{*}	118	Trdan and Hoeh (1993)
Epioblasma triquetra	Clinton River, MI	0.52^{ns}	804	Trdan and Hoeh (1993)
Epioblasma florentina aureloa	Indian Creek, VA	0.36^{*}	88	Rogers et al. (2001)
Lampsilis siliquoidea	Iatt Creek, LA	0.51^{ns}	39	W. R. Haag (unpublished data)
Lampsilis siliquoidea	East Fork Little Miami River, OH	0.67^{*}	54	Perles et al. (2003)
Lampsilis straminea	Little Noxubee River, MS	0.25^{**}	32	W. R. Haag (unpublished data)
Lampsilis ornata	Sipsey River, AL	0.83^{***} (0.03)	40	Haag and Staton (2003)
Lampsilis ornata	Sipsey River, AL[b]	0.63^{ns}	41	W. R. Haag (unpublished data)
Lampsilis ornata	Sipsey River, AL[c]	0.56^{ns}	81	W. R. Haag (unpublished data)
Lampsilis teres	Chewacla Creek, AL	0.82^{***}	71	J. Stoeckel (unpublished data)

Family or tribe Species	Site	Sex ratio[a]	*N*	Source
Leptodea leptodon	Gasconade River, MO	0.83***	57	Barnhart (2000)
Ligumia subrostrata	Davis Lake, MS	0.46^{ns}	292	W. R. Haag (unpublished data)
Medionidus acutissimus	Sipsey River, AL[c]	0.55^{ns}	300	W. R. Haag (unpublished data)
Obliquaria reflexa	Little Tallahatchie River, MS	0.49^{ns}	41	Haag and Staton (2003)
Obovaria unicolor	Sipsey River, AL[c]	0.62*	108	W. R. Haag (unpublished data)
Toxolasma parva	Davis Lake, MS	0.00*** (1.00)	38	W. R. Haag (unpublished data)
Toxolasma parva	Natchez Trace Lake, MS	0.00*** (1.00)	41	W. R. Haag (unpublished data)
Toxolasma texasensis	Iatt Creek, LA	0.63^{ns}	33	W. R. Haag (unpublished data)
Venustaconcha ellipsiformis	Ore Creek, MI	0.54^{ns} (0.01)	238	van der Schalie and van der Schalie (1963)
Pleurobemini				
Elliptio arca	Sipsey River, AL	0.48^{ns}	81	Haag and Staton (2003)
Elliptio arctata	North Mosquito Creek, FL	0.49^{ns} (0.03)	126	Heard (1979)
Elliptio complanata[d]	Spring Creek, FL	0.49^{ns} (0.02)	266	Heard (1979)
Elliptio complanata	Morice Lake, NB	0.60*	100	Paterson (1985)
Elliptio complanata	Lac de l'Achigan, QB	0.61* (0.06)	421	Downing et al. (1989)
Elliptio icterina	Steinhatchee River, FL	0.50^{ns} (0.02)	310	Heard (1979)
Elliptio jayensis	Myakka River, FL	0.44^{ns} (0.05)	59	Heard (1979)
Fusconaia cerina	Sipsey River, AL	0.53^{ns}	61	Haag and Staton (2003)
Pleurobema cordatum	Tennessee River, AL	0.55^{ns}	306	Yokely (1972)
Quadrulini				
Cyclonaias tuberculata	Tennessee River, AL	0.52^{ns} (0.01)	234	Haggerty et al. (1995)
Cyclonaias tuberculata	New River, WV	0.61*	90	Jirka and Neves (1992)
Megalonaias nervosa	Mississippi River, WI	0.28***	220	Woody and Holland-Bartels (1993)
Quadrula asperata	Buttahatchee River, MS	0.52^{ns}	46	Haag and Staton (2003)

(continued)

Table 6.1 *(continued)*

Family or tribe Species	Site	Sex ratio[a]	N	Source
Quadrula asperata	Sipsey River, AL	0.77^{**}	165	Haag and Staton (2003)
Quadrula cylindrica	Clinch River, VA	0.47^{ns}	74	Yeager and Neves (1986)
Quadrula metanevra	Tennessee River, TN	0.40^{**} (0.02)	227	Garner et al. (1999)
Quadrula pustulosa	Little Tallahatchie River, MS	0.63^{**} (0.01)	92	Haag and Staton (2003)

Note: Asterisks denote significant departures from 1:1 sex ratio: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, ns = not significant (goodness-of-fit test, 1 df, hermaphrodites not included).

[a] Proportion of hermaphrodites observed in population is given in parentheses if > 0.

[b] Collection of individuals killed by drought.

[c] Grand total from 10 years combined survey data with whole-substrate excavation.

[d] Includes two shell forms of unknown taxonomic status; neither shell form deviated from 1:1 individually.

of either males or females, but sex ratios of large populations approach 1:1 (Zouros 1994; Kenchington et al. 2002). Consequently, local sex ratios could vary due to stochastic factors, especially in small populations, and slightly skewed sex ratios may be of little or no adaptive significance (e.g., Dolgov 1991).

The significance of variable sex ratios is clouded further by potential bias in many reported ratios. Sex ratios are reported commonly but are often based on small sample sizes. Even though sex in completely gonochoristic species has only two states (male or female), obtaining a precise estimate of sex ratio with a standard error 10 percent of the mean (e.g., an estimate of 50% male with 95% confidence interval of 40%–60%) requires a sample size of about 100 individuals (Rohlf and Sokal 1969). Other reported sex ratios may be influenced by mussel behavior. Sampling in the fall with mask and snorkel revealed a strongly male biased sex ratio for the southern pocketbook, *Lampsilis ornata* (greater than 5:1), but a large collection of individuals killed later by drought and results of whole–substrate sampling both revealed a 1:1 sex ratio (Table 6.1). This discrepancy likely is due to differences in burrowing behavior between sexes, which biased visual sampling. The golden riffleshell, *Epioblasma florentina aureola*, showed strong seasonal variation among sexes in burrowing; visual sampling revealed a sex ratio of 7–20 percent male from February to June but more than 70 percent male in August and September (Rogers et al. 2001). Finally, potential size- and age-related factors are not accounted for in most reports of sex ratios (see subsequent discussion).

Occasional simultaneous hermaphrodites may occur in gonochoristic species, but they typically compose a low percentage of a population (less than 10%) and usually have a small percentage of gonads of the opposite sex (van der Schalie 1970; Heard 1975; Kat 1983; Jirka and Neves 1992; Garner et al. 1999; Table 6.1). In these occasional hermaphroditic individuals, gonads of the dominant sex are often more fully developed than the minor sex (van der Schalie 1970), and individuals with less than 50 percent ovarian tissue do not produce eggs or glochidia (Downing et al. 1989). Furthermore, in individuals in which gills are modified for brooding glochidia, gonads are dominated by ovarian tissue (Heard 1975). Hermaphrodites occasionally compose a higher percentage of a population. Only 20 percent of eastern elliptio, *Elliptio complanata*, in a Quebec lake were entirely one sex, but as in other populations, the percentage of gonads of the opposite sex in most individuals was less than 10 percent (Downing et al. 1989). These observations suggest that, despite having gonads of both sexes, most hermaphroditic individuals are functionally gonochoristic. Explanations for the occurrence of occasional hermaphrodites in otherwise gonochoristic species include developmental errors and trematode infestation (van der Schalie 1969; Kat 1983), but these ideas have not been tested. Regardless, these occasional hermaphrodites are considered of little reproductive significance from a population perspective (Heard 1979).

In North America, functionally hermaphroditic populations are restricted to a few species in the Anodontini (*Lasmigona compressa, L. subviridis*, and *Utterbackia imbecillis*), Lampsilini (*Toxolasma parva*), and perhaps Margaritiferidae (*Margaritifera falcata*) (Ortmann 1919; Tepe 1943; van der Schalie 1970; Heard 1970, 1975). Functional hermaphroditism appears to have arisen independently in these lineages (Heard 1975; Hoeh et al. 1995). These species are all simultaneous hermaphrodites in which individuals possess both male and female gonadal tissue. Unlike primarily gonochoristic species, functional simultaneous hermaphroditism appears to have a strong adaptive basis. A classical explanation of the benefit of simultaneous hermaphroditism is that species occurring in low-density populations have a higher probability of fertilization (because of the ability to self-fertilize), and hermaphroditism doubles the effective population size relative to gonochorism (Ghiselin 1969). This adaptation is thought to allow simultaneous hermaphrodites, including freshwater fingernail clams (Sphaeriidae) and *Corbicula*, to rapidly colonize vacant habitats (Ghiselin 1969; McMahon and Bogan 2001).

With the exception of *M. falcata*, all predominantly hermaphroditic North American species are short-lived and occur in very small streams or isolated lentic habitats. In such places, they may be the only mussel species present, but they are usually rare in larger streams with more diverse assemblages (Ortmann 1919; van der Schalie 1969). In addition, the lilliput, *T. parva*, and paper pondshell, *U. imbecillis*, can rapidly colonize newly created habitats (W. R. Haag, observation). These observations are consistent with the prediction that "short-lived selfers do well where immediate fitness is crucial; in the long run . . . they are less successful" (Ghiselin 1969, 191–192). In *T. parva*, all populations that have been examined were composed exclusively of hermaphroditic individuals (Sterki 1898; Tepe 1943; van der Schalie 1970; W. R. Haag, unpublished data), suggesting that hermaphroditism is a characteristic and invariant trait in this species. In *U. imbecillis*, the proportion of hermaphrodites and the relative allocation to each sex are highly variable among populations (Heard 1975; Kat 1983; Johnston et al. 1998), and populations range from predominantly outcrossing to having 100 percent self-fertilization (Johnston et al. 1998). This suggests that the mating system of *U. imbecillis* is highly labile and may change in response to environmental variables (Hoeh et al. 1998). On the basis of classical theory (Ghiselin 1969; see previous discussion), Kat (1983) proposed the incidence of hermaphroditism and patterns of gonadal allocation are influenced by population density, but he provided scant support for this idea, and his methods of determining gonadal allocation were questioned by Johnston et al. (1998). No other studies have examined relationships between environmental variables and mussel mating systems.

In a few cases, individuals of primarily gonochoristic species appear able to change to hermaphrodites, and these observations support Kat's (1983) idea that environmental factors or population density influence sexuality. *Anodonta* in the Rhine River, Germany, were exclusively gonochoristic, and sex ratios were 1:1, but the incidence of hermaphroditism was higher in floodplain ponds and increased with increasing isolation from the river (Ghiselin 1969, citing Weisensee 1916). A high percentage of female *Margaritifera margaritifera* changed to hermaphrodites after being transplanted from a high-density to a low-density site, a result explained as an adaptation to deal with a shortage of sperm (Bauer 1987). Most margaritiferid populations are gonochoristic, but other occurrences of hermaphroditism in the group have been attributed potentially to low population density (Grande et al. 2001). Change of gonochoristic individuals to hermaphrodites appears to be rare in the Unionidae and is reported only for the washboard, *Megalonaias nervosa* (Heinricher and Layzer 1999).

Sex change occurs in many snails and marine bivalves but is limited almost exclusively to protandry (i.e., sequential hermaphroditism involving a change from male to female) (Wright 1988; Yusa 2007). In protandry, all small individuals are usually males, but nearly all later change to females or hermaphrodites (e.g., Dolgov 1991). There is little evidence for sex change or protandry in freshwater mussels. Seasonal variation in sex ratios of European *Unio pictorum* and *U. tumidus* was interpreted as evidence of sex reversals (Tudorancea 1972); however, confidence intervals around sex ratio estimates (estimates ranging from 46% to 63% male, $n = 50–252$) overlap widely and thus provide no support for sex change. Sex change was reported in *Anodonta cygnea* (Bloomer 1934), but these findings were viewed with skepticism by Heard (1975) on methodological grounds, and he found no evidence of sex change in several North American anodontines. Protandry was suggested by Kat (1983) based on anecdotal evidence that juvenile individuals of several species were all male, but other studies have not found differences in sex ratios among age classes (Smith 1979; Haag and Staton 2003). In a population of *Elliptio complanata*, the smallest size class (15–50 mm) was male biased to a greater extent than larger size classes, and this was interpreted as evidence of protandry (Downing et al. 1989). However, in contrast to the nearly complete sex reversal seen in most protandrous marine mollusks, all size classes of *E. complanata* were male biased, and the difference in sex ratios among size classes was small (ranging from 55% to 79% male), suggesting that differences may have been be due to random factors.

Protandry is favored when the increase in reproductive success with age or size is small for males but large for females, and it produces strong size dimorphism among sexes (Charnov 1982). The best-known examples of protandry in marine invertebrates are colonial species that occur in very dense aggregations (within 1–2 mm or often on top of each other); in these situations, highly efficient fertilization allows decreased investment in male gametes (e.g., oysters, *Crassostrea*, slipper shell snails, *Crepidula*; Hoagland 1978; Wright 1988). Few mussel species regularly occur in such close proximity – even in dense mussel beds – and the sparse distribution of most species would make protandry untenable (but not simultaneous hermaphroditism). The few species that do occur in very dense, discrete aggregations (e.g., spectaclecase, *Cumberlandia monodonta*; *Margaritifera*) show no evidence of protandry (Smith 1979; Baird 2000). Furthermore, many mussel species show no sexual dimorphism in size or growth (Haag and Rypel 2011), which is often a hallmark of protandry. Protandry or a change to hermaphroditism also may be prohibited by physiological or genetic constraints, such as in birds and mammals, which often have distinct sex-specific life histories and morphology (Charnov 1982). Accordingly, sex change seems especially unlikely in mussel species with permanent sexual characteristics such as shell dimorphism, female gill modifications, or mantle lures.

Female mussels often have high fertilization rates even in headwater streams or other habitats with low mussel density (Barnhart 1997; Haag and Staton 2003; Moles and Layzer 2008; W. R. Haag, observations). This consistent phenomenon could be explained by facultative hermaphroditism that allows self-fertilization at low densities. Downing et al. (1993) reported a positive relationship between fertilization success and mussel density for *Elliptio complanata* and proposed that individuals occurring at local densities less than $10/m^2$ would experience reproductive failure unless they self-fertilize. However, there was no evidence of hermaphroditism in several species that had high fertilization at densities much less than $10/m^2$ (Haag and Staton 2003). In experiments in hatchery ponds, female southern fatmuckets, *Lampsilis straminea*, a species widespread in headwater streams in the southeastern United States, did not become gravid in the absence of males (T. Mosley, J. Stoeckel, and W. R. Haag, unpublished data). Furthermore, in the presence of males, fertilization of females was consistently high (more than 90% of eggs fertilized), with or without current and even when females were separated from males by 25 m. These results do not support facultative hermaphroditism but rather show that at least some species have highly efficient sperm transfer (e.g., spermatozeugmata; Section 1.4.C) that allows fertilization and outcrossing even at low densities.

It is clear from this discussion that our understanding of the ecological factors that influence sexuality in mussels is very poor. Simultaneous hermaphroditism appears to have a clear adaptive basis, but this strategy occurs in few species and the factors that influence its expression are not well understood. In gonochoristic species, sex ratios vary widely at multiple scales, but it is possible that this variation has a large random component and therefore is of less ecological significance than variation in other life history traits such as growth and age at maturity. Nevertheless, environmentally-mediated changes in sex ratios are documented in many other mollusks (e.g, Yusa 2007) and this possibility cannot be ruled out for mussels. The breadth of these questions and the challenges involved in addressing them was recognized long ago by Sterki (1898:30) who stated "That would be a task for persons with a good deal of time at their disposal."

6.2.B. Age at maturity

Mussels are typically characterized as having delayed maturity. Similar to previous generalizations about growth and longevity, this notion is informed mostly by *Margaritifera margaritifera*, which does not mature until about 11 years of age (Young and Williams 1984a). Another long-lived margaritiferid, *Cumberlandia monodonta*, matures at about age 10 (Baird 2000). However, these are rather extreme values for freshwater mussels as a whole. In the Unionidae, most species for which data are available become sexually mature at age 6 or before, and many mature at age 2–4 (Figure 6.6). Most surprisingly, several species become mature and produce viable glochidia during their first year (age 0). In hatchery ponds, nearly all female pond-mussels, *Ligumia subrostrata*, and giant floaters, *Pyganodon grandis*, that recruited in late winter or spring 2009 were gravid by November, at which time individuals were less than 9 months old (W. R. Haag and J. Stoeckel, unpublished data). *Lampsilis ornata, Leptodea fragilis, Medionidus acutissimus, Potamilus ohiensis, Utterbackia imbecillis*, and the Asian species *Sinanodonta woodiana* also can become gravid before age 1 (Coker et al. 1921; Dudgeon and Morton 1983; Haag and Staton 2003; W. R. Haag, unpublished data). Maturity of *P. grandis*, *Truncilla donaciformis*, and *U. imbecillis* is reported by age 1 (van der Schalie and Locke 1941; Stansbery 1967). Heard (1975) estimated maturity at age 4–6 for several species of *Anodonta, Pyganodon*, and *Utterbackia*, but his samples included few young individuals, and it is possible that he overestimated the age of these rapidly growing species.

Species also differ in the degree of synchrony in maturation among individuals in a population. Species with early maturity appear to become reproductively active during a short time period. The majority of *Elliptio arca* and *Lampsilis ornata* matured

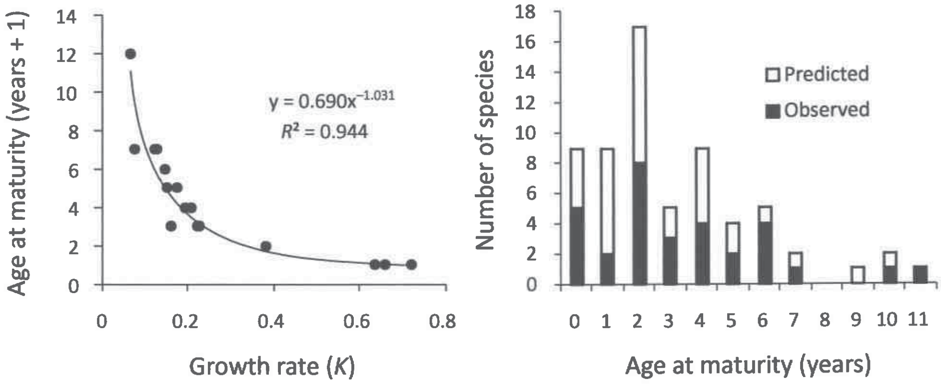

Figure 6.6. Age at maturity for North American freshwater mussels (including European *Margaritifera margaritifera*). (left) Relationship between the von Bertalanffy growth parameter, *K*, and observed age at maturity for 16 species (see Appendix A; for *M. margaritifera*, age at maturity is for a Scottish population (Young and Williams 1984a), and *K* is the median value of 16 Scottish populations (Hastie et al. 2000b)). Note that the *y* axis is expressed as age at maturity + 1 for computational purposes. (right) Distribution of age at maturity among 60 species. Values for individual species are given in Appendix A. Predicted values were generated from the regression equation in the left figure using values of *K* reported in the literature (Haag and Rypel 2011; Jones and Neves 2011). Values include two populations of threeridge, *Amblema plicata*, and purple wartyback, *Cyclonaias tuberculata*, with widely divergent values of *K*; for all other species represented by multiple populations, *K* is the median reported value.

between the ages of 1–2 and 0–1, respectively (Haag and Staton 2003), and nearly all females of *Leptodea fragilis* and *Medionidus acutissimus* become gravid by age 1 (W. R. Haag, observation). Species with later maturity show greater variation among individuals in the timing of maturation. In *Megalonaias nervosa*, *Quadrula asperata*, and *Q. pustulosa*, the percentage of mature individuals increased gradually between ages 3 and 6, but 100 percent maturity was not reached until ages 7–9 (Woody and Holland-Bartels 1993; Haag and Staton 2003).

Determination of age at maturity requires examination of large numbers of young individuals, but these size classes can be difficult to obtain or are absent in many populations. Consequently, estimates of this important life history parameter are available for few species (about 30, or 10% of the North American fauna; Appendix A). Life history theory predicts that age at maturity should covary with other traits such as body size, longevity, and growth rate (e.g., Stearns 1983), and growth rate is inversely correlated with age at maturity in fishes (He and Stewart 2002). In mussels, age at maturity is inversely related to life span (16 species, $R^2 = 0.717$) and growth rate (*K*), but *K* explains a remarkably high percentage of the observed variation (Figure 6.6). This relationship suggests that *K* is a useful predictor of age at maturity, and indeed, the distribution of predicted values for 35 species is similar to observed values of age at maturity (Figure 6.6). Predicted values range from early maturity (age 0–2) for fast-growing, short-lived species, such as *Alasmidonta*, *Epioblasma*, *Lampsilis teres*, *Lasmigona*, *Ligumia recta*, *Potamilus purpuratus*, *Strophitus*, *Toxolasma*, and *Villosa*, to later maturity (age 4–7) for longer-lived species, such as *Cyclonaias*, *Elliptio crassidens*, *Fusconaia*, *Plectomerus*, *Pleurobema*, *Ptychobranchus*, and *Reginaia* (Appendix A).

The relationship between age of maturity and *K* also predicts that, similar to life span, age at maturity may be plastic and vary in response to environmental factors that influence growth rate. Observed age at maturity was about 3 years for a fast-growing, short-lived population of *Amblema plicata* in the Little Tallahatchie River, Mississippi (maximum age 18 years), but predicted age at maturity was 9 years for a slow-growing, long-lived population in the Sipsey River, Alabama (maximum age 54 years; see Haag and Rypel 2011). Similarly, predicted age at maturity for *Cyclonaias tuberculata* in West Virginia was 4 years in the New River but 7 years in a slower-growing population in the Greenbrier River (growth rates from Jirka and Neves 1992).

6.2.C. Fecundity and reproductive output

Compared to many organisms, including other mollusks, mussels have very high fecundity. For example, some freshwater fingernail clams (Sphaeriidae) produce clutches of fewer than 20 eggs (McMahon and Bogan 2001). However, mussel fecundity is more variable among species than perhaps any other life history trait, and categorizing mussels uniformly as having high fecundity masks this variation. Mean annual fecundity varies among mussel species by nearly 4 orders of magnitude, ranging from fewer than 2,000 for the little-wing pearlymussel, *Pegias fabula*, to more than 8 million for the fragile papershell, *Leptodea fragilis* (Figure 6.7). Because fecundity is strongly related to mussel size, individual fecundity is even more variable, ranging from 49 for a small *Quadrula asperata* to more than 23 million for a large *L. fragilis* (Haag and Staton 2003; Haag, in press). Other aspects of reproductive output vary widely among species, including timing of brood production, glochidial size, and the amount of energy devoted to reproduction. For example, glochidial size varies by almost a factor of 7, from the 60 μm glochidia of *Cumberlandia monodonta* and *Truncilla* spp., to the nearly 400 μm glochidia of many anodontines (Barnhart et al. 2008).

6.2.C.1. Timing and periodicity of brood production

Females reproduce from the onset of maturity throughout the remainder of their lives (Bauer 1987; Haag and Staton 2003). Species with early maturity and short life spans produce large numbers of glochidia soon after maturation, but species with later maturity may produce very few offspring in their first few years of reproductive activity. An age 0, *Lampsilis ornata* produced about 48,000 glochidia (representing 17% of mean adult fecundity), but in *Quadrula asperata* and *Q. pustulosa*, age 3–4

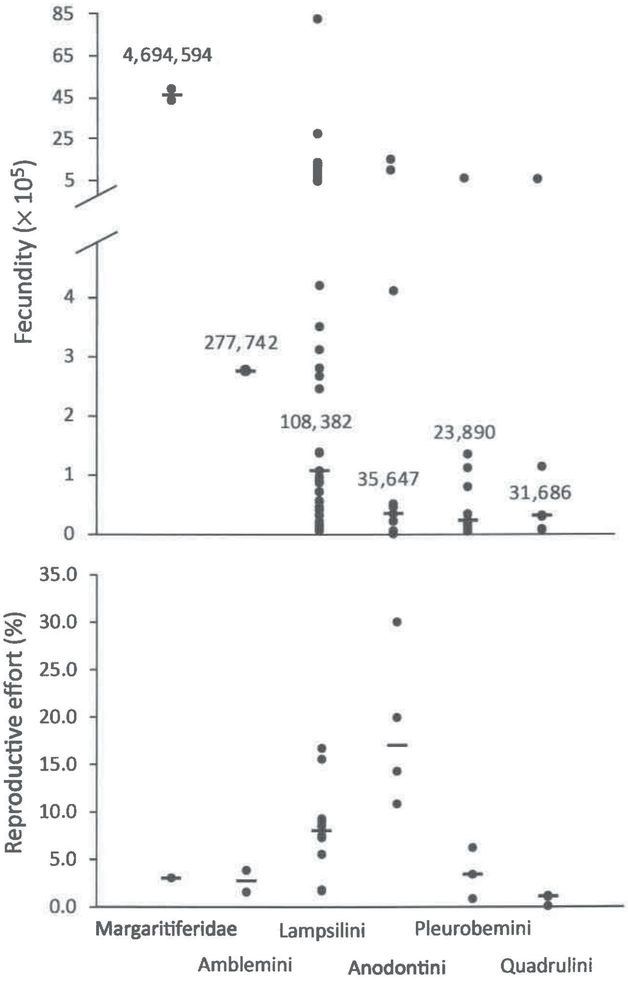

Figure 6.7. Variation in fecundity and reproductive effort among mussel groups. Dashes and numbers represent median values for each phylogenetic group. Note break in *y* axis scale on upper panel (from Haag, in press).

individuals (the earliest ages at which individuals attain maturity) produced as few as 250 and 49 glochidia, respectively (3.0% and 0.2% of mean adult fecundity) (Haag and Staton 2003).

Reproductive senescence, in the form of a decline in reproductive output with increasing age, has been reported for a few species, but the evidence for this is equivocal (see Section 6.2.C.2). However, reproduction may be reduced or terminated in some individuals by digenetic trematodes that castrate mussels by feeding on gonadal tissue (reviewed in Fuller 1974; Taskinen and Valtonen 1995). Trematode infestation often is more prevalent in older individuals, giving the appearance of reproductive senescence, but in some populations, infestation appears non–size selective (Zale and

Neves 1982a; Taskinen and Valtonen 1995; Haag and Staton 2003). Trematode infestations are rare in most populations (affecting less than 5% of individuals) but can vary among mussel species and occasionally occur at higher frequencies (Zale and Neves 1982a; Haag and Staton 2003). In extreme cases, trematodes may castrate the majority of individuals in a population, resulting in greatly lowered reproductive output. In the Pearl River, Mississippi, 90 percent of yellow sandshells, *Lampsilis teres* ($n = 56$), were castrated by trematodes such that no recognizable gonadal tissue remained, but other species at the site had lower incidence of infestation (0%–26%) (W. R. Haag and A. Rypel, unpublished data). Parasitism or opportunistic predation of gravid female gills by mites and dragonfly larvae may also result in lowered reproductive output (Gangloff et al. 2008; Levine et al. 2009).

In the absence of heavy parasitism, a high percentage of females typically reproduce each year. In 13 species, including representatives of all unionid tribes, except the Amblemini, 85–100 percent of mature females were gravid during the brooding period, and in many cases, the few nongravid individuals were young, suggesting that they had only recently reached sexual maturity (Haag and Staton 2003 and citations therein; Haggerty et al. 2011; data on *Ligumia subrostrata* from W. R. Haag, unpublished data; 91% gravid, $n = 80$, December 2009). In four other species, including *Amblema plicata*, the percentage of gravid females was lower, ranging from 64–77 percent (Haag and Staton 2003 and citations therein). *Margaritifera margaritifera* appears to have a consistently lower rate of female reproduction, with an average of 64 percent of females producing glochidia each year (Bauer 1987). It is unknown whether the apparent lower female participation in reproduction in some populations is due to a protracted brooding period with low synchrony among individuals or to environmental factors that influence either fertilization success or availability of resources necessary for egg production. In unfertilized hatchery ponds, a high percentage of *Ligumia subrostrata* and *Pyganodon grandis* were gravid in November 2010, but at the same time, few individuals of either species were gravid in adjacent ponds that had been fertilized and supported heavy growths of algae and aquatic macrophytes (A. Gascho-Landis, J. Stoeckel, and W. R. Haag, unpublished data).

Most evidence supports production of only a single brood per year for most species (reviewed in Haag and Staton 2003; see also White et al. 2008; Haggerty et al. 2011), but this has rarely been examined directly. Production of multiple clutches is especially unlikely in long-term brooders due to the lengthy, overwintering brooding period of these species. Production of multiple clutches is plausible for short-term brooders, but most evidence for this is equivocal. Multiple brood production was proposed for *Cumberlandia monodonta*, *Elliptio*, *Glebula rotundata*, and *Popenaias popei*, based on the occurrence of gravid females in a population over an extended period (Howard 1915; Parker et al. 1984; Gordon and Smith 1990; Heard 1998; Smith et al.

2003). However, because gravidity of specific individuals was not followed over time, apparent multiple broods could have been the result of asynchronous reproduction among individuals. An intensive, yearlong study of *C. monodonta* showed that females were gravid during only a short period in April and May, indicating production of a single brood (Baird 2000). *Elliptio jayensis* (as *E. buckleyi*) in south Florida (27°N latitude) showed a bimodal brooding pattern with gravid individuals present from January to May and again from September to November, providing convincing evidence of at least two broods per year, and other Florida *Elliptio* populations had gravid individuals for extended periods (Heard 1998).

Only a few studies have examined brood production by direct, repeated observations of marked individuals, and they present evidence of multiple broods in European *Unio* (one to five broods; Hochwald 2001) and North American *Elliptio* (one to three broods; Price and Eads 2011). However, because short-term brooders frequently abort their broods in response to disturbance (Section 5.3.B), multiple brood production by marked individuals could have been caused by loss of the initial brood due to handling. The maximum number of broods produced in these studies increased with the frequency at which marked females were examined (i.e., European *Unio* were examined more frequently). A convincing example of multiple brood production is an individual of the Tar spinymussel, *Elliptio steinstansana*, in captivity that produced and released five mature broods between April and July, even though the individual was not removed from the substrate or handled (S. Fraley, personal communication).

Multiple broods also are reported in *Utterbackia*, and consequently, its brooding strategy (short or long term) is not clear. Allen (1924) concluded that paper pondshells, *U. imbecillis*, produced multiple, consecutive broods based on observations of marked individuals having embryos in the gills in midsummer that matured and were released within 3–4 weeks, followed by deposition of another brood 2–14 days later. *Utterbackia* does not abort glochidia on disturbance, and the pattern is in marked contrast to other long-term brooding anodontines; however, observations were made only from July to September, and brooding behavior for the remainder of the year was unknown. Multiple brood production in *Utterbackia* appears to be a variable trait. Heard (1975, 1998) reported two gametogenic and brooding cycles per year in one population of Florida floaters, *U. peggyae*, but only one cycle per year in another population and in a population of *U. imbecillis*. Other anodontines in Florida appeared to produce only one brood, but the winter brooding period was much shorter than in populations farther north (Heard 1998).

Most reports of multiple brood production in the wild are from southerly populations below about 31°N latitude (e.g., Florida *Elliptio*, *Glebula*, *Popenaias*), suggesting that milder winters facilitate extended reproductive periods. Moreover, the flat spike, *Elliptio jayensis* (as *E. buckleyi*), appears to be nongravid only during June–July (Heard 1998), the main period of gravidity for northern short-term brooders. Because of their tendency to abort glochidia, it is difficult to study directly reproductive periodicity of short-term brooders in the wild, but this is an important question that needs more study.

6.2.C.2. Patterns of fecundity and reproductive effort

Fecundity differs among phylogenetic groups, but variation within most groups is so great that few useful generalizations can be made (Figure 6.7). Fecundity is uniformly high in the Margaritiferidae and is by far the highest on average of any group, but fecundity of smaller species, such as the Alabama pearlshell, *Margaritifera marrianae*, is unknown. The Amblemini and Lampsilini have moderately high fecundity, but fecundity of the Lampsilini spans an enormous range. Several lampsilines have relatively low fecundity (less than 20,000; e.g., *Epioblasma, Lemiox, Medionidus*), but others, including *Actinonaias, Glebula, Lampsilis, Leptodea, Ligumia recta, Potamilus*, and *Truncilla*, produce more than 500,000 glochidia, and fecundity of *Leptodea fragilis* exceeds that of even the Margaritiferidae. The Anodontini, Pleurobemini, and Quadrulini all have similar, lower median fecundities, but each group has conspicuous outliers with very high fecundity (Anodontini: *Arcidens confragosus, Pyganodon grandis*; Pleurobemini: *Elliptio crassidens*; Quadrulini: *Megalonaias nervosa*) (Haag, in press).

Patterns of energetic investment in reproduction among phylogenetic groups differ in several important ways from patterns of total fecundity (Figure 6.7). Because of their large glochidia, reproductive effort (the ratio of offspring mass to adult mass) is highest in the Anodontini, despite their relatively low mean fecundity, and RE is also high in the Lampsilini. In contrast, the Margaritiferidae have the lowest mean reproductive effort of any group, despite their high fecundity, a result that is explained by the diminutive glochidia of this group. Reproductive effort is low in the Amblemini, Pleurobemini, and Quadrulini, similar to the low fecundity of the latter two groups.

Among individuals in a population, fecundity is closely related to body size. Fecundity usually increases with shell length via a power function such that larger females have much higher fecundity than smaller individuals (Haag, in press; Figure 6.8). Other measures of body size, such as mass and shell volume, are also strongly positively related to fecundity but do not add appreciable explanatory power because of the close relationship between these variables and shell length (R^2 typically > 0.95; Haag, in press; see Benke et al. 1999). In a few cases, fecundity may reach an apparent asymptote or may even decline slightly in large individuals (Haag and Staton 2003). Residual variation in size–fecundity relationships may be explained by differences in energetic status among females and can be substantial in some populations (Bauer 1998). Body size explained little or no variation in reproductive effort among individuals in a population, but this relationship has been examined for few species (Haag, in press).

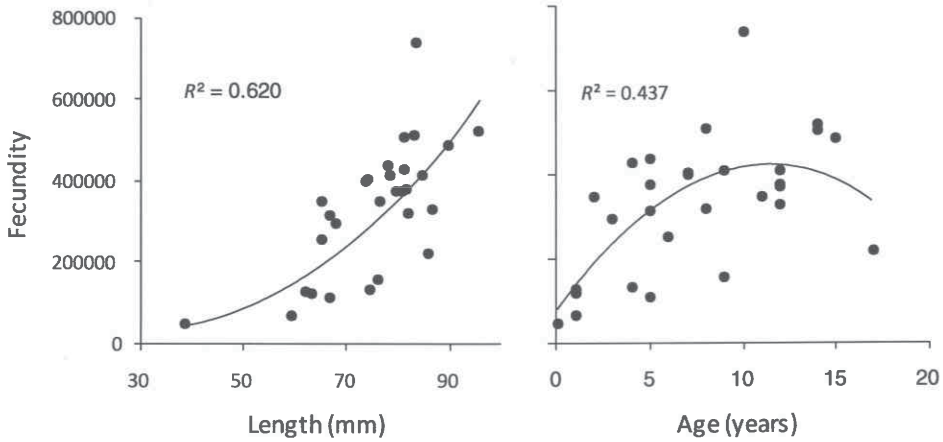

Figure 6.8. Relationships between fecundity, body size, and age for the southern pocketbook, *Lampsilis ornata*. The length relationship is a power curve, and the age relationship is a second-order polynomial (redrawn from Haag and Staton 2003).

Fecundity also generally increases with age, but this relationship is more variable than for length, and age is a less useful predictor of fecundity (Figure 6.8). Fecundity can appear to decline with increasing age, and this has been interpreted as evidence of reproductive senescence (Bauer 1987; Haag and Staton 2003; Figure 6.8). However, this pattern also may be due to variation in length at age among individuals. Although fecundity appears to decline with age in *Lampsilis ornata* and *Quadrula asperata* (Haag and Staton 2003), when the effect of length is accounted for, age is not a significant predictor of fecundity (analysis of covariance: *L. ornata*, $p < 0.385$, $F = 1.19$, 15 df; *Q. asperata*, $p < 0.500$, $F = 0.97$, 16 df; interaction between length and age not significant for either species). Nevertheless, the possibility of reproductive senescence is an important issue for conservation and needs more study. For example, large relict populations of the elephant-ear, *Elliptio crassidens*, exist in many streams but are composed exclusively of old individuals (often more than 50 years old) and show no evidence of recent recruitment (Section 10.5.A). The lack of recruitment is likely attributable to disruption of migratory host fish movement by dams, but it is difficult to find gravid females in these populations (W.R. Haag, observations); it is unknown whether this is due to senescence in these old individuals or simply an extremely short reproductive period.

Little is known about variation in fecundity or reproductive effort among populations or years. In four species, populations at different sites in a river or in different rivers had similar length-specific fecundities (Haag and Staton 2003). Length-specific fecundity of the threeridge, *Amblema plicata*, differed between two rivers, and differed among sites in a single river for the southern clubshell *Pleurobema decisum*. Length-specific fecundity of the threehorn wartyback, *Obliquaria reflexa*, did not differ between rivers, but mean fecundity differed because of differences in mean size

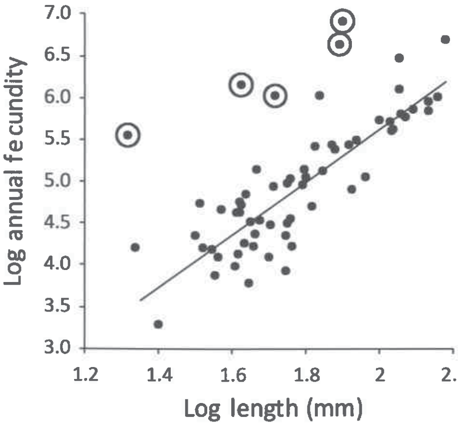

Figure 6.9. Relationship between annual fecundity and body size among 71 species. Regression line (log fecundity $= 3.146$(log length) $- 0.672$, $R^2 = 0.751$, $p < 0.001$) is for the data set excluding significant outliers (circled points, studentized residuals ≥ 2.0 in full data set). Outliers are *Leptodea fragilis, L. leptodon, Margaritifera margaritifera, Truncilla donaciformis*, and *T. truncata* (from Haag, in press).

between these populations. Differences in fecundity among populations over greater geographical scales have not been studied. Differences in mean fecundity are expected in populations with different mean sizes, but the causes or significance of differing length-specific fecundity among populations are unknown. In transplant experiments, European *Anodonta piscinalis* had higher reproductive output (measured as gravid gill mass) at sites where mussels grew fastest (Jokela and Mutikainen 1995a). This result was explained by assuming that sites with faster growth were more productive and provided more energy for reproduction; however, productivity was not measured directly, and the effect of transplant site on reproductive output was relatively low and was confounded to some extent by site of origin. Haukioja and Hakala (1978) reported differences in reproductive effort (based on the ratio of glochidial to somatic mass) among years in *A. piscinalis*, which they proposed were due to annual differences in resource availability. No other studies have examined annual differences in fecundity, and apparently none have directly assessed the role of productivity or other factors (e.g., stream discharge, water temperature).

Similar to variation among individuals in a population, variation in fecundity among species is explained primarily by body size. Fecundity increases with size via a power function, and size explains about half of the variation in fecundity among species ($R^2 = 0.512$; Haag, in press). However, this relationship is influenced by five outliers representing species with very high length-specific fecundity (*Leptodea fragilis, L. leptodon, Margaritifera margaritifera, Truncilla donaciformis*, and *T. truncata*). After omitting these outliers, length explains a much higher proportion of the variation in fecundity among species (75%; Figure 6.9). Shell volume (a surrogate for body mass) was a nearly equivalent predictor of fecundity (Haag, in press).

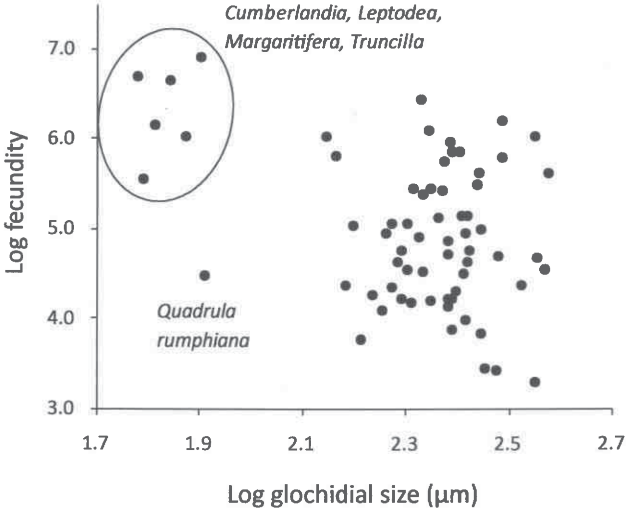

Figure 6.10. Relationship between fecundity and glochidial size (from Haag, in press).

6.2.C.3. Trade-offs and adaptive significance of fecundity

In many organisms, differences in reproductive investment among species follow predictable patterns representing trade-offs between fecundity, offspring size, and life span. Having smaller offspring and reduced parental care can allow higher fecundity because of lower energetic investment in individual offspring (e.g., Winemiller and Rose 1992). Similarly, short-lived species may have high annual fecundity or reproductive effort such that lifetime fecundity is comparable to longer-lived species with low annual fecundity (e.g., Charnov et al. 2007). Mussels are notable for their deviation from many of these pervasive patterns.

There is little relationship between fecundity and offspring size or the time invested in brooding offspring. Bauer (1994) proposed a trade-off between glochidial size and fecundity similar to that seen in other organisms, but this study was based on only seven species. Across 67 species, there is a negative but weak relationship between fecundity and glochidial size (Figure 6.10). However, this relationship is driven by six species with very small glochidia and high fecundity; these species include the five species identified previously as outliers in the length-fecundity relationship (Section 6.2.C.2) and also *Cumberlandia monodonta*. Omitting these species revealed no relationship between glochidial size and fecundity for the remaining 61 species, and fecundity of the ridged mapleleaf, *Quadrula rumphiana*, which also has miniature glochidia, is similar to other *Quadrula* with larger glochidia (Haag, in press). Species that invest more time in brooding glochidia (long-term brooders) produce on average *more* and larger glochidia and have higher reproductive effort than short-term brooders, contrary to predictions of life history theory (Haag, in press). However, these relationships are relatively weak, and fecundity and glochidial size overlap greatly among brooding

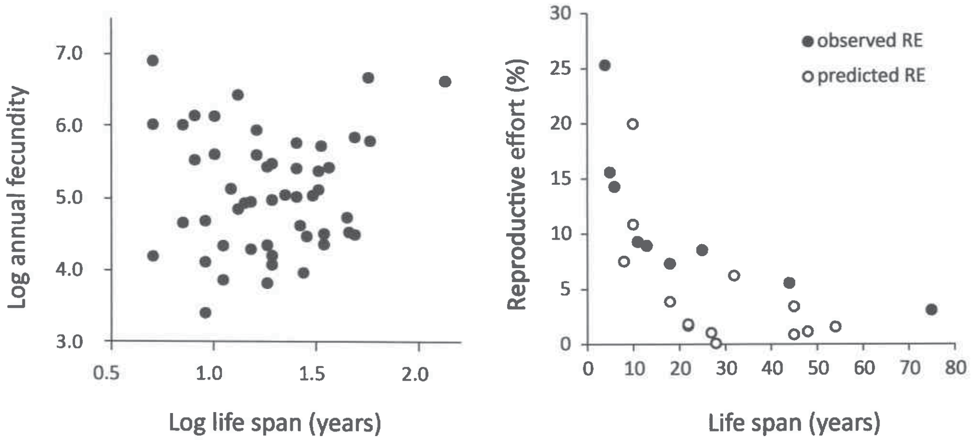

Figure 6.11. Relationships between annual fecundity, annual reproductive effort (RE), and life span in freshwater mussels. Annual fecundity was not related to life span. Regression equation for reproductive effort is arcsin RE $= -16.564$(log life span) $+ 35.254$; $p < 0.0001$, $R^2 = 0.632$ (observed and predicted RE combined); predicted RE was calculated based on length-dry mass relationships (from Haag, in press).

strategies. In a few species, reduced energetic investment in individual glochidia (due to their small size) may facilitate extraordinarily high fecundity, and this trade-off may incur the cost of requiring a prolonged period of glochidial attachment, during which chances for host death are increased (Chapter 5). For most species, glochidial size and brooding time have little, if any, bearing on reproductive output.

Annual fecundity in mussels is not related to life span (Figure 6.11); at each extreme of the life span spectrum are found species with both very high and very low fecundities (Table 6.2). Lifetime fecundity is positively related to life span, but life span explains little of the variation in lifetime fecundity ($R^2 = 0.167$) and this relationship may be largely an artifact of the weak, positive relationship between life span and body size (Section 6.1); rather, lifetime fecundity is simply a strong function of annual fecundity ($R^2 = 0.882$; Haag, in press). In contrast, annual reproductive effort decreases sharply with increasing life span as predicted by theory (Figure 6.11). This provides compelling evidence for a strong trade-off between life span and reproductive effort.

Because of the great variation among species in host use and infection strategies (Chapter 5), it is reasonable to expect these factors to be related to fecundity. For example, highly efficient host infection strategies should require lower fecundity compared to less efficient strategies (Wächtler et al. 2001). However, there are few strong patterns of differing fecundity among host strategies (Haag, in press). Fecundity is highest for specialists on freshwater drum or salmonids, but there are few significant differences among other host-use groups. Generalists have among the lowest mean fecundity of any group, suggesting that a broad host range requires lower fecundity,

Table 6.2. *Patterns of annual fecundity, lifetime fecundity, and life span for selected mussel species*

Species	Life span (years)	Annual fecundity	Lifetime fecundity
Leptodea fragilis	5	9,586,987	47,934,935
Medionidus acutissimus	5	16,258	65,032
Pyganodon grandis	11	412,300	4,535,300
Epioblasma florentina aureola	11	7,213	79,343
Lampsilis ornata	17	281,776	4,790,192
Plectomerus dombeyanus	33	553,500	18,265,500
Fusconaia cerina	34	23,890	812,260
Quadrula pustulosa	48	28,369	1,361,712
Elliptio crassidens	57	651,250	37,121,250
Margaritifera margaritifera	132	4,421,688	583,662,816

Note: Data are from Haag and Rypel (2011) and Haag (in press).

but the range of fecundity in this strategy overlaps widely with others. The high fecundity of drum and salmonid specialists may be related not to host use specifically but to the fact that some of these mussel species may be broadcasters (e.g., *Leptodea fragilis*, *Margaritifera margaritifera*). Species that apparently broadcast free glochidia have higher fecundity than those with other host infection strategies, suggesting that this is an inefficient strategy and that these species are under selective pressure to maximize fecundity at the expense of offspring size (see previous discussion). There are no significant differences in fecundity among other host infection strategies, suggesting that they have similar efficiencies or that differences in infection efficiency do not impose strong selection pressure on fecundity. There is a trend for lower fecundity in species that use pelagic conglutinates or mantle magazines, and that broadcast glochidia in mucus webs. However, these differences may be confounded with phylogenetic relationships among species or structural constraints on fecundity (e.g., unfertilized structural eggs in pelagic conglutinates). Overall, host use and host infection strategies add little explanatory power beyond that provided by the strong relationship between body size and fecundity (Haag, in press).

Unlike the strong associations between other life history traits such as growth, life span, and age at maturity, patterns of fecundity show little evidence of trade-offs despite the great variation in fecundity among species. For species that broadcast free glochidia, extraordinarily high fecundity at the cost of reduced glochidial size may be selected for to maximize chances of host infection. Otherwise, fecundity appears to be primarily a function of body size at both the population and species level. This suggests that mussels simply maximize glochidial production within the physical and energetic constraints imposed by body size and the size of glochidia necessary for rapid metamorphosis.

By integrating fecundity, glochidial size, and body mass, reproductive effort seems a more valuable measure of reproduction allocation, and the negative relationship between reproductive effort and life span is indicative of a strong trade-off between reproduction and other functions. High and early investment in reproduction can decrease life span because of diversion of resources from somatic maintenance, and also because of adult mortality associated with reproductive behaviors. Consequently, long-lived organisms are expected to devote less energy to reproduction per unit time compared with short-lived organisms (Williams 1966; Stearns 1992; Charlesworth 1994). Nevertheless, reproductive effort is generally low in mussels; among 19 species, RE averaged only 7% and exceeded 10% in few species (Haag, in press; Figure 6.11). This contrasts markedly with marine bivalves, for which RE often exceeds 40% (Dame 1996), and suggests that production of glochidia incurs comparatively little cost, and consequently, patterns of reproductive allocation may have had little role in shaping mussel life histories (see Tuomi et al. 1983; Haag, in press). However, estimates of reproductive effort remain unavailable for most species, and methods to accurately estimate inclusive costs of reproduction for mussels need refinement. For example, available estimates of reproductive effort for mussels do not consider potential differences in caloric content of reproductive versus somatic tissue, lifetime schedules of production and reproductive activity, or costs of brooding, conglutinate production, and reproductive behaviors such as lure display (Haag, in press). Additional studies of reproductive effort are clearly needed to further elucidate patterns of life history diversification in mussels.

6.3. Life history strategies and some outliers

It is clear that life history traits vary greatly among mussel species, but does this variation show consistent patterns that are useful in an ecological context? In the following section, I explore patterns of variation in mussel life histories to test for the existence of strategies that can represent groups of species with similar traits. I compiled information on the following life history traits for 47 populations of 45 species: maximum life span, age at maturity, mean fecundity, maximum adult size, glochidia size, and duration of glochidial brooding (short or long term). These species represent a cross section of North American mussel diversity and include multiple members of all families and tribes. Values and sources for this data set are presented in Appendix A. If multiple values were available for a trait, I used the mean of these values. All traits are represented by observed values, except for age at maturity. Observed estimates of age at maturity were available for 20 species in the data set; for the remaining species, I used estimates predicted from growth rate (K; Figure 6.6), when this value was available. I assumed that glochidial size and brooding period were relatively invariant within species (see Kennedy and Haag 2005; Section 1.4.C). For *Hamiota altilis* and *Ptychobranchus fasciolaris*, I used fecundity estimates for the closely related *H. australis* and *P. subtentum*, respectively. Life span, fecundity, and size of *Amblema plicata* varied considerably among populations in the data set. Because two populations had fairly complete life history information, the data set contains three entries for this species: a population in the Little Tallahatchie River, Mississippi; a population in the Sipsey River, Alabama; and a composite entry representing mean values across these and other populations. I did not use growth rate (K) or reproductive effort (RE) as variables because they were not available for all species, they are highly correlated with life span, and K was used as a predictor for age at maturity.

I explored patterns of variation in life history traits using nonmetric multidimensional scaling (NMS). NMS is similar conceptually to other ordination methods (e.g., principal component analysis) but differs in that it is distribution-free and therefore often provides a more flexible and generalizable representation of ecological data (McCune and Grace 2002). I omitted brooding period from the final analysis because the categorical nature of this variable tended to swamp continuous variables and simply clustered species into two groups (short- or long-term brooders). The best solution to this reduced data set portrayed variation in life history traits along two axes (Figure 6.12). Axis 2 described most of the variation among species (72%) and represented a continuum from short-lived species with early maturity to long-lived species with late maturity. Axis 1 described only 24 percent of the observed variation and represented a continuum from small species with low fecundity to large species with high fecundity. Although on each axis, the two most important variables are intercorrelated, inclusion of these partially redundant variables provides additional separation among species. For example, the Alabama spike, *Elliptio arca*, matures at an early age (age 2), but its greater life span separates it on axis 2 from other species with early maturity but shorter lives. On axis 1, species with similar fecundity were separated by size, describing differences in length-specific fecundity. Glochidial size was not an important variable for describing patterns of life history variation; species with diminutive glochidia (e.g., *Leptodea fragilis, Margaritifera margaritifera, Quadrula rumphiana*) appear throughout the ordination space. The low contribution of fecundity in depicting life history differences among species is concordant with the idea that variation in fecundity has less adaptive significance than other traits (Section 6.2.C). Nevertheless, fecundity did provide additional discrimination among species, particularly those with extremely high fecundity. Because mussel life history is described well by only two traits, life span (and the related age at maturity) and fecundity (and the related body size), patterns of covariation in these traits can be portrayed on a bivariate plot, which further emphasizes the great differences among species (Figure 6.13).

The spatial pattern of species in life history space suggests three divergent life history strategies for North American mussels. To describe these strategies, I have drawn from concepts in fish and plant ecology, particularly Winemiller and Rose (1992)

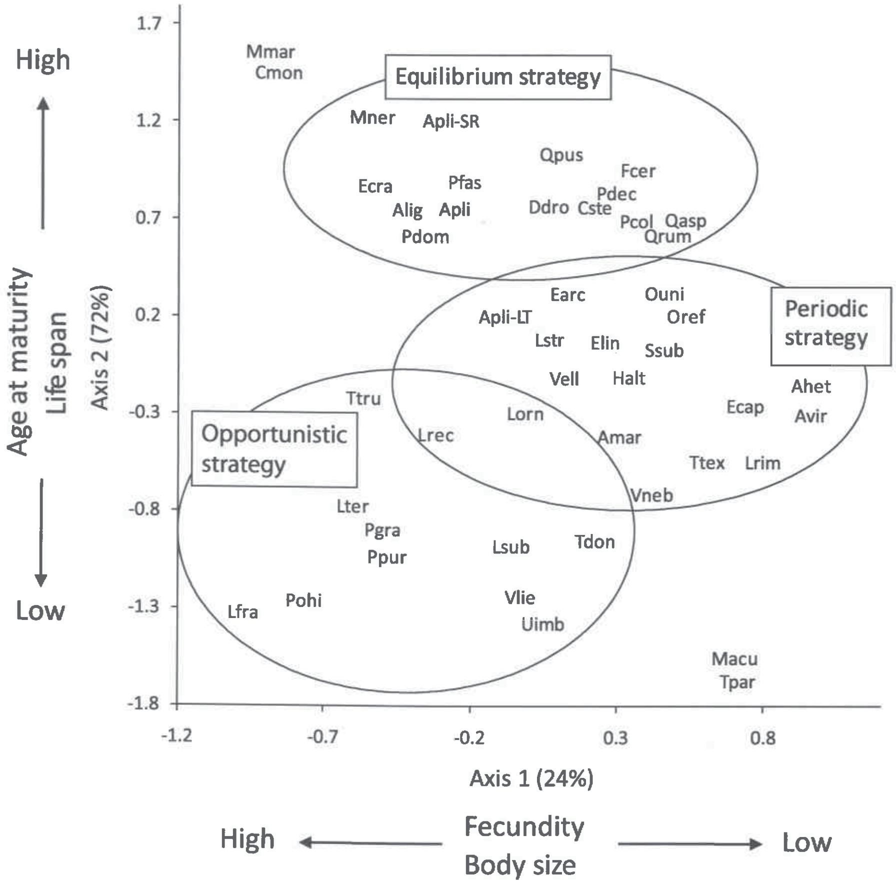

Figure 6.12. Ordination of 45 mussel species based on five life history traits (maximum life span, age at maturity, annual fecundity, glochidial size, and maximum adult size; nonmetric multidimensional scaling based on Sørensen distance, PC-ORD; McCune and Mefford 1999). All traits were log-transformed (age at maturity + 1) and relativized by column (trait) totals to account for the differing units and scales of life history traits. The best solution was two-dimensional (96% of variation among species, final stress = 9.27, instability = 0.00001). Numbers in parentheses on axis titles give the percentage of variation explained by that axis; note that axis 2 explains the most variation. Traits with the highest correlations on each axis are indicated along with the relative magnitude of each trait (from low to high). Species codes are as follows: Ahet, *Alasmidonta heterodon*; Amar, *A. marginata*; Avir, *A. viridis*; Alig, *Actinonaias ligamentina*; Apli, mean values for *Amblema plicata* (see text); Apli-LT, *A. plicata*, Little Tallahatchie River; Apli-SR, *A. plicata*, Sipsey River; Cmon, *Cumberlandia monodonta*; Cste, *Cyprogenia stegaria*; Ddro, *Dromus dromas*; Earc, *Elliptio arca*; Ecra, *E. crassidens*; Ecap, *Epioblasma capsaeformis*; Elin, *Ellipsaria lineolata*; Fcer, *Fusconaia cerina*; Halt, *Hamiota altilis*; Lfra, *Leptodea fragilis*; Lorn, *Lampsilis ornata*; Lstr, *L. straminea*; Lter, *L. teres*; Lrec, *Ligumia recta*; Lsub, *L. subrostrata*; Lrim, *Lemiox rimosus*; Macu, *Medionidus acutissimus*; Mmar, *Margaritifera margaritifera*; Mner, *Megalonaias nervosa*; Oref, *Obliquaria reflexa*; Ouni, *Obovaria unicolor*; Pcol, *Pleurobema collina*; Pdec, *P. decisum*; Pdom, *Plectomerus dombeyanus*; Pfas, *Ptychobranchus fasciolaris*; Pgra, *Pyganodon grandis*; Pohi, *Potamilus ohiensis*; Ppur, *P. purpuratus*; Qasp, *Quadrula asperata*; Qpus, *Q. pustulosa*; Qrum, *Quadrula rumphiana*; Ssub, *Strophitus subvexus*; Tdon, *Truncilla donaciformis*; Ttru, *T. truncata*; Tpar, *Toxolasma parva*; Ttex, *T. texasensis*; Uimb, *Utterbackia imbecillis*; Vell, *Venustaconcha ellipsiformis*; Vlie, *Villosa lienosa*; Vneb, *V. nebulosa*.

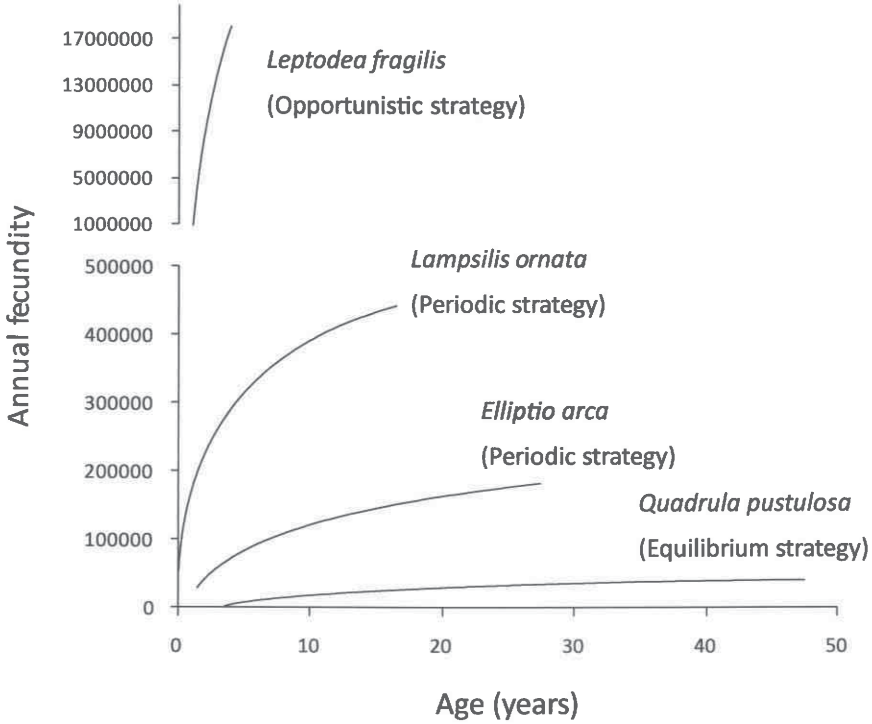

Figure 6.13. Relationship between individual age and fecundity for four North American mussel species. Note the difference in scale on the *y* axis for *Leptodea fragilis* (data from Haag and Staton 2003; Haag and Rypel 2011; Haag, in press).

and Grime (2001). Both frameworks use a triangular continuum with three end point strategies to represent patterns of life history variation. These frameworks are viewed as improvements or alternatives to the concept of *r* and *K* selection, which portrays life history variation along a continuum with only two end points (Pianka 1970). The C-S-R framework of Grime (2001) for plants employs the strategies: competitors, stress tolerators, and ruderals. The C-S-R framework was used to describe life history variation in freshwater snails (Dillon 2000). I adapted the terminology of Winemiller and Rose (1992) for fishes, which identifies three divergent life history strategies: *opportunistic*, *equilibrium*, and *periodic* (Table 6.3). In the following paragraphs, I describe each of these strategies as it applies to mussels and compare the strategies with those described for fishes and plants as well as with the concept of *r* and *K* selection.

6.3.A. Opportunistic strategy

The opportunistic strategy for mussels is characterized by short life span, early maturity, high fecundity, and, to a lesser extent, moderate to large body size (Table 6.3). These species also have the fastest growth rates and highest reproductive effort (despite

Table 6.3. *Life history strategies of North American freshwater mussels*

Traits	Opportunistic strategy	Periodic strategy	Equilibrium strategy
Life span (years)	low (≤10)	moderate (8–30)	high (>25)
Age at maturity (years)	low (0–2)	low–moderate (1–3)	high (>3)
Fecundity	moderate–very high	low–moderate	variable; typically low, but broadcasters high
Max. adult size (mm)	moderate–large	small–moderate	moderate–large
Brooding strategy	long-term or multicyclic[a]	mostly long-term	mostly short-term
Growth rate (*K*)	high	moderate–high	low–moderate
Taxonomic representation	Anodontini: *Anodonta*, *Lasmigona complanata*, *Pyganodon*, *Utterbackia* Lampsilini: *Lampsilis teres*, *Leptodea*, *Ligumia subrostrata*, *Potamilus*, *Toxolasma parva*, *Truncilla*, some *Villosa* (e.g., *V. lienosa*)	Anodontini: *Alasmidonta*, *Strophitus*, most *Lasmigona*, *Pegias*, *Simpsonaias* Lampsilini: *Ellipsaria*, *Epioblasma*, *Hamiota*, most *Lampsilis*, *Lemiox*, *Ligumia recta*, *Medionidus*, *Obliquaria*, *Obovaria*, some *Toxolasma*, *Venustaconcha*, most *Villosa* Pleurobemini: some *Elliptio* Quadrulini: *Q. cylindrica* (?), *Uniomerus* (?)	Margaritiferidae Amblemini Lampsilini: *Actinonaias*, *Cyprogenia*, *Dromas*, *Ptychobranchus* Pleurobemini: some *Elliptio*, *Fusconaia*, *Pleurobema*, *Pleuronaia* most Quadrulini incertae sedis: *Reginaia ebena*, *Plectomerus dombeyanus*

[a] Only for *Utterbackia*.

the low-moderate fecundity of some Anodontini) of any North American species. The high investment in reproduction is further illustrated in that high fecundity is achieved soon after maturation, and nearly all species are long-term brooders. The opportunistic strategy occurs only in the Anodontini and Lampsilini, and extreme examples include *Lampsilis teres*, *Leptodea fragilis*, *Potamilus* spp., *Pyganodon grandis*, and *Utterbackia imbecillis* (Figure 6.12). The suite of traits that characterize the opportunistic strategy for mussels is shared by ruderal plant species in the C-S-R model and by *r*-selected species. In fishes, the opportunistic strategy differs only in having low batch fecundity, but overall reproductive effort is higher because these fishes usually have multiple spawnings per year. This feature of fish life history has one known analog for mussels: *Utterbackia imbecillis* has relatively low fecundity (but high reproductive effort) but may produce multiple consecutive broods in a single season. This trait is not accounted for in the data set because the number of broods produced is unknown and apparently variable among populations (Section 6.2.C). Production of multiple broods would result in higher fecundity and placement of this species nearer to the end point for the opportunistic strategy. For all organisms, fast growth, short life, early maturity, and high reproductive effort are considered adaptations for rapid colonization and persistence in disturbed and unstable but productive habitats (Chapter 8).

6.3.B. Equilibrium strategy

The equilibrium strategy for mussels is characterized primarily by long life span and late maturity. Fecundity is uniformly low in most species and is high only in generalists that use a broadcasting host infection strategy (e.g., *Actinonaias*, *Amblema*, *Margaritifera*, *Megalonaias*); however, reproductive effort of most of these species, especially *Margaritifera*, is low, despite high fecundity. In addition, unlike opportunists and periodic species, fecundity increases slowly after maturation, further delaying attainment of maximal reproductive output (Section 6.2.C). Many equilibrium species with low investment in fecundity also are short-term brooders. Body size is highly variable, but very small species are absent in this strategy. The equilibrium strategy occurs primarily in the Amblemini, Pleurobemini, and Quadrulini but also in a few lampsiline genera (Table 6.3), and the Margaritiferidae appear to represent extreme examples of the strategy (Figure 6.12). This strategy is broadly analogous to the equilibrium strategy for fishes, the competitor strategy for plants, and to *K*-selected species. These suites of life history traits are considered to be favored in stable, productive habitats.

6.3.C. Periodic strategy

The periodic strategy for mussels is characterized by moderate to high growth rate, low to intermediate life span, age at maturity, and fecundity but generally smaller body size than opportunistic species (Table 6.3). Most species are long-term brooders. This strategy encompasses the widest taxonomic breadth of any strategy, potentially including members of all unionid tribes, but is dominated by species in the Anodontini and Lampsilini. Species near the end point for this strategy include *Alasmidonta* spp., the oyster mussel, *Epioblasma capsaeformis*, and the birdwing pearlymussel, *Lemiox rimosus* (Figure 6.12). The periodic strategy for mussels occupies an intermediate position between the end points of the *r*- and *K*-selection continuum but deviates in several respects from the periodic strategy for fishes (high fecundity and late age at maturity) and the stress-tolerant strategy for plants (low fecundity and growth rate, late age at maturity). However, for both fishes and plants, these strategies are considered adaptations to allow species to persist in unproductive habitats or habitats that are subjected to large-scale, cyclical environmental variation or stress.

Similar to life history frameworks for other organisms, proposal of these strategies for mussels is not meant to imply that they represent black boxes into which all species can be placed cleanly; rather, this framework represents a trilateral continuum of life history variation, and the boundaries of the ellipses I have drawn to represent these strategies are arbitrary. Some species have suites of traits that clearly represent the end points of the continuum, such as the fragile papershell, *Leptodea fragilis*, and pink papershell, *Potamilus ohiensis* (opportunistic strategy); dwarf wedgemussel, *Alasmidonta heterodon*, and slippershell mussel, *A. viridis* (periodic strategy); and the washboard, *Megalonaias nervosa* (equilibrium strategy). Other species fall along this continuum in a position that does not allow them to be classified easily into a particular strategy. For example, the southern pocketbook, *Lampsilis ornata*, and black sandshell, *Ligumia recta*, are intermediate between the end points for the opportunistic and periodic strategies, and the Alabama spike, *Elliptio arca*, may be classified as either an equilibrium or periodic strategist (Figure 6.12). Furthermore, because of phenotypic plasticity in life history traits, strategies may vary among populations for some species. The long-lived population of threeridge, *Amblema plicata*, in the Sipsey River and the composite suite of traits for this species fall well within the equilibrium strategy. However, the shorter-lived and earlier-maturing population in the Little Tallahatchie River is best classified within the periodic strategy but is near the equilibrium strategy, similar to *E. arca*.

A few species are notable outliers in this framework. The spectaclecase, *Cumberlandia monodonta*, and eastern pearlshell, *Margaratifera margaritifera*, appear to represent extreme examples of the equilibrium strategy based on their high life span and age at maturity but also have extremely high fecundity, similar to opportunistic species. *Margaritifera* deviates further from other equilibrium species by its occurrence primarily in low-productivity habitats (Section 4.1.C), contrary to predictions of life history theory. This suite of life history traits is seen in no other mussel species, highlighting the unique ecological role of the Margaritiferidae (Section 8.6). The Alabama moccasinshell, *Medionidus acutissimus*, and lilliput, *Toxolasma parva*, grouped together far from all other species based on their diminutive size, low fecundity, very short life spans, and maturity at age 0–1 (Figure 6.12). However, these species occur in very different habitats, suggesting that their life histories represent similar solutions to different challenges. *Medionidus* is most prevalent in small to medium-sized streams, which are dominated by periodic strategists (Chapter 8). Other *Medionidus* (e.g., *M. conradicus*) appear to mature at a slightly later age and have longer life spans (Zale and Neves 1982a), placing them more firmly within the periodic strategy. In contrast, *T. parva* occurs in a wide variety of habitats, including ditches, wetlands, and highly disturbed streams. In these habitats, it typically occurs with opportunistic species but is often the only species in a water body, indicating that it has very high colonizing ability. These traits, along with reliance on simultaneous hermaphroditism (similar to *Utterbackia imbecillis*), suggest that *T. parva* represents an unusual but extreme example of the opportunistic strategy.

At this time, comprehensive life history information is unavailable for most North American species. However, because classification of life history strategies is determined primarily by life span, age at maturity, fecundity, and body size, other species with limited life history information may be placed provisionally into these strategies. The anodontine genera *Lasmigona* (except *L. complanata*), *Pegias*, and *Simpsonaias* have one or more of the following traits characteristic of the periodic strategy: small size, low to moderate fecundity, and low to moderate age at maturity and life span (Appendix A); *L. complanata* appears to represent the opportunistic strategy on the basis of its large size, high fecundity, and short life span (Haag in press; W.R. Haag, unpublished data). The rabbitsfoot, *Quadrula cylindrica*, has a shorter life span than other equilibrium species in the Quadrulini, suggesting that this species may fall nearer the periodic strategy. *Pleuronaia* (Pleurobemini) and the ebonyshell, *Reginaia ebena* (incertae sedis), have long life spans and low fecundity typical of the equilibrium strategy. Life span and age of maturity of *Uniomerus* are unknown, but the pondhorn, *U. tetralasmus*, has very low fecundity (Haag, in press). Although *Uniomerus* often occurs with opportunistic species in disturbed or ephemeral habitats, the unusual ability of these species to aestivate for extended periods (Section 4.1.D.1) may allow them to cope with frequent or cyclic disturbance in a manner similar to periodic strategists. Additional information about mussel life histories, particularly estimates of reproductive effort, will allow refinement of these classifications and likely will reveal other variations on these strategies.

Far from the previous generalized depictions of mussel life history, North American mussels encompass a diverse array of life history strategies. These strategies do not appear to be simply phylogenetic artifacts resulting from suites of traits inherited within lineages; rather, most phylogenetic groups have representatives in multiple strategies, suggesting that unrelated species have found similar solutions to common ecological challenges. These fundamental differences among species have far-reaching consequences for mussel ecology and conservation.

An important feature of life history frameworks for other organisms is that they specify the relative importance to each strategy of competition and other biotic interactions, as well as disturbance and environmental stress, and how these factors influence survivorship and population growth (Winemiller and Rose 1992; Grime 2001). Similarly, the concept of r and K selection is predicated on the type of selection operating on a population, specifically, whether or not the population is limited by density dependence (Pianka 1970). These mechanisms largely determine the composition of biological communities in different habitats and generate predictions that can be used to test ideas about life history divergence. In Chapter 7, I examine how these life history strategies influence population dynamics and the potential influence of biotic interactions on population growth. Then, in Chapter 8, I attempt to integrate these ideas, along with patterns of habitat and host use from Chapters 4 and 5, into a framework that can explain how mussel assemblages are structured. Finally, in Chapters 10 and 11, I examine how life history strategies influence the vulnerability of mussel species to human impacts and how understanding life history diversity may allow us to more effectively conserve these animals.

Plate 1. Variation in shell form and coloration in North American mussels I: Ovate or elliptical shells (specimen shell length in parentheses). (left, from top) Fine-lined pocketbook, *Hamiota altilis* (53 mm); eastern elliptio, *Elliptio complanata* (82 mm); painted creekshell, *Villosa taeniata* (54 mm); fat pocketbook, *Potamilus capax* (107 mm). (right, from top) Round hickorynut, *Obovaria subrotunda* (65 mm); barrel floater, *Anodonta couperiana* (68 mm); yellow sandshell, *Lampsilis teres* (107 mm); Altamaha arc-mussel, *Alasmidonta arcula* (47 mm) (Richard T. Bryant, photos).

Plate 2. Variation in shell form and coloration in North American mussels II: Triangular or quadrate shells. (left, from top) Deertoe, *Truncilla truncata* (67 mm); shiny pigtoe, *Fusconaia cor* (36 mm); rabbitsfoot, *Quadrula cylindrica* (65 mm); threehorn wartyback, *Obliquaria reflexa* (42 mm). (right, from top) Mapleleaf, *Quadrula quadrula* (49 mm); Ohio pigtoe, *Pleurobema cordatum* (71 mm); pimpleback, *Quadrula pustulosa* (23 mm); threehorn wartyback, *Obliquaria reflexa* (43 mm); both individuals of *O. reflexa* are from the same population showing distinct external color phases (Richard T. Bryant, photos).

Plate 3. Evolutionary convergence in shell morphology I: Lanceolate shells. (from top) Altamaha lance, *Elliptio shepardiana* (Unionidae, Pleurobemini, North America, 133 mm); *Lamproscapha ensiformis* (Mycetopodidae, South America, 124 mm); *Lanceolaria grayana* (Unionidae, Unionini, Southeast Asia, 94 mm) (Richard T. Bryant, photos).

Plate 4. Evolutionary convergence in shell morphology II: Dorsal wings. (clockwise from top left) Winged floater, *Anodonta nuttalliana* (Anodontini, North America, 61 mm); *Hyriopsis cumingii* (Unionini, Southeast Asia, 131 mm); pink papershell, *Potamilus ohiensis* (Lampsilini, North America, 108 mm); Alabama heelsplitter, *Lasmigona alabamensis* (Anodontini, North America); all Unionidae (Richard T. Bryant, photos).

Plate 5. Sexual dimorphism in North American mussels. Males (M) are to the left. (from top) Leafshell, *Epioblasma flexuosa* (M, 55 mm; F, 59 mm); Duck River dartersnapper, *Epioblasma ahlstedti* (M, 53 mm; F, 54 mm); little spectaclecase, *Villosa lienosa* (M, 44 mm; F, 47 mm); scaleshell, *Leptodea leptodon* (M, 80 mm; F, 49 mm); pistolgrip, *Quadrula verrucosa* (M, 94 mm; F, 107 mm) (Richard T. Bryant, photos).

Plate 6. Evolutionary convergence in shell morphology III: Dorsal slope sculpture. (clockwise from top left) Alabama pearlshell, *Margaritifera marrianae* (Margaritiferidae, 65 mm); fluted elephant-ear, *Elliptio mcmichaeli* (Unionidae, Pleurobemini, 35 mm); fluted kidneyshell, *Ptychobranchus subtentum* (Unionidae, Lampsilini, 59 mm); *Lasmigona costata* (Unionidae, Anodontini, 76 mm); all North American (Richard T. Bryant, photos).

Plate 7. Evolutionary convergence in shell morphology IV: Parallel ridge sculpture. (clockwise from top left) Threeridge, *Amblema plicata* (Amblemini, 96 mm); fat threeridge, *Amblema neislerii* (Amblemini, 70 mm); washboard, *Megalonaias nervosa* (Quadrulini, 120 mm); rock-pocketbook, *Arcidens confragosus* (Anodontini, 104 mm); all Unionidae and North American (Richard T. Bryant, photos).

Plate 8. Evolutionary convergence in shell morphology V: Tubercles. (clockwise from top left) Orange-foot pimpleback, *Plethobasus cooperianus* (Pleurobemini, North America, 69 mm); Alabama orb, *Quadrula asperata* (Quadrulini, North America, 52 mm); *Lamprotula coreana* (Unionini, Southeast Asia, 56 mm); fanshell, *Cyprogenia stegaria* (Lampsilini, North America, 53 mm); all Unionidae (Richard T. Bryant, photos).

Plate 9. Altamaha spinymussel, *Elliptio spinosa* (North America, 78 mm) (Richard T. Bryant, photo).

Plate 10. Variation in nacre color in North American mussels I. (left, from top) Altamaha arc-mussel, *Alasmidonta arcula* (47 mm); bleufer, *Potamilus purpuratus* (195 mm); threeridge, *Amblema plicata* (117 mm); downy rainbow, *Villosa villosa* (52 mm). (right, from top) Hickorynut, *Obovaria olivaria* (55 mm); ring pink, *Obovaria retusa* (67 mm); black sandshell, *Ligumia recta* (149 mm); Cumberland moccasinshell, *Medionidus conradicus* (44 mm) (Richard T. Bryant, photos).

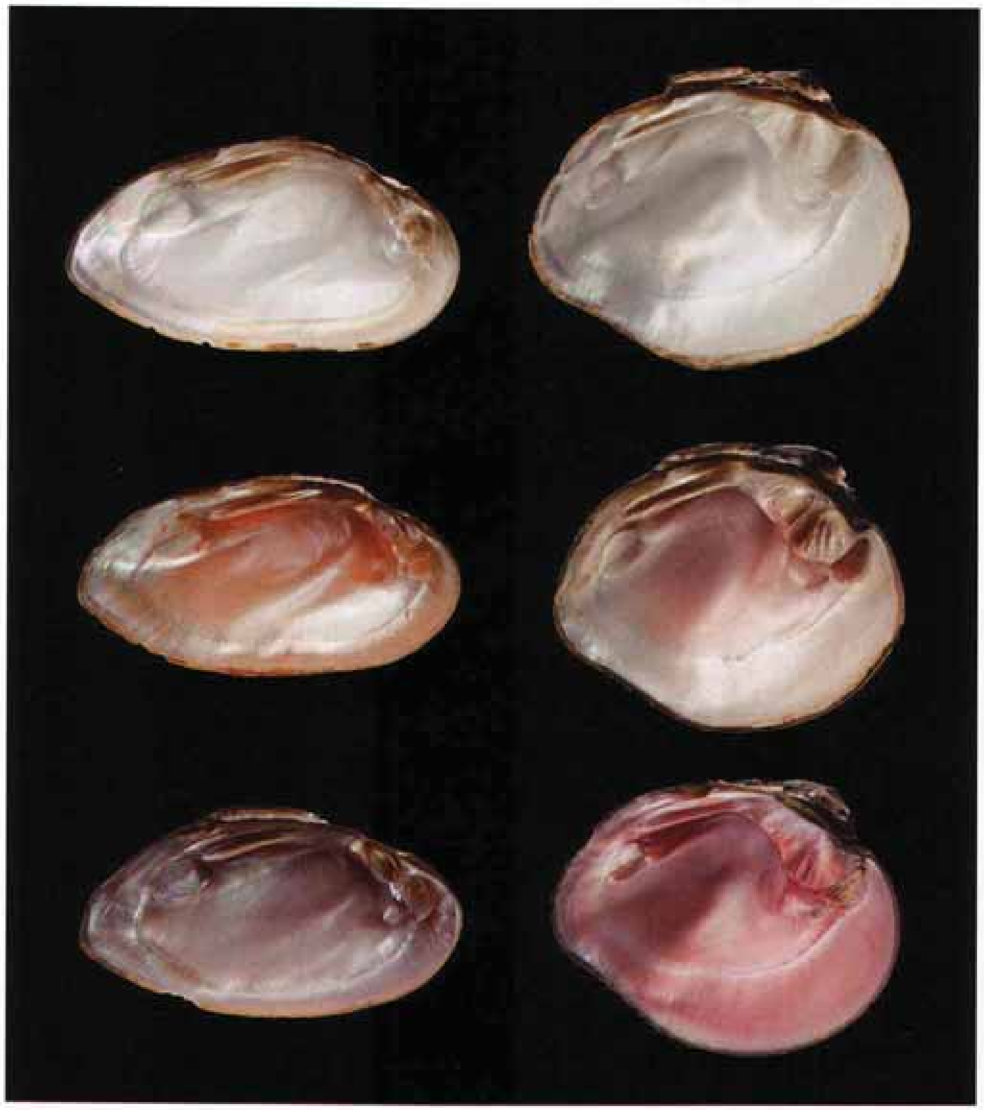

Plate 11. Variation in nacre color in North American mussels II. (left) Polymorphic variation in the Alabama spike, *Elliptio arca*, showing distinct, non-intergrading color phases (white, orange, and purple). (right) Continuous variation in the threehorn wartyback, *Obliquaria reflexa*, from a single population, showing intergrade (center) between white and red nacre (Richard T. Bryant, photos).

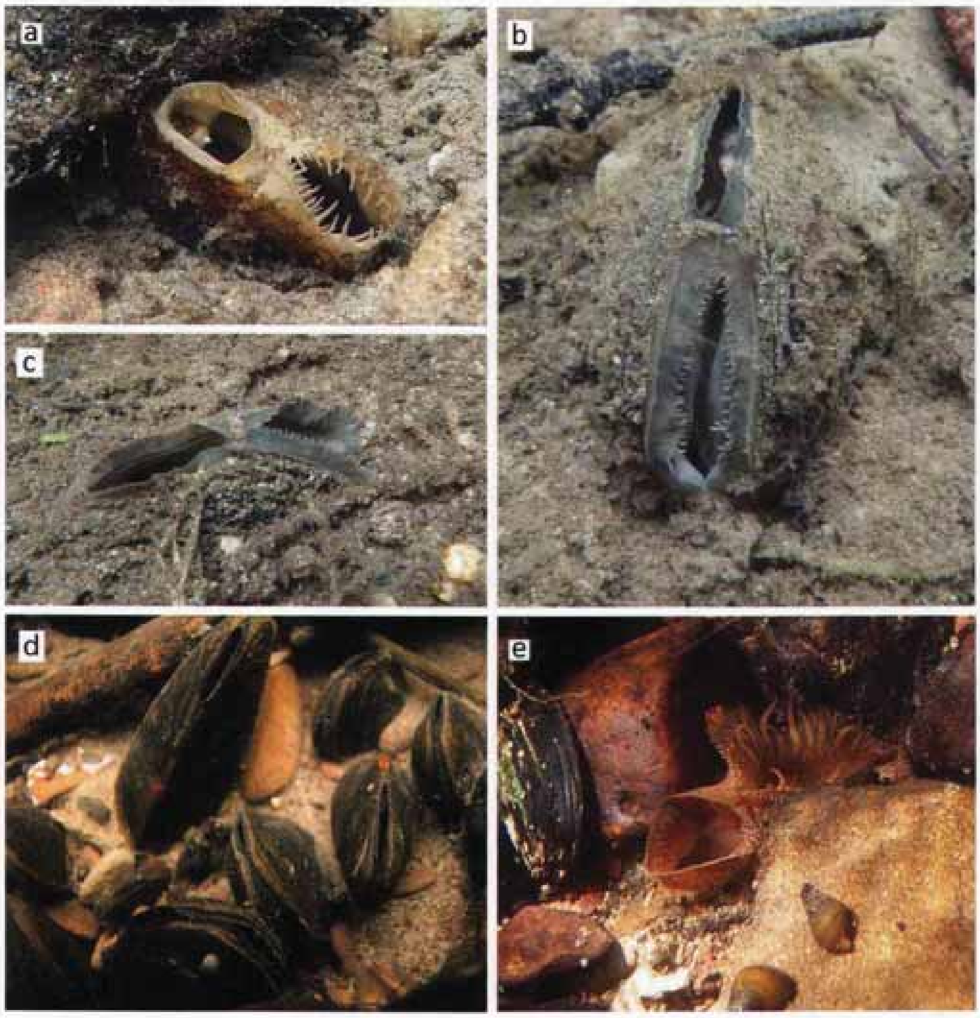

Plate 12. Mussels oriented naturally in stream sediments and actively filtering. Inhalant apertures are ornamented with papillae, but exhalent apertures are unornamented. (a) southern pigtoe, *Pleurobema georgianum* (Alabama Aquatic Biodiversity Center (AABC), photo, courtesy Paul Johnson). (b, c) Alabama creekmussel, *Strophitus connasaugensis*. Individual in (b) is only partly buried, but note heavy accumulation of sediment and biofilm on shell (AABC, photos, courtesy Paul Johnson). (d) Western pearlshell, *Margaritifera falcata* (Jeremy Monroe, photo, courtesy Freshwaters Illustrated). (e) Southern pocketbook, *Lampsilis ornata* (Paul Freeman, photo).

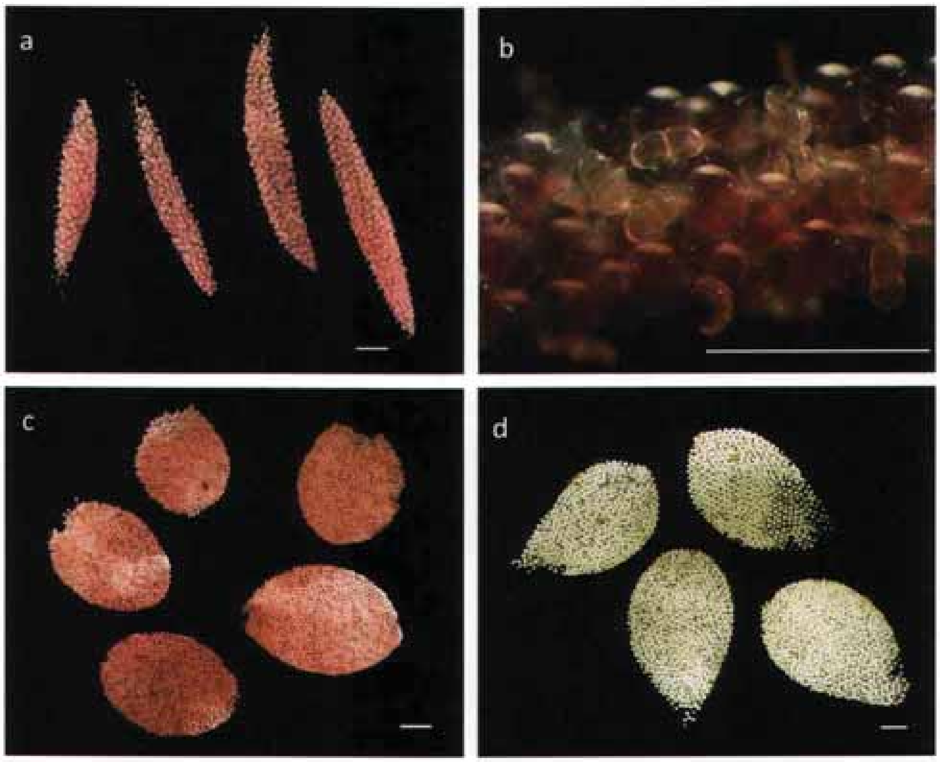

Plate 13. Pelagic conglutinates. (a) Gulf pigtoe, *Fusconaia cerina*. (b) *F. cerina* detail showing pigmented, undeveloped eggs and colorless, mature glochidia. (c, d) Southern clubshell, *Pleurobema decisum*, showing two conglutinate color phases; scale bar = 1 mm in all (W. R. Haag, photos).

Plate 14. Demersal conglutinates. (a) Ouachita kidneyshell, *Ptychobranchus occidentalis*, larval fish or insect mimic. (b) Fluted kidneyshell, *P. subtentum*, blackfly pupa mimic. (c) Triangular kidneyshell, *P. greenii*, fish egg mimic (conglutinates within gill). (d) Western fanshell, *Cyprogenia aberti*, worm mimic. (c, Paul Hartfield, photo; all others, Chris Barnhart).

Plate 15. Superconglutinates of the orange-nacre mucket, *Hamiota perovalis*. (a–c) Early stages of release showing paired superconglutinates; mucus tube tethering superconglutinates to female is not visible. (d) Later stage of release showing single superconglutinate after disassociation; mucus tube is indicated by arrow. (a, b, Chris Barnhart, photos; c, d, William Roston, photos).

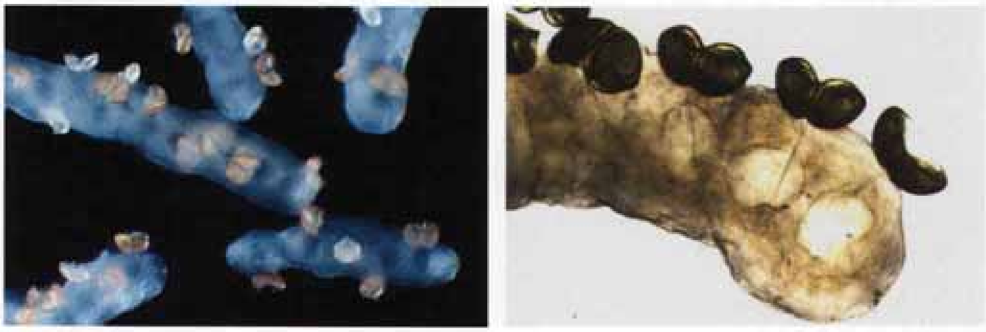

Plate 16. Conglutinates of the creeper, *Strophitus undulatus*. In right photograph, note larval thread tethering glochidia to conglutinate (Chris Barnhart, photos).

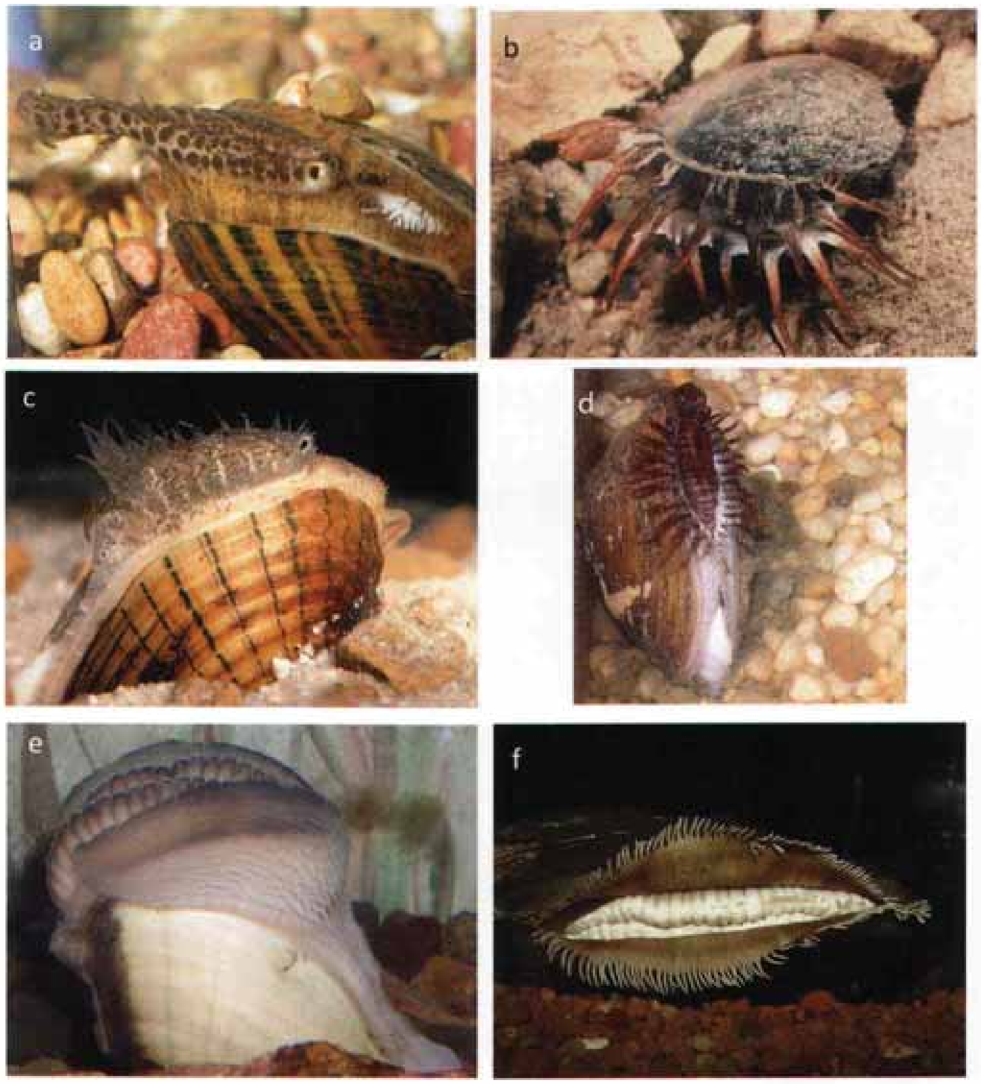

Plate 17. Large mantle lures. (a) Broken-rays, *Lampsilis reeviana*, fish mimic (Chris Barnhart, photo). (b) Rainbow, *Villosa iris*, crayfish mimic (William Roston, photo). (c) Fine-lined pocketbook, *Hamiota altilis*, generalized papillae with eyespot (W. R. Haag, photo). (d) *Hamiota altilis* alternate lure morphology with elongated tentacle-like papillae (Alabama Aquatic Biodiversity Center, photo, courtesy Paul Johnson). (e) Yellow sandshell, *Lampsilis teres* (Paul Frese, photo). (f) Black sandshell, *Ligumia recta* (Chris Barnhart, photo).

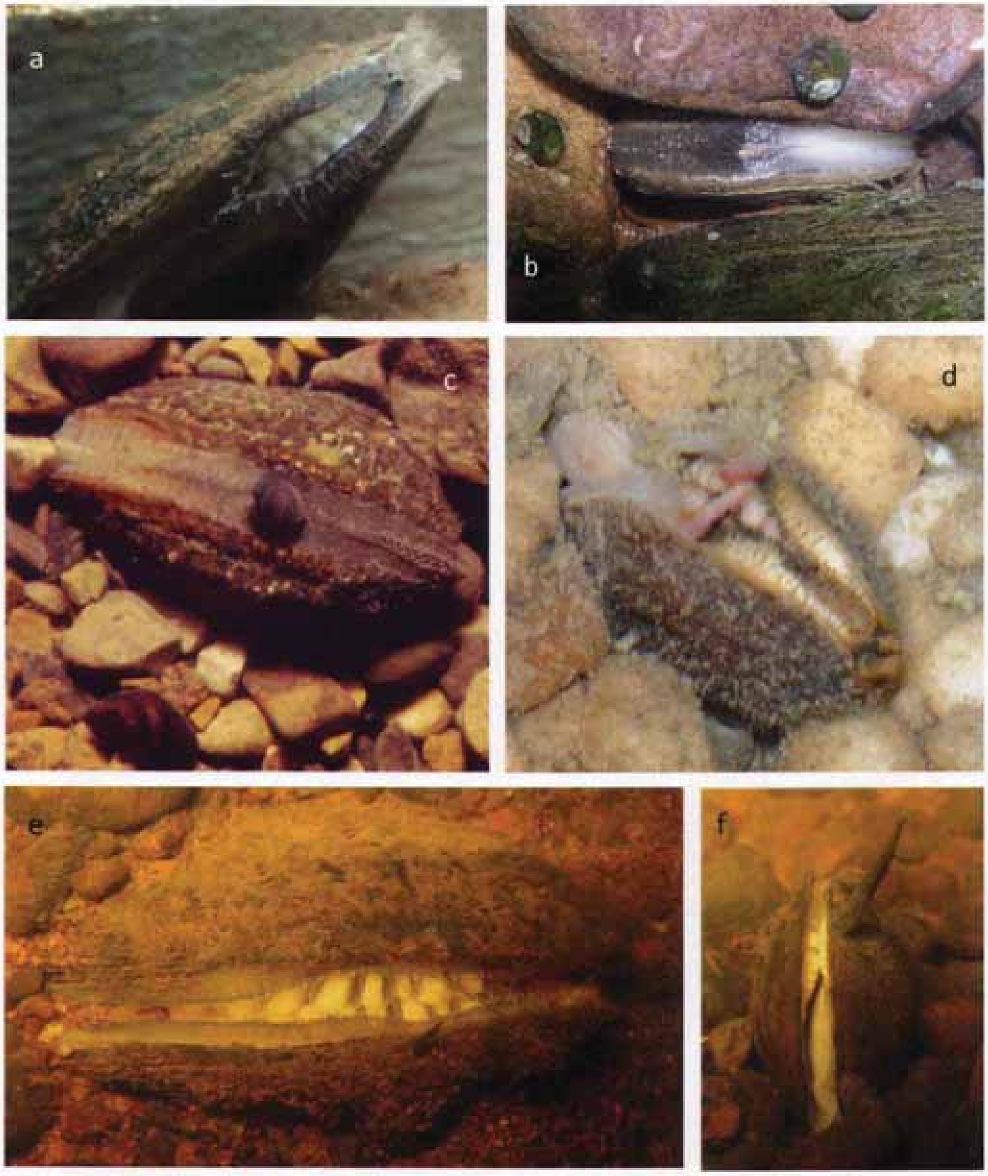

Plate 18. Cryptic lures. (a) Pondmussel, *Ligumia subrostrata*, papillae and egg mimic gravid gills (James Stoeckel, photo). (b) Cumberland moccasinshell, *Medionidus conradicus*, hidden among stones; note white patch with paired papillae to left of patch (Bernard Sietman, photo). (c) Birdwing pearlymussel, *Lemiox rimosus*, snail mimic; note live snail at lower left (Jess Jones, photo). (d) Pale lilliput, *Toxolasma cylindrellus*, caruncles (elongated pink structures) and egg mimic gravid gills (Alabama Aquatic Biodiversity Center, photo, courtesy Paul Johnson). (e, f) Potential cryptic lures of the butterfly, *Ellipsaria lineolata*, and deertoe, *Truncilla truncata* (elongated object on shell is a leech) (Bernard Sietman, photos).

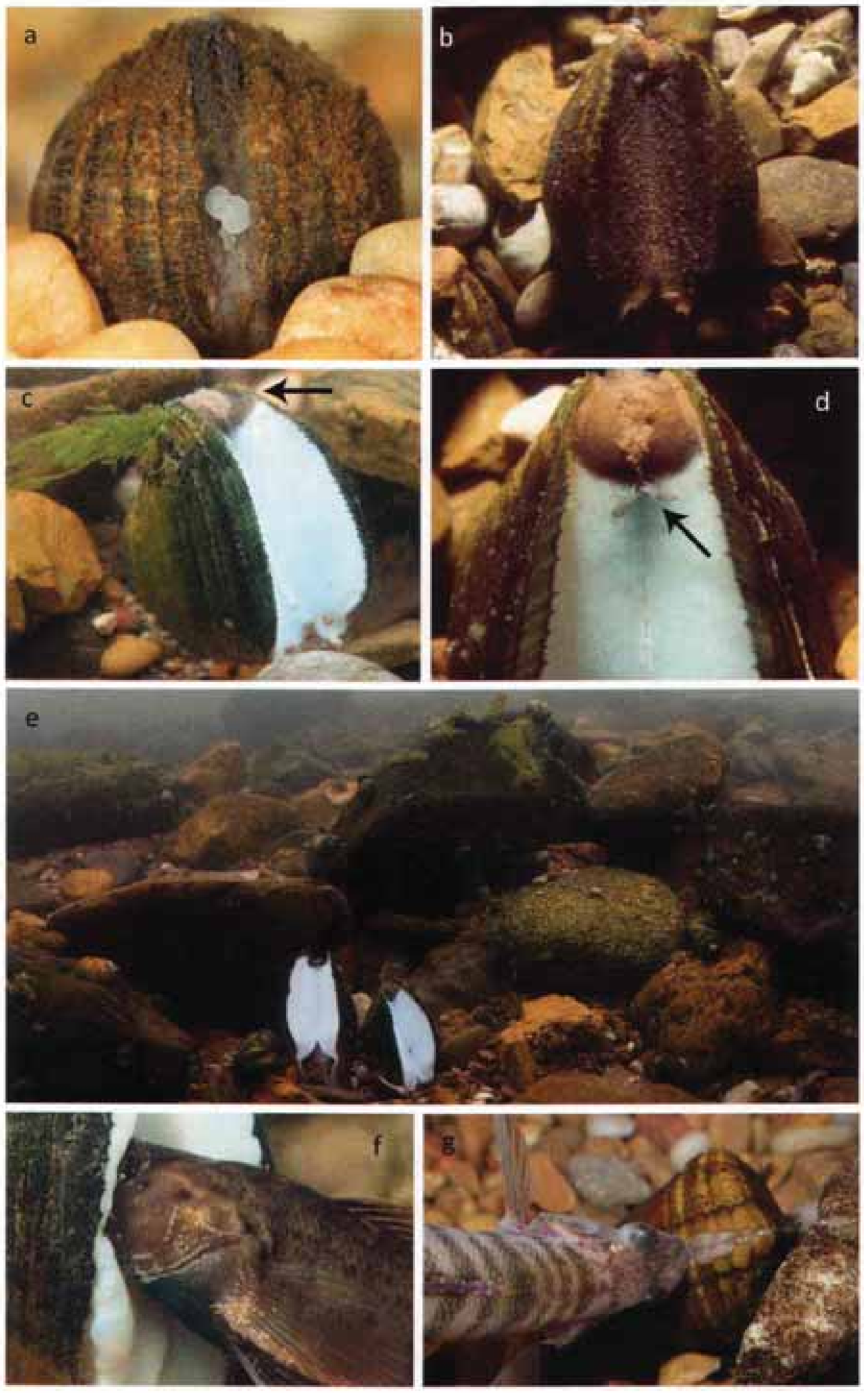

Plate 19. Cryptic lures and host trapping in *Epioblasma*. (a) Southern combshell, *E. penita*, fish egg mimic (Alabama Aquatic Biodiversity Center, photo, courtesy Paul Johnson). (b) Tan riffleshell, *E. florentina walkeri* (Jess Jones, photo). (c) Oyster mussel, *E. capsaeformis* (arrow shows location of detail d) (Bernard Sietman, photo). (d) Detail of *E. capsaeformis* showing paired microlure filaments (arrow) (Jess Jones, photo). (e) Displaying *E. capsaeformis* in the Clinch River, Tennessee (David Herasimtschuk, photo, courtesy Freshwaters Illustrated). (f) Bluebreast darter (*Etheostoma camurum*) captured by *E. capsaeformis*; note glochidia attached to fish's opercle and pectoral fin (David Herasimtschuk, photo, courtesy Freshwaters Illustrated). (g) Logperch (*Percina caprodes*) captured by a snuffbox, *E. triquetra* (Chris Barnhart, photo).

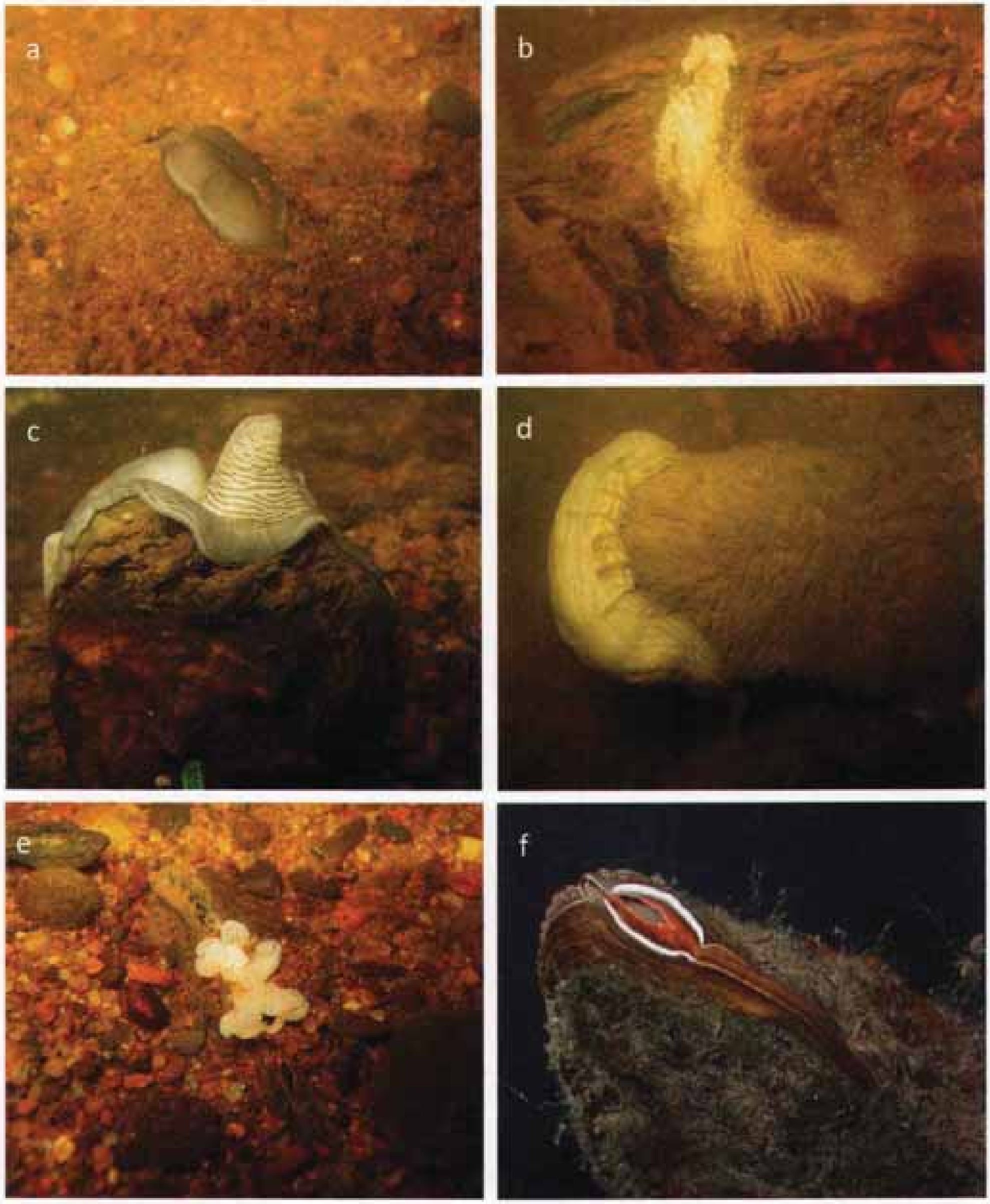

Plate 20. Mantle magazines and mucoid conglutinates. (a) Pimpleback, *Quadrula pustulosa*. (b) Purple wartyback, *Cyclonaias tuberculata*, with mucoid conglutinate streaming from exhalent aperture; inhalant aperture is visible to the left. Note parallel white stripes at lower portion of conglutinate representing contents of individual gill water tubes. (c) Winged mapleleaf, *Q. fragosa*, mantle magazine; magazine is the conical structure associated with the exhalant aperture; inhalent aperture is visible to the right. (d) Pistolgrip, *Q. verrucosa*. (e) Monkeyface, *Q. metanevra*; inhalant aperture is visible above and to left of magazine. (f) Rabbitsfoot, *Q. cylindrica* (f, Chris Barnhart, photo; all others Bernard Sietman).

Plate 21. Graves decorated with mussel shells at Hill Grove Missionary Baptist Church, Edmonson County, Kentucky. Species visible in lower left photo include *Actinonaias ligamentina*, *Cyclonaias tuberculata*, *Lampsilis ovata*, and *Pleurobema cordatum* (W. R. Haag, photos).

Chapter 7

Mussel population biology

Life history traits of mussel species such as life span, individual growth rate, age at maturity, fecundity, and host use interact to determine the demographic structure of populations and the rate at which populations grow. Differences in survival and population growth among habitats are the ultimate selective forces responsible for the divergence of life history strategies, and these patterns are central in understanding how mussel assemblages are structured. From a conservation perspective, the growth rate of a population is the ultimate measure of its health or stability and can provide a clear picture of how different life histories respond to environmental alteration.

Despite its importance, less is known about mussel population biology than almost any other facet of their ecology. This is understandable because until recently, we knew little about more basic aspects of mussel ecology, and life history information remains unavailable for many species. As with other aspects of mussel ecology, a lack of information led to widely accepted generalizations based primarily on the best-studied species, *Margaritifera margaritifera*. *Margaritifera margaritifera* has high adult survival but low annual recruitment, and consequently, populations grow slowly and are dominated by large individuals. These populations seem almost inert, changing little over time (in the absence of human impacts), and a similar view was ascribed by default to mussels as a whole. But obviously, the population biology of an animal like the fragile papershell, *Leptodea fragilis*, which can reach reproductive maturity in its first year and lives less than 10 years, cannot be characterized in this way. Given the great differences in life history strategies among species, we expect to see similar differences in population biology.

7.1. Age and size structure of populations

A commonly reported feature of mussel populations is a predominance of large individuals and a dearth or absence of small size classes (Figure 7.1). These left-skewed size-frequency distributions may appear to have a single mode, but they

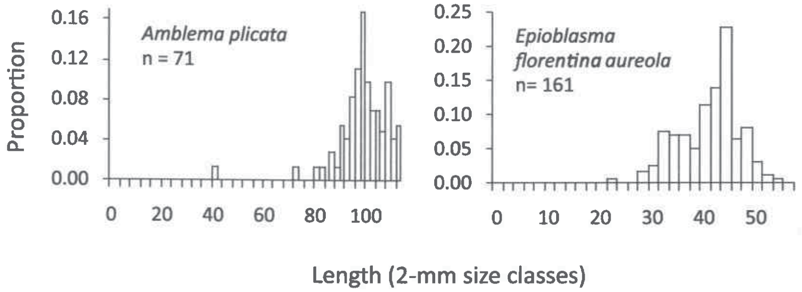

Figure 7.1. Size-frequency distributions of mussel populations obtained from human-impacted streams (left) or with conventional sampling methods (right). *Amblema plicata*, Big Sunflower River, Mississippi (W. R. Haag, unpublished data); *Epioblasma florentina aureola*, Indian Creek, Virginia (data from Rogers et al. 2001).

typically are composed of multiple, older age classes. This pattern seems a natural characteristic of *Margaritifera margaritifera* because of its low recruitment rate and high adult survival (Bauer 1983; Hastie et al. 2000b). In many other, if not most, species, a left-skewed length-frequency distribution appears to be an artifact of two factors. First, recent recruitment is suppressed by human impacts in many populations, leading to an absence of young individuals and dominance by older individuals that recruited prior to habitat alteration (Chapter 10). Second, conventional surveys are strongly biased against small size classes, which are difficult to detect by visual methods. Because of the prevalence of these sources of bias, left-skewed distributions are reported widely and have been considered characteristic of mussel populations.

Obtaining unbiased estimates of size structure requires excavation of the substrate, ideally collecting whole substrate samples and examining them across a series of sieves to allow consistent detection of small individuals (Miller and Payne 1988; Haag and Warren 2007). This painstaking method has been used rarely, but the results of such studies show a picture of size structure that differs markedly from conventional methods. In relatively healthy streams, populations comprise individuals in many size classes, but at least three types of size structure are evident: *cohort-dominated* distributions, *uniform* distributions, and *right-skewed* distributions (Figure 7.2). Cohort-dominated populations are composed predominantly of one or a few size classes representing strong year–class cohorts with few individuals in other size classes. As individuals grow, these cohorts can be followed over time, and they may dominate populations of long-lived species for many years (Payne and Miller 2000). This type of distribution was the first to be revealed by demographically unbiased sampling – in a population of *Reginaia ebena* in the Ohio River (Payne and Miller 1989) – and it quickly supplanted the left-skewed distribution as the generalized depiction of mussel population size structure. However, no other examples of cohort-dominated populations have been reported, and uniform or right-skewed distributions appear to be much more common.

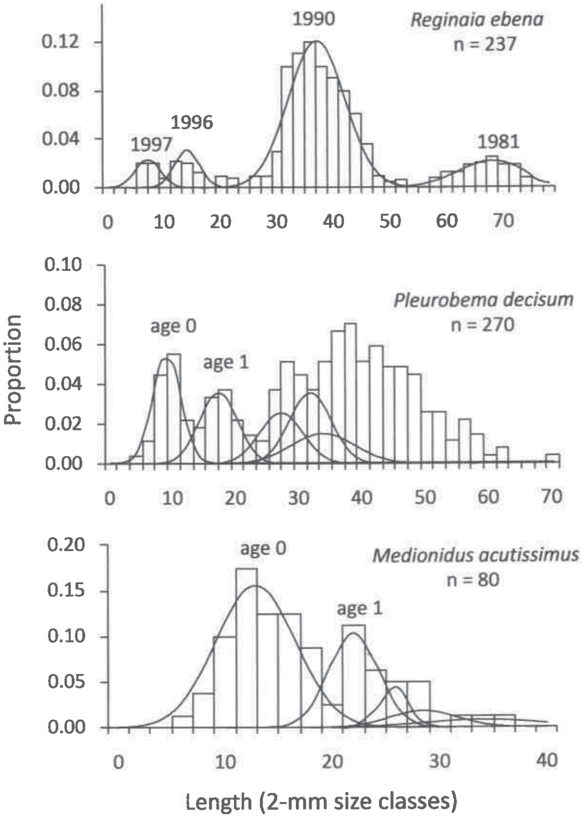

Figure 7.2. Three types of size-frequency distributions of mussel populations obtained with demographically unbiased methods. Normal curves represent cohort size-frequency distributions computed from the observed mean cohort length and standard deviation and the cumulative frequency distribution of the population (Ebert 1999). (top) Age-class dominated (adapted from Payne and Miller 2000); cohorts are indicated by probable birth year. (middle) Uniform distribution. (bottom) Right-skewed distribution (middle and bottom adapted from Haag and Warren 2010). In the lower two panels, the first five cohorts are shown, but only the first two are labeled; note increasing overlap in size distributions among older cohorts.

Uniform size distributions are characterized by relatively even occurrence of individuals across size classes. These populations may be dominated numerically by larger or mid-sized individuals due to accumulation of multiple cohorts within these size classes as growth slows in older individuals and length at age overlaps broadly; however, distinct cohorts are evident among smaller individuals (Figure 7.2). Uniform size distributions are reported for a number of long-lived species, including the periodic and equilibrium life history strategists *Amblema, Fusconaia, Obliquaria, Obovaria, Pleurobema*, and *Quadrula* (Miller and Payne 1993; Haag and Warren 2007, 2010). Right-skewed distributions are characterized by a preponderance of individuals in small size classes with successively fewer numbers of larger individuals.

As with the left tail of uniform distributions, right-skewed distributions often show distinct cohort size structure (Figure 7.2). Right-skewed distributions are reported primarily for short-lived species, including periodic and opportunistic strategists *Epioblasma, Leptodea*, and *Medionidus* (Crabtree and Smith 2009; Haag and Warren 2010; Jones and Neves 2011; W. R. Haag, unpublished data). Size distributions intermediate between uniform and right skewed are reported for *Amblema* and *Elliptio* (Haag and Warren 2007, 2010).

Age structure based on demographically unbiased sample methods differs to an even greater extent from the picture provided by conventional methods. In contrast to the preponderance of old, large individuals suggested by conventional methods, most populations from healthy streams show strongly right-skewed age distributions dominated by young age classes (Figure 7.3). Uniform and right-skewed size distributions differ in the proportional representation of young individuals and the persistence of older individuals, and these differences are commensurate with species life spans. In short-lived species, the first year class often represents more than 40 percent of the population, and the number of individuals in older age classes dwindles rapidly. In an extreme example, 82 percent of individuals in a population of *Leptodea fragilis* were less than 1 year old, and there were no individuals older than 4 years (Figure 7.3). In long-lived species, the first year class makes up less than 20 percent of the population, and representation in older age classes diminishes slowly.

Similar to the continuous variation in life history traits that defines end points of life history strategies (Chapter 6), patterns of population size and age structure vary along broad gradients. The great demographic differences among species suggest that there are comparably large differences in survival and birth (recruitment) schedules, the two most fundamental processes that determine the dynamics of a population.

7.2. Survival (and mortality)

High adult survival is one of the most widely cited attributes of mussel populations. Like most generalizations, this applies to at least some species, but it is by no means an accurate characterization of the group as a whole. Annual adult survival more than 90 percent is reported for *Amblema, Elliptio, Fusconaia, Lampsilis*, and *Margaritifera* (Bauer 1983; Hart 1999; Hart et al. 2001; Villella et al. 2004; Hastie 2006). With the exception of *Lampsilis*, these species are uniformly long-lived, providing little context for examining differences in survival among life history strategies. Furthermore, adult mortality is only one of several factors that influence population growth and stability.

Catch curve analysis is a standard technique in fisheries biology that provides an estimate of mortality based on the age structure of the population. Assuming constant mortality, the number of individuals in a cohort is expected to decline exponentially over time, and the logarithm of this rate is the instantaneous mortality rate, Z (Haddon 2001). Annual survival (S) is related to Z by the equation $S = e^{-Z}$. Further

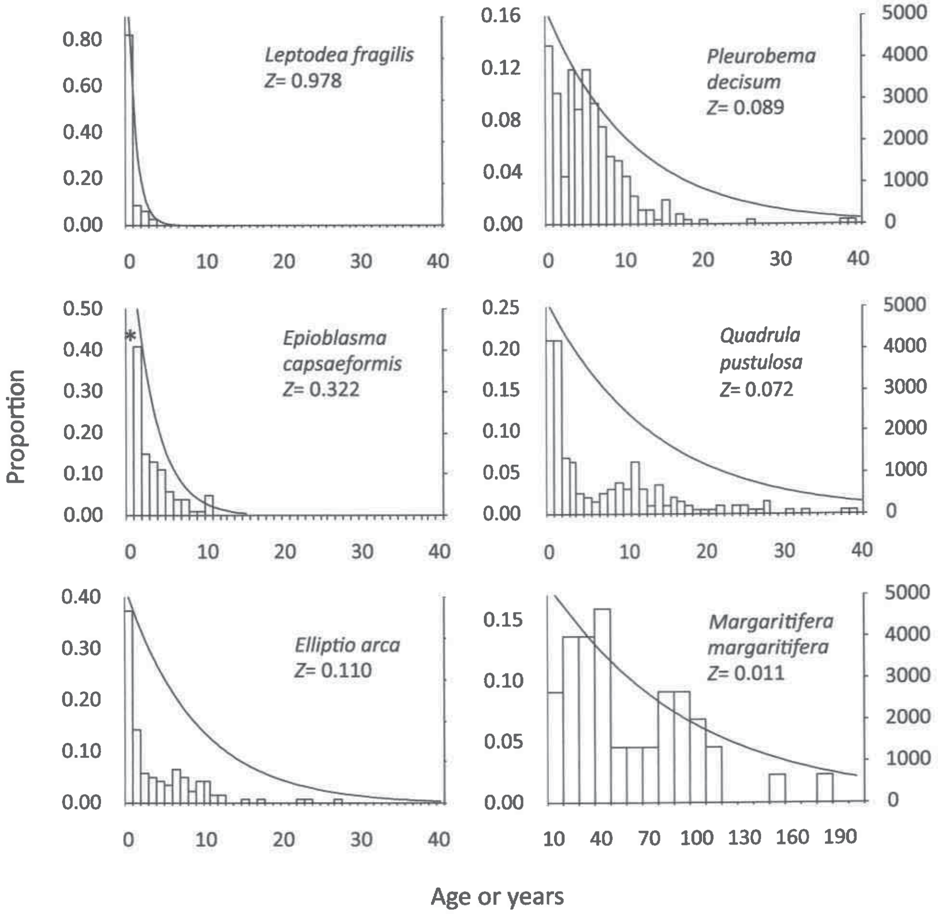

Figure 7.3. Age-frequency distributions and catch curve analysis for representative mussel populations. Left *y* axis is the proportion of individuals in each age class (histogram); note difference in axis scale for each species. Number of age 0 individuals was unavailable for *E. capsaeformis* (*). For most species, ages were predicted from lengths using von Bertalanffy growth equations. Right *y* axis is the predicted number of individuals in a cohort over time (line) based on an initial cohort size of 5,000 and the indicated value of *Z* (data from Ziuganov et al. 2001; Haag and Warren 2007, 2010; Jones and Neves 2011; W. R. Haag, unpublished data).

assuming constant recruitment, the rate of decline in abundance of successive age classes in a population at equilibrium also is described by *Z*. These assumptions are obviously unrealistic for natural populations, and catch curve methods have the further disadvantage of relying on ages predicted from length, which can be inaccurate for older individuals (Haag 2009). Nevertheless, catch curve analysis provides a simple measure of survival and can be applied easily to a large number of species.

Catch curve estimates of survival vary substantially across mussel life histories (Figure 7.3). Consistent with previous generalizations, high annual survival (more

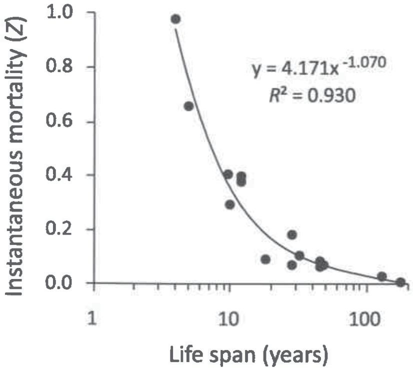

Figure 7.4. Relationship between instantaneous mortality (Z) and life span for 14 mussel species (15 populations). Values of Z were reported or calculated from data in Michaelson and Neves (1995), Hastie et al. (2000), Ziuganov et al. (2001), Haag and Warren (2007, 2010), Crabtree and Smith (2009), Jones and Neves (2011), and W. R. Haag (unpublished data). Values of life span are from these sources or Haag and Rypel (2011).

than 90%) is characteristic of equilibrium species such as *Fusconaia*, *Pleurobema*, and *Quadrula* and is nearly 99 percent for *Margaritifera*. However, opportunistic and periodic species have much lower survival, as low as 38 percent for *Leptodea fragilis*, and survival varies broadly between these two extremes. There is a remarkably strong, negative relationship between instantaneous mortality rate (Z) and life span (Figure 7.4). This relationship is curvilinear, indicating a rapid decline in mortality with increasing life span and uniformly low mortality in species with life spans more than 30 years. However, it is clear from Figure 7.3 that assumptions of catch curve analysis are violated in many cases. For example, the inordinate prominence of the first one to two age classes for the Alabama spike, *Elliptio arca*, and pimpleback, *Quadrula pustulosa*, suggests that these individuals experience much higher mortality than subsequent age classes, but such a pattern also could be caused by variable recruitment among years. For the clubshell, *Pleurobema decisum*, mortality seems to be uniformly low in about the first seven age classes but increases sharply thereafter.

Survival indeed varies among mussel life history stages. Most notably, survival from the glochidial stage to the benthic recruit stage is exceptionally low, on the order of 10^{-5}–10^{-6}, meaning that individual females produce only 0.1–1.3 juveniles/yr, despite production of many thousands or millions of glochidia (Young and Williams 1984a; Jansen et al. 2001; Haag 2002). There is no information about survival of recruits in the wild immediately after settlement. In hatchery raceways, mortality of newly settled juveniles was about 50 percent during the first 50 days after excysting from hosts but declined subsequently (Hanlon and Neves 2006). Survival of recruits during their first year was estimated at 16–50 percent for short-lived species and as high as 83 percent for long-lived species, but these estimates do not include early mortality of individuals less than about 4 mm in length (Haag and Warren, in preparation).

Table 7.1. *Variation in survival among mussel species and life history stages*

Species	Life span (years)	Recruit survival	CV (%)	Adult survival	CV (%)
Leptodea fragilis	5	0.42	97.2	0.51	68.1
Medionidus acutissimus	5	0.47	85.5	0.61	37.5
Truncilla donaciformis	8	0.37	147.6	0.36	59.7
Potamilus purpuratus	10	0.43	–	0.54	38.1
Amblema plicata	18	0.34	113.0	0.76	14.0
Lampsilis ornata	18	0.73	50.2	0.75	44.8
Elliptio arca	32	0.76	37.6	0.73	38.5
Obliquaria reflexa	35	0.60	66.2	0.82	34.1
Fusconaia cerina	45	0.85	21.6	0.87	9.9
Pleurobema decisum	45	0.98	0.8	0.88	9.3
Quadrula pustulosa	48	0.84	27.7	0.96	3.8

Note: Survival is mean annual survival across 9 years with coefficients of variation (CV) in the Little Tallahatchie River, Mississippi, and Sipsey River, Alabama (data from Haag and Warren, in preparation).

After the initial settlement stage, survival is high for some species but not for others. In equilibrium species, including *Fusconaia, Pleurobema*, and *Quadrula*, mean annual survival of recruits to their second year was more than 80 percent and did not differ substantially from adult size classes (Table 7.1). In contrast, mean recruit survival during the same period ranged from only 37 to 47 percent for the opportunists and periodic species *Leptodea, Medionidus, Potamilus*, and *Truncilla* and was only 34 percent in a short-lived population of *Amblema plicata*. Furthermore, estimated recruit survival of these latter species was highly variable and was less than 10 percent in some years. As suggested by catch curve analysis, adult survival in most short-lived species also was low, and it was similar to or only slightly higher than survival of earlier life stages. This suggests that growth rate and life span have a pervasive effect on survival throughout a species' life history. However, patterns of recruit and adult survival differ consistently across a range of species in that recruit survival typically is more variable among years (Table 7.1).

Regardless of overall differences in survival among species, mortality is expected to increase in older age classes as individuals approach the end of their life spans. European *Anodonta anatina* showed no measurable mortality from age 1 to 4, but mortality increased sharply from age 5 to 8, and few individuals older than 8 years were present (Negus 1966). At the other end of the life span spectrum, annual mortality of "younger" *Margaritifera margaritifera* and *M. falcata* (less than 40 and less than 20 years, respectively) was less than 2 percent but increased to 20 percent in older individuals (Bauer 1983; Howard and Cuffey 2006b). This pattern often is not evident in studies based on size-specific mortality because multiple age classes are represented in the largest size class (e.g., Haag 2002; Haag and Warren, in preparation).

7.2.A. Sources of mortality: Predation

Mussels are preyed on by a wide variety of terrestrial and aquatic organisms, from flatworms and insect larvae to turtles, fishes, and wading birds. Because few organisms appear to prey heavily and consistently on adults and adult mortality for some species is low, the importance of predation in regulating and structuring mussel populations has been downplayed (e.g., Haag and Warren 1998). However, with the exception of the muskrat, few studies have quantified the strength of predation pressure, particularly for early life stages that may be more vulnerable to predation.

The most conspicuous predator of mussels in much of North America is the muskrat (*Ondatra zibethicus*). Muskrats are largely herbivorous, but they also prey heavily on mussels. Large middens of empty mussel shells near muskrat burrows and smaller accumulations at satellite feeding stations are a familiar sight along streams and lakes (Figure 7.5). Muskrats open thin-shelled species by breaking one valve in a characteristic pattern (Hanson et al. 1989; Zahner-Meike and Hanson 2001). Muskrats do not break heavier-shelled species, and how these are opened is poorly known. Apgar (1887) proposed that muskrats pinch the shells together between their jaws, trapping the mussel's foot in an extended position, which causes the shell to gape on release due to "the pain produced." Other observers report muskrats quickly inserting a claw or incisor into the shell before the shell closes completely or leaving larger mussels on the bank until they gape (Butler 1885; Lee 1886). Heavy-shelled species killed by muskrats typically bear characteristic and extensive scratch marks on the shell, but the shell margin is undamaged (Figure 7.5); these marks could only be made by the teeth and with great force applied by the jaws, lending credence to Apgar's seemingly unlikely hypothesis.

Muskrat predation shows strong size and species selectivity. Muskrats typically prey preferentially on medium-sized mussels (about 40–80 mm; Figure 7.6), representing a trade-off between handling costs and prey energy content (Neves and Odum 1989; Tyrrell and Hornbach 1998; Owen et al. 2011). Small mussels (less than 20–30 mm) are rarely taken, probably because of the difficulty of finding these individuals and their low energetic return. Large mussels are similarly avoided in most cases because of the difficulty of transporting and opening the shells. Large unopened mussels apparently beyond the handling capabilities of muskrats are occasionally found in middens. Shell shape also influences selection as muskrats prefer round, inflated shells as opposed to elongated, compressed shells (Owen et al. 2011). This shape preference was explained by the difficulty of harvesting compressed species that may have greater anchoring and burrowing ability, but it also could be related to the ratio of flesh to shell mass (see subsequent discussion). Patterns of species selection are explained largely by differences in size and shape among species or life stages. For example, large threeridge, *Amblema plicata*, were avoided by muskrats at one site, but smaller individuals were preyed on heavily at another site (Watters 1995).

Figure 7.5. Muskrat predation on mussels. (a) Muskrat returning to feeding station with a mussel held between its incisors; note other discarded shells (Robert Scholl, photo). (b) Muskrat feeding on giant floater, *Pyganodon grandis*, after breaking right shell valve (Allan Oman, photo). (c) Large muskrat midden among tree roots on shore (Ethan Nedeau, photo). (d) Characteristic scratches on shell of round pigtoe, *Pleurobema sintoxia*, harvested by a muskrat (Richard T. Bryant, photo).

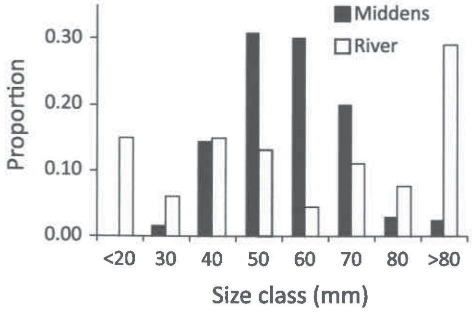

Figure 7.6. Representation of mussel size classes in muskrat middens and in the live mussel assemblage in the Mississippi River, Minnesota, showing preferential selection of medium-sized mussels by muskrats (redrawn from Tyrrell and Hornbach 1998).

Selectivity also is influenced by prey availability and other species-specific attributes. Muskrats avoided small deertoe, *Truncilla truncata*, at sites with an abundance of medium-sized mussels but selected them at a site where optimally sized mussels were rare (Tyrrell and Hornbach 1998). Similarly, where nonnative *Corbicula fluminea* is abundant, muskrats often prey preferentially on this species, despite its small size (Neves and Odum 1989). Muskrat predation on *Margaritifera margaritifera* showed typical selection for medium-sized individuals, but muskrats consistently selected larger eastern floaters, *Pyganodon cataracta* (Zahner-Meike and Hanson 2001). This was explained by the difficulty of transporting and opening large, heavy-shelled *Margaritifera* and its decrease in flesh to shell mass ratio with increasing size. In contrast, the flesh to mass ratio of *P. cataracta* increased with increasing size, and muskrats were able to open large individuals because of this species' thin shell. Preferential selectivity of large individuals is reported for other thin-shelled species (Convey et al. 1989; Hanson et al. 1989; Jokela and Mutikainen 1995b). Differences in taste and odor among species also have been proposed as a basis for species selectivity (Watters 1995; Diggins and Stewart 2000), but others claim that muskrats locate mussels primarily by touch (Zahner-Meike and Hanson 2001), and within the optimal size and shape range, muskrats may prey on mussel species roughly in proportion to their occurrence in a stream (Neves and Odum 1989).

Muskrat predation can have a significant impact on mussel population abundance and size structure. Muskrats removed about 16 percent of the adult mussels (across all species) at a site in a small river over 8 years, but some species suffered as much as 47 percent mortality (Neves and Odum 1989). In another stream, mussels were nearly absent in the vicinity of muskrat burrows, but abundance increased with distance from burrows (Jokela and Mutikainen 1995b). In a lake, muskrats ate up to 350 mussels/day and a total of nearly 37,000 mussels over 1 year, representing 31 percent of annual production (Hanson et al. 1989). Muskrat predation effectively eliminated

Figure 7.7. Limpkin feeding on freshwater mussel in southern Florida (John T. Ratcliff, photo).

medium-sized *Margaritifera margaritifera* at one site relative to a control site in the same stream not experiencing muskrat predation (Zahner-Meike and Hanson 2001).

Muskrat predation varies widely across time and space. It is claimed that muskrat predation is highest in winter when plant material is scarce, but heavy predation can occur any time of the year and shows no clear seasonal pattern (reviewed in Zahner-Meike and Hanson 2001). Predation is most intense at sites with high mussel abundance, but it varies dramatically from year to year, and muskrats may quickly locate and exploit newly established mussel assemblages (Neves and Odum 1989; Diggins and Stewart 2000). Heavy predation was observed only once in 10 years at one river site, but never at another, despite the presence of dense mussel populations at both sites (Haag and Warren, in preparation). Similar to size selectivity, the occurrence of muskrat predation likely follows an optimal foraging model by which muskrats move to other locations when returns begin to decline. Furthermore, predation on mussels probably varies with availability of other food items, and muskrat populations fluctuate widely.

Other terrestrial predators occasionally eat mussels, including raccoons, otters, and skunks (reviewed in Fuller 1974; Tyrrell and Hornbach 1998). Simpson (1899) described crows dropping mussels from the air to break their shells. In Florida, limpkins (*Aramus guarauna*) are frequent predators of mussels (Figure 7.7). Limpkins prey primarily on apple snails (*Pomacea*), but their discrete feeding stations – similar to muskrat middens – often contain large numbers of mussel shells, which they open deftly with their long, curved bills (Cottam 1936). Diving ducks eat large numbers of fingernail clams (Sphaeriidae) and invasive *Dreissena*, and 8–15 percent of Canvasbacks, Lesser Scaup, and Common Goldeneye collected from the upper Mississippi River had eaten unionids (Thompson 1973; Hamilton et al. 1994).

Several widespread North American fishes are frequent or specialized predators of mussels. Freshwater drum (*Aplodinotus grunniens*) have long been recognized as specialized molluscivores that prey heavily or primarily on mussels (Rafinesque 1820; Forbes 1888), and its colloquial name in Louisiana, "gaspergou," is a corruption of the French *casse burgau* (mussel breaker). Drum forage by suction feeding in the substrate and have massive pharyngeal teeth for crushing. Drum diets vary according to life history stage and local prey availability, but bivalves, including native freshwater mussels, *Corbicula*, *Dreissena*, and brackish-water *Rangia cuneata*, can be important prey items, especially for larger individuals (Darnell 1961; Bur 1982; Morrison et al. 1997; Rypel and Mitchell 2007). Large catfishes, including channel (*Ictalurus punctatus*), blue (*I. furcatus*), and flathead catfish (*Pylodictus olivaris*), also feed on mussels, which, similar to drum, they crush in the rear of the throat. Catfishes also have diverse diets, but mussels can be seasonally dominant prey items (Neumann 2008; reviewed in Hove et al. 2011; Tiemann et al. 2011; Sietman et al. 2012). River redhorse (*Moxostoma carinatum*) are specialized molluscivores having heavy, molariform pharyngeal teeth and enlarged skull musculature and bone structure compared with other redhorses (Jenkins and Burkhead 1994). Some sunfishes (*Lepomis*) also have molariform pharyngeal teeth and feed extensively on snails and small bivalves. Bowfin, sturgeon, bullhead catfishes, yellow perch, darters, turtles, and crayfishes feed at least opportunistically on mollusks (reviewed in Robinson and Wellborn 1988; Dillon 2000).

Most reports of fish predation on mussels are incidental, and no studies have focused on this source of mortality. However, fish predation may be a widespread and important factor regulating mussel populations. In the Little Tallahatchie and Sipsey rivers, 87 and 70 percent, respectively, of mussels in the recent dead shell assemblage were crushed (Haag and Warren, in preparation). Shells were collected from quadrat samples, which often included multiple fragments from the same individual, suggesting that fishes had crushed the shells at the site. Furthermore, these lowland rivers lacked large rocks or other objects capable of routinely crushing shells, and one of the rivers was impounded and never experienced turbulent flows. The occurrence of these crushed shells was remarkably consistent among years and represented a substantial percentage of the population. In the Little Tallahatchie River, total annual mussel mortality across all species from apparent fish predation ranged from 17 to 38 percent (mean = 27%, coefficient of variation = 27.0) over 9 years. Mortality from this source was lower and more variable in the Sipsey River during the same time ranging from 5 to 29 percent (mean = 15%, CV = 60.5).

Table 7.2. *Relative intensity of apparent fish predation among mussel species based on the proportion of crushed individuals in the recent dead shell assemblage*

Species	Sipsey River	Little Tallahatchie River
Potamilus ohiensis		1.000
Pyganodon grandis		1.000
Lampsilis teres	1.000	0.948
Potamilus purpuratus		0.970
Leptodea fragilis	0.905	0.999
Medionidus acutissimus	0.939	
Villosa lienosa	0.918	
Amblema plicata		0.908
Lampsilis ornata/cardium	0.706	1.000
Elliptio arca	0.807	
Truncilla donaciformis	0.667	0.838
Quadrula verrucosa	0.520	0.936
Obovaria unicolor	0.683	
Fusconaia cerina	0.668	
Pleurobema decisum	0.588	
Obliquaria reflexa	0.250	0.919
Quadrula rumphiana/quadrula	0.136	0.714
Quadrula asperata/pustulosa	0.195	0.624

Note: Species are ordered according to the mean proportion between the two rivers (data from Haag and Warren, in preparation).

Thin-shelled species appeared to suffer proportionally higher fish predation (Table 7.2), and some species were found only as crushed shells and never alive, suggesting that they were actively selected by fishes. The size distribution of crushed shells also differed among species according to shell thickness (Figure 7.8). For thin-shelled species, fish predation occurred in roughly equal proportions across size classes and included even large individuals. For thick-shelled species, fish predation was mostly limited to individuals less than 50 mm in length, and the size distribution of these crushed shells differed significantly from the live assemblage. The size distribution of whole dead shells (i.e., not crushed) was similar to the live assemblage, providing further evidence that crushed shells were the product of selective fish predation. We occasionally found larger crushed shells (up to 80 mm) of even heavy-shelled species (Figure 7.9). These shells were typically found in aggregations under submerged logs or undercut banks and are likely attributable to large flathead catfish, which commonly reside in such sheltered locations.

Large individuals capable of crushing large, thick-shelled mussels typically compose a small percentage of catfish or drum populations, but predation by more abundant, smaller individuals on thin-shelled or young mussels appears intense and of regular occurrence. A wide variety of other aquatic predators prey on small mollusks,

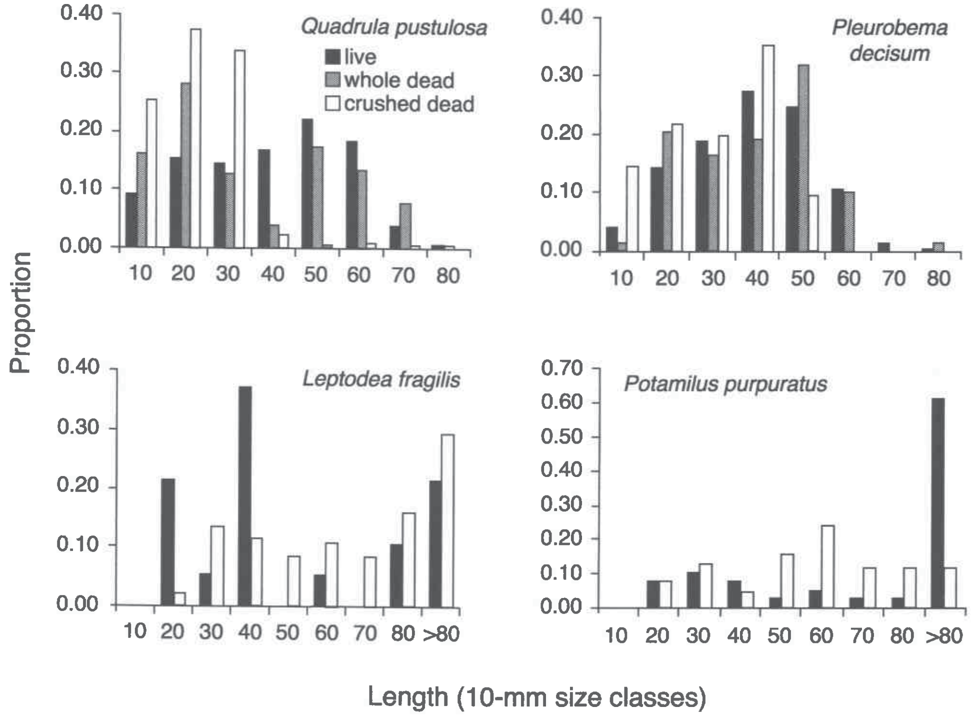

Figure 7.8. Size selectivity of apparent fish predation on mussels in relation to shell thickness (*Quadrula pustulosa* and *Pleurobema decisum*, thick shelled; *Leptodea fragilis* and *Potamilus purpuratus*, thin shelled). Crushed shells are considered indicative of fish predation and whole shells indicative of other sources of mortality; whole shells were rare for thin-shelled species and are not plotted (from Haag and Warren, in preparation).

particularly snails (reviewed in Dillon 2000). Newly settled juvenile mussels may be especially vulnerable to predation and could be preyed on by a wider range of fishes and other organisms. Crayfishes preyed on juvenile *Corbicula* (less than 6 mm shell length; Covich et al. 1981), and predaceous flatworms may be a significant source of mortality for newly settled native mussels (Zimmerman and Neves 2003). On the upper Mississippi River, the wintering population of diving ducks consumed an estimated 2 million kg of fingernail clams (Sphaeriidae), representing 25 percent of the standing crop (Thompson 1973); although unionids were a small percentage of bivalves consumed, this could represent a substantial source of mortality for juvenile mussels.

7.2.B. Other sources of natural mortality

Mussels can experience high mortality from catastrophic events. A major flood in Scotland killed an estimated 50,000 *Margaritifera margaritifera*, representing 4–8

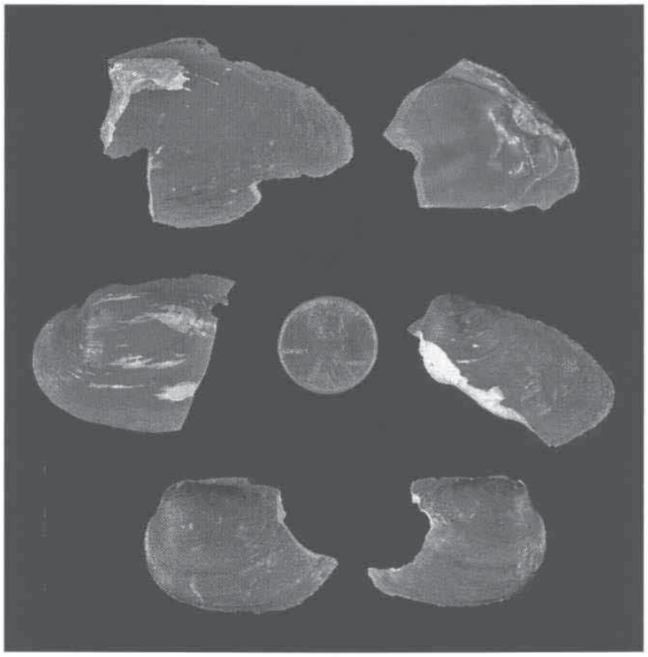

Figure 7.9. Large, thick-shelled mussels crushed by unknown predator, potentially large flathead catfish. Note abrasion on some of the shells. Clockwise from top left: *Elliptio arca*, *E. arca*, *Pleurobema decisum*, *P. decisum* (both valves of single individual), *Lampsilis straminea* (W. R. Haag, photo).

percent of the population (Hastie et al. 2001), and severe drought can reduce mussel abundance by more than 50 percent (Golladay et al. 2004; Haag and Warren 2008). These events are localized and of irregular occurrence and are likely more severe in small streams or isolated lentic habitats (Section 4.1.D.1). Seasonal periods of low oxygen doubtlessly have a major influence on assemblage composition and abundance in isolated lakes, but this source of mortality is probably low in streams in the absence of human impacts.

Apart from predation and catastrophic events, little is known about natural causes of mortality or factors that influence temporal or spatial variation in survival. Villella et al. (2004) reported lower survival in winter compared with spring and summer but suspected that this was an artifact of lower capture probability in winter due to mussel burrowing. In another study, survival was negatively related to stream discharge in summer but not in winter, suggesting that high, scouring flows when mussels are active and near the surface incur higher mortality than high flows in winter, when mussels are buried more deeply (Peterson et al. 2011). Jones and Neves (2011) proposed that display of lures may incur higher female mortality than in other times of the year. Similar to predation, sources of natural mortality may be more varied for newly settled juveniles. For example, large numbers of juveniles may settle in inappropriate

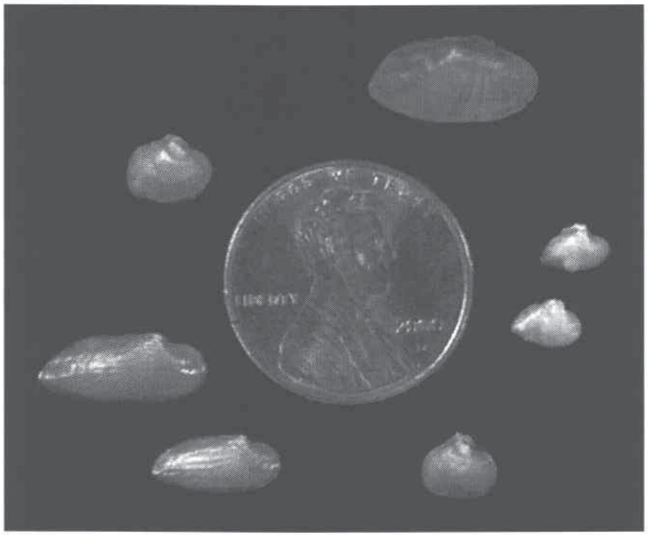

Figure 7.10. Age 0 recruits from the Sipsey and Little Tallahatchie rivers. Clockwise from top right: Alabama spike, *Elliptio arca*; threehorn wartyback, *Obliquaria reflexa* (two specimens); pimpleback, *Quadrula pustulosa*; yellow sandshell, *Lampsilis teres* (two specimens); threeridge, *Amblema plicata* (W. R. Haag, photo).

habitats, where they may be washed away or buried in sediments (Zimmerman and Neves 2003; Morales et al. 2006a).

7.3. Recruitment

The difficulty of finding small individuals and the resulting left-skewed length-frequency distributions of many populations (Section 7.1) have led to the widely accepted notion that mussel recruitment occurs infrequently. This idea was solidified by the finding that strong year classes of the ebony shell, *Reginaia ebena*, in the regulated Ohio River occurred only about once in a decade (Payne and Miller 2000). However, as indicated by the length- and age-frequency distributions in Figures 7.2 and 7.3, recruitment appears to be a regular feature of most healthy populations, and the absence or rarity of young age classes is either a sampling artifact or symptomatic of human impacts. Individuals less than 5 years old composed 40–62 percent of mussels in the upper Mississippi River, and these young individuals comprised multiple age classes, indicating regular and high recruitment (Newton et al. 2011). In a given year, recruits can make up from 1 to more than 50 percent of a population (Negus 1966; Villella et al. 2004; Jones and Neves 2011). These studies defined recruitment as the addition to the population of individuals greater than a minimum size for visual detection (usually more than 1–3 years of age). Consequently, recruitment of age 0 individuals may be considerably higher (Figure 7.10).

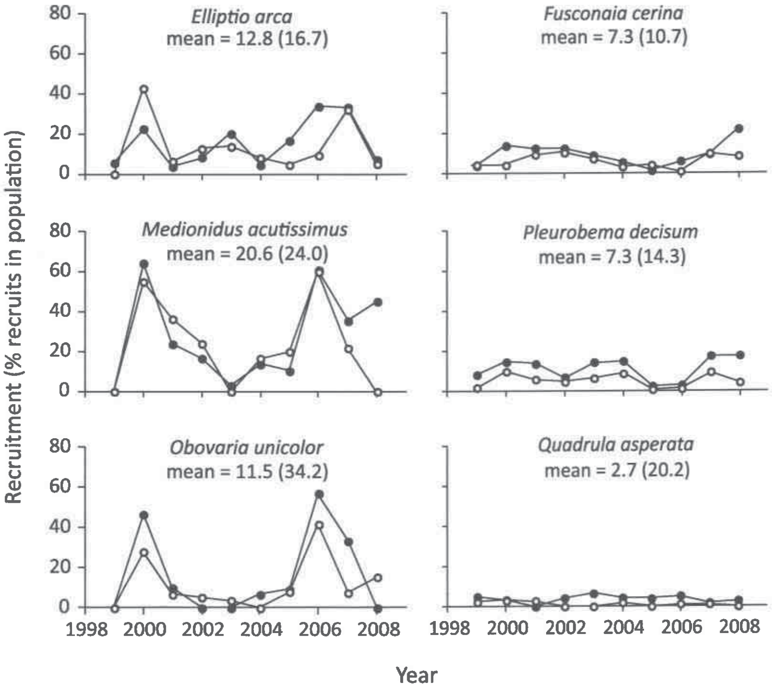

Figure 7.11. Two types of annual variation in recruitment in the Sipsey River, Alabama. (left column) High and variable recruitment. (right column) Low and constant recruitment. Recruitment is the percentage of age 0 individuals in the population in early autumn. The two lines and symbols on each graph represent two different sites in the river. Mean and coefficients of variation (in parentheses) were calculated across years for both sites combined and are back-transformed from arcsine-transformed proportions (from Haag and Warren, in preparation).

Recruitment appears to show two major patterns, low and constant or high and variable (Figure 7.11), and these patterns are concordant with life history strategies. Haag and Warren (in review) measured recruitment for 10 consecutive years in the Sipsey River, Alabama, and the Little Tallahatchie River, Mississippi. In the Sipsey River, five equilibrium strategists (*Fusconaia cerina, Pleurobema decisum, Quadrula asperata, Q. rumphiana*, and *Q. verrucosa*) had consistently low mean annual recruitment ranging from 3 to 7 percent (percentage of age 0 individuals in the population). Recruitment was evident in most years for these species but exceeded 20 percent only once (for one species) and, in general, exhibited low annual variation. Recruitment varied similarly among sites but was not correlated among species. In contrast, four periodic species (*Elliptio arca, Lampsilis ornata, Medionidus acutissimus*, and *Obovaria unicolor*) had higher mean annual recruitment ranging from 12 to 21 percent. Recruitment was highly variable, including years with no apparent recruitment punctuated by years in which more than 50 percent of the population was composed of recruits. Annual patterns of recruitment were highly consistent among sites

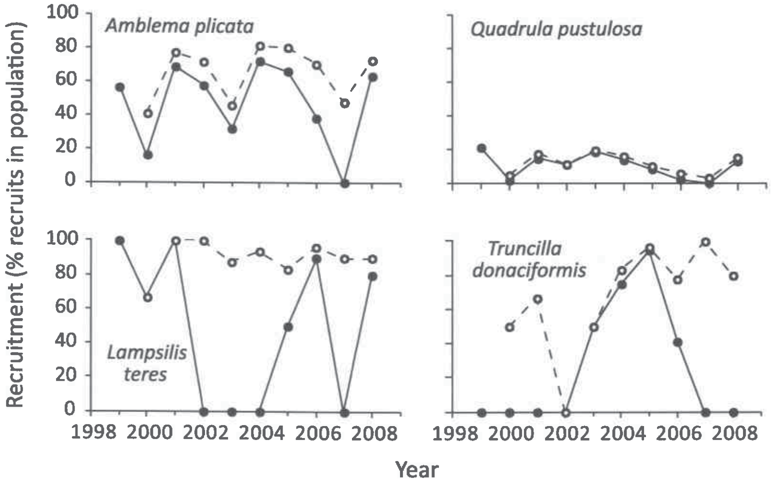

Figure 7.12. Patterns of recruitment and recruit mortality in the Little Tallahatchie River, Mississippi. Solid symbols and lines are percentage of live recruits (age 0 individuals) in the population in early autumn. Open symbols and dashed lines are percentage of live recruits + percentage of recently dead recruits (from Haag and Warren, in preparation).

and species, suggesting that pervasive factors influence recruitment at large scales. A similar dichotomy existed in the Little Tallahatchie River (Figure 7.12). Mean recruitment for the equilibrium species *Quadrula pustulosa* was 10 percent and varied little among years, but recruitment for the periodic species *Amblema plicata* and *Obliquaria reflexa* was 47 percent and 22 percent, respectively, and was highly variable. *Lampsilis teres*, *Leptodea fragilis*, *Truncilla donaciformis*, and other opportunistic species represented extreme examples of the high and variable recruitment strategy. In some years, samples of these species were composed entirely of recruits, and adult abundance was below detectable limits, but there was no measurable recruitment in other years (Figure 7.12). In two other studies, variability in annual recruitment also was higher for species with higher mean annual recruitment (Villella et al. 2004; Jones and Neves 2011).

In addition to the general concordance with life history strategies, specific traits that define these strategies are good predictors of annual recruitment (Figure 7.13). Recruitment was negatively related to life span, suggesting a decreasing importance of recruitment to maintenance of populations of long-lived species (Section 7.4). Recruitment also was positively related to annual fecundity, but fecundity explained less variation in recruitment than life span. Life span is not related to fecundity for the species in this analysis or for mussels overall (Chapter 6). Because many short-lived species appear to have low recruit survival, high fecundity may be selected for to compensate for high recruit mortality. The low annual recruitment of *Margaritifera margaritifera* despite its extremely high fecundity was a strong outlier in this

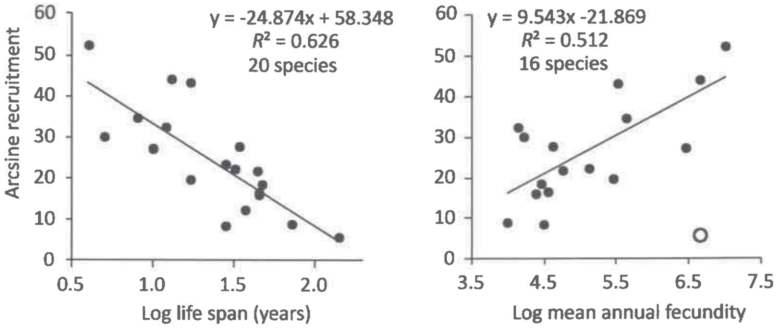

Figure 7.13. Relationships between mean annual recruitment (% of recruits in population) and life history variables. Regression line for fecundity was computed omitting *Margaritifera margaritifera* (open circle); both regressions are significant at $p < 0.001$ (recruitment data from Hastie et al. 2000; Jones and Neves 2011; Haag and Warren, in preparation; life span and fecundity data from Haag and Rypel 2011; Haag, in press). Recruitment of *M. margaritifera* was reported as percentage of individuals less than 10 years old (see Hastie et al. 2000); I estimated annual recruitment by dividing this number by 10 and taking the average for nine populations.

relationship and illustrates its unusual life history strategy that departs from other equilibrium species (Section 8.6).

Haag and Warren (in review) defined recruitment as the number of age 0 individuals present near the end of the growing season when their samples were taken (late August to October). However, based on the abundance of dead recruits in their samples, total initial recruitment appears to be considerably higher for some species. For the opportunists *L. teres*, *L. fragilis*, *T. donaciformis*, and *Potamilus purpuratus*, dead recruits were consistently abundant, but in many years, few survived to the end of the growing season (Figure 7.12). This suggests that for these species, recruitment is consistently high but early recruit survival is highly variable. For other species, early recruit survival appears to be high, and the abundance of dead recruits adds little to total annual recruitment and tracks the number of live recruits closely.

In unregulated rivers, recruitment of species with high and variable recruitment, and in *Margaritifera falcata*, is consistently greatest in low-flow years (Howard and Cuffey 2006b; Jones and Neves 2011; Haag and Warren, in preparation; Figure 7.14). These studies proposed several explanations for this phenomenon. First, low flow may increase chances of glochidial encounters with hosts by concentrating fishes in a smaller volume of water and reducing fish mortality and emigration. Second, low flow may enhance juvenile survival because of decreased scour. Third, greater water clarity in low-flow conditions could increase the visibility of lures used to attract host fishes. Fourth, variation in recruitment may have an energetic component. Mussel growth is highest in low-flow years, potentially because of decreased food processing costs resulting from lower suspended solid concentrations or higher concentrations of algae and other autochthonous food sources under conditions of increased water

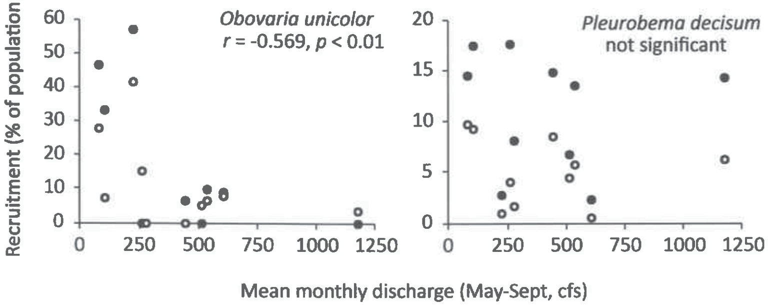

Figure 7.14. Annual variation in recruitment of two representative species in the Sipsey River, Alabama, in relationship to streamflow. Symbols represent two different sites in the river; correlation coefficients are for both sites combined and are based on arcsine recruitment and log discharge (from Haag and Warren, in preparation).

clarity and retention time (Rypel et al. 2009). A more favorable feeding environment may enhance juvenile survival. In a lake, poor recruitment coincided with years of low adult growth (Hanson et al. 1988), further suggesting that juvenile survival depends on an abundant and available food supply. The pervasive relationship between flow and recruitment shows that large-scale climatic phenomena can have a strong effect on mussel population dynamics. However, in another stream, the proportion of individuals in young age classes varied among sites, suggesting that local factors also influence recruitment or juvenile survival (Crabtree and Smith 2009).

In contrast to the strong coupling of recruitment with flow in some species, equilibrium species with low and constant recruitment exhibited no such relationship (Figure 7.14), and the factors that influence their recruitment are unknown. In the regulated and impounded Little Tallahatchie River, relationships between flow and recruitment were opposite to those seen in unregulated streams. In this stream, annual recruitment was correlated among all species, regardless of mean annual recruitment strength, and was lowest in low-flow years (Haag and Warren, in preparation). Recruitment may be limited by low oxygen concentration during years of reduced dam release, and indeed, no recruitment was observed in a year when dam maintenance resulted in extremely low flow. In the same river, mussel growth also was decoupled from relationships with streamflow seen in unregulated rivers (Rypel et al. 2008). In a stream affected by water withdrawal for irrigation, recruitment was also positively related to streamflow, further suggesting that hydrologic alteration disrupts natural recruitment patterns (Peterson et al. 2011). Accordingly, disruption of natural hydrological cycles may be responsible for the infrequent recruitment seen in *Reginaia ebena* in the regulated Ohio River (Payne and Miller 2000).

7.4. Population growth and stability

Schedules of birth and death are the primary variables that determine the rate at which populations grow or decline. Consequently, given the great differences among species

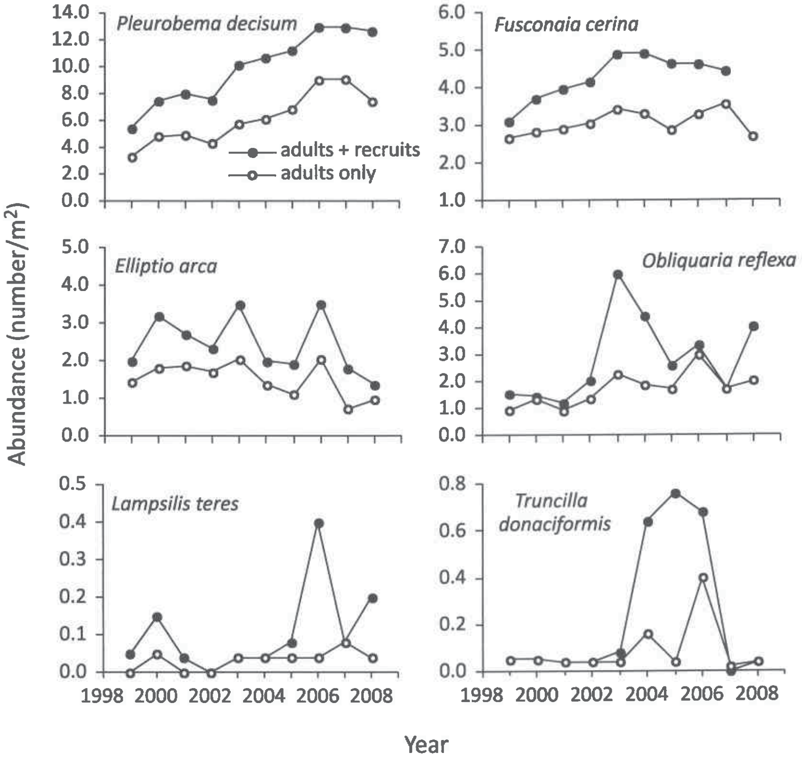

Figure 7.15. Stability of mussel populations in the Little Tallahatchie and Sipsey rivers over 10 years (from Haag and Warren, in preparation).

in survival and recruitment rates, we expect similarly wide variation in population growth rate and stability. The proportional increase in population size over a specific time interval can be expressed by the finite rate of increase (λ). This value is 1 for stable populations, less than 1 for declining populations, and more than 1 for growing populations.

In the absence of human impacts, mussel populations can remain nearly stable for many years and have λ near 1 (Villella et al. 2004; Jiao et al. 2008). In the Sipsey River, Alabama, total mussel abundance (all species) remained remarkably constant over 10 years but appeared to oscillate slightly around a median value (Haag and Warren, in preparation). Abundance of most equilibrium species was stable and varied little among years. At one site, abundance of *Pleurobema decisum* approximately doubled over 10 years, but it increased steadily by only about 10 percent per year (Figure 7.15). Populations of periodic and opportunistic species in the Sipsey and Little Tallahatchie rivers appeared to fluctuate more widely. However, much of this variation was due to highly variable recruitment for these species, and for most, adult population size showed much less fluctuation and λ was near 1, similar to long-lived species (Figure 7.15).

In some cases, populations of periodic or opportunistic species do appear to fluctuate dramatically. In the Little Tallahatchie River, the fawnsfoot, *Truncilla donaciformis*, increased rapidly over 3 years – both in total and adult population size – but then crashed abruptly the following year (Figure 7.15). In the Clinch River, Tennessee, two periodic species, the Cumberlandian combshell, *Epioblasma brevidens*, and oyster mussel, *E. capsaeformis*, increased by 21 percent and 33 percent, respectively, over 4 years, but a third, the wavy-rayed lampmussel, *Lampsilis fasciola*, declined by 24 percent during the same period (Jones and Neves 2011). In experiments of mussel recruitment in hatchery ponds, initial populations of 10 females of the opportunistic species the pondmussel, *Ligumia subrostrata*, and giant floater, *Pyganodon grandis*, increased to as much as 521 individuals in 1 year, representing an astounding λ of 53.1 (W. R. Haag and J. Stoeckel, unpublished data). Rapid colonization and population growth in ponds is reported for other opportunistic species (Coker et al. 1921; Diggins and Stewart 2000). These observations show that opportunistic and periodic species have the potential for rapid population growth, but growth is often limited by environmental and biotic factors such as predation. Similarly rapid population growth is not reported for equilibrium species, but there remain few studies of mussel population dynamics.

Other demographic attributes show fundamental differences among life history strategies. The stable stage distribution of a population is the proportional representation of individuals among life history stages when the population is at a steady state and is determined by the survival and recruitment schedules of each stage. Stable stage distributions for species in the Little Tallahatchie and Sipsey rivers differed markedly according to life history strategy (Figure 7.16). Populations of opportunistic species are expected to be dominated by recruits and have decreasing representation of older stages. In contrast, populations of equilibrium species are dominated by adult stages. As with other life history traits, periodic species fall between these two extremes and have a relatively uniform distribution of individuals among stages. The observed representation of individuals within stages was similar to expectations for most populations, suggesting that the size structure is stable over time and characteristic of these species. Surprisingly, the threeridge, *Amblema plicata*, had a stable stage distribution similar to opportunistic species (Figure 7.16). Most populations of this species are long-lived and slow growing, placing them in the equilibrium life history strategy (Section 6.3). However, the population in the Little Tallahatchie River grows rapidly, has a modest life span (about 20 years), and has highly variable recruitment and recruit survival, aligning it more closely with the periodic or opportunistic strategies.

Changes in survival or recruitment rates alter the population growth rate and size distribution. The relative effect on population growth of changes in these rates is measured by the elasticity index; changes in demographic rates with higher elasticity values have a proportionally greater effect on population growth rate (de Kroon et al. 1986). Elasticity values for species in the Little Tallahatchie and Sipsey rivers further illustrate the great differences in population dynamics among life history

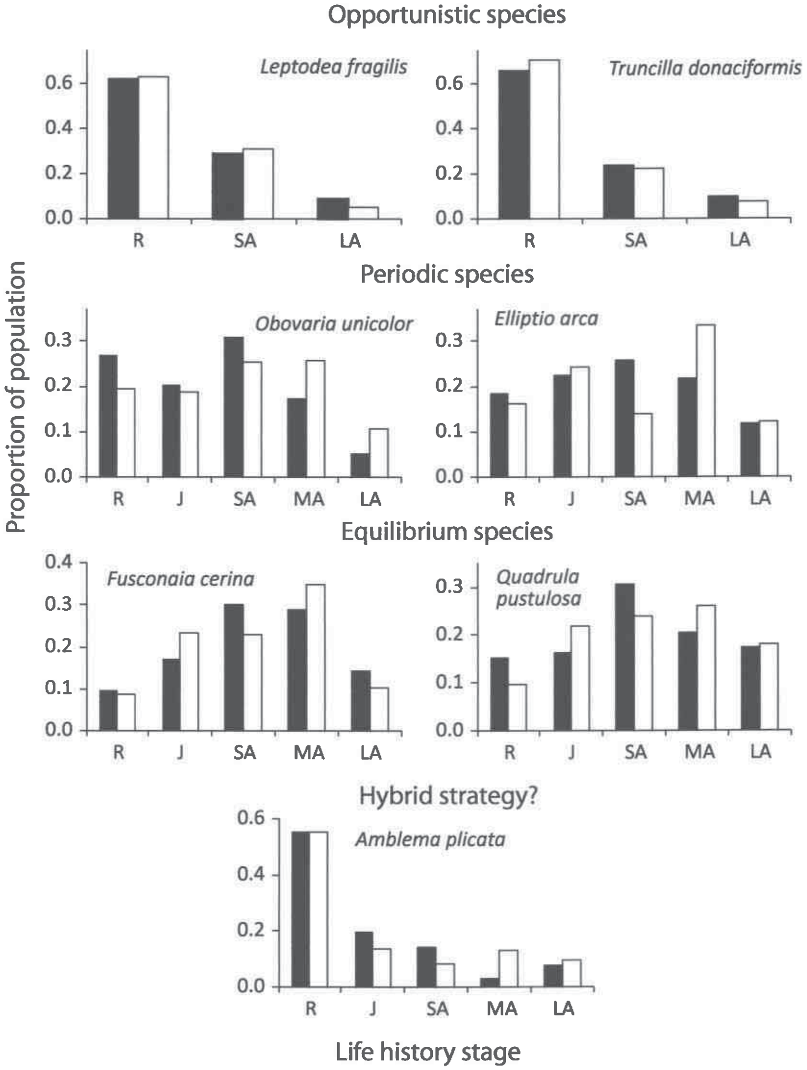

Figure 7.16. Stable stage distributions for mussel populations in the Little Tallahatchie and Sipsey rivers. Solid bars are predicted distributions and white bars are observed distributions of all individuals across 10 years. Life history stages are: R, recruits; J, juveniles (defined as > age 0 but not reproductively mature); SA, small adults; MA, medium adults; LA, large adults (from Haag and Warren, in preparation).

strategies (Table 7.3). Population growth rate of opportunistic species is most sensitive to changes in recruit survival and recruitment (as measured by fertility, defined as the number of recruits produced by individual females). Other species fall along a gradient representing declining influence of recruitment but greater sensitivity to changes in survival of increasingly larger adult size classes. At the opposite end of the gradient, population growth of equilibrium species is influenced most strongly by changes in large adult survival and minimally by changes in recruitment or recruit survival. Although *Amblema plicata* has a stable stage distribution similar to opportunistic

Table 7.3. *Transition matrix elasticity values for mussel populations in the Little Tallahatchie and Sipsey rivers based on mean survival and recruitment rates over 10 years*

	Elasticity of survival (S)					Elasticity of fertility (F)			
Species	S_{R}	S_{J}	S_{SA}	S_{MA}	S_{LA}	F_{R}	F_{SA}	F_{MA}	F_{LA}
Leptodea fragilis	**0.348**	–	0.194	–	0.105	0.006	**0.229**	–	0.118
Truncilla donaciformis	**0.328**	–	**0.229**	–	0.115	–	0.099	–	**0.229**
Medionidus acutissimus	**0.281**	–	**0.257**	–	0.181	–	0.024	–	**0.257**
Obovaria unicolor	0.125	**0.164**	**0.398**	0.129	0.059	–	0.059	0.048	0.018
Elliptio arca	0.082	0.116	**0.205**	**0.407**	0.109	–	0.002	0.046	0.034
Fusconaia cerina	0.083	0.169	**0.277**	**0.280**	0.109	–	0.018	0.032	0.033
Pleurobema decisum	0.088	0.130	**0.291**	**0.272**	0.132	–	0.021	0.027	0.040
Quadrula pustulosa	0.073	0.102	**0.242**	**0.242**	**0.268**	–	0.007	0.026	0.040
Amblema plicata	0.052	0.052	0.087	0.196	**0.560**	–	0.007	0.006	0.040

Note: See Figure 7.16 legend for definition of life history stages. Highest values for each species are bolded. Dashes indicate that the transition does not exist for that species (data from Haag and Warren, in preparation).

species, its elasticity values were similar to equilibrium species. This is explained in part by the fact that *Amblema* is one of the few species in this data set for which adult survival is much higher than recruit survival (Table 7.1). This apparent hybrid life history strategy highlights the plasticity of life history traits in *Amblema*.

7.5. Factors that regulate population growth

The factors that regulate population growth and how they differ among species and habitats are of central importance to mussel evolutionary biology and conservation. The fundamental differences in population dynamics among life history strategies suggest that these strategies have evolved to cope with very different environmental and biotic challenges. For opportunistic and periodic life history strategists, small increases in recruitment and recruit survival during favorable environmental conditions such as low streamflow can result in rapid population growth. This ability – coupled with early maturity – may allow these species to recover rapidly from stressful conditions and promotes persistence in frequently disturbed habitats (Chapter 8).

In contrast, equilibrium species appear to have limited potential for rapid population growth. Population growth of equilibrium species is most sensitive to changes in adult survival, but because adult survival is normally high, there is little scope for increased survival even during favorable conditions. Along with later maturity, low potential for rapid growth may limit equilibrium species in frequently disturbed habitats and restrict them to more stable environments where populations change slowly.

Ecological theory predicts that the potential for biotic interactions, such as competition and predation, to regulate populations increases in stable habitats. The role of competition in regulating mussel populations is poorly known (Chapter 8). The role of predation in regulating mussel populations also has received minimal attention. Simulated population dynamics models predict that increased mortality from predation can have important effects on population growth and evolution of life history traits such as age at maturity (Heino and Kaitala 1997). The apparent intensity of predation in some situations suggests that this can be an important if not primary regulating factor (Section 7.2.A). Because mussels have poorly developed anti-predator shell adaptations (Section 1.3.C), this challenge may be dealt with primarily by life history diversification in accordance with the variable effects of predation among life history strategies and habitats.

Muskrat predation could be important in regulating populations of equilibrium species because it targets medium-sized adults, for which decreased survival is predicted to result in sharply decreased population growth. Muskrat predation could also negatively affect population growth of opportunistic and periodic species by increasing mortality of large adult females – especially for thin-shelled species – resulting in decreased recruitment. However, muskrat predation is expected to have lesser effects on these species because muskrats typically avoid small individuals and therefore should not influence recruit survival. Despite the potential for muskrats to have a large effect on some species, muskrat predation is highly variable and transient. Furthermore, because they are terrestrial animals, muskrats may have minimal impact on mussel populations in deeper, mid-channel habitats in large rivers. For these reasons, muskrat predation may have had little long-term effect on mussel populations historically, despite sporadically intense mortality. Today, small, isolated populations of endangered species may be threatened by muskrat predation (Neves and Odum 1989; Hoggarth et al. 1995). Similarly, muskrats were introduced to Europe from North America and represent a novel threat to mussel populations already reduced by human impacts (Zahner-Meike and Hanson 2001).

Fish predation is potentially a more widespread and important but largely overlooked regulating factor. Fish predation can exert substantial control on the invasive bivalves *Corbicula* and *Dreissena*, limiting abundance and influencing size structure (Robinson and Wellborn 1988; Bowers and de Szalay 2007). Exceptionally dense aggregations of *Corbicula* are often found in shallow water immediately adjacent to the shore and within dead, native mussel shells or other enclosed spaces, suggesting that these places represent refuges from fish predation (W. R. Haag, observations). Similarly, fish predation can limit snail and fingernail clam populations in lakes, and beds of aquatic vegetation or other structure are important refuges from predation (reviewed in Dillon 2000).

Unlike muskrats, fishes are in constant proximity to mussels and have access to most parts of a river channel, and fish predation appears to be consistently high in some habitats (Section 7.2.A). Fish predation may be particularly important in limiting populations of opportunistic and periodic species. Fish predation focuses on small individuals and recruits as well as adult individuals of thin-shelled species, and increased mortality of these life history stages is expected to strongly reduce population growth. In contrast, only the largest fishes can prey on adult individuals of heavy-shelled equilibrium species, and even juveniles appear to suffer lower fish predation than similarly sized thin-shelled species. Fish predation is therefore likely to have lesser effects on equilibrium species for which adult survival is most important to population growth. Fish predation also is likely most important in mid-sized and large streams where molluscivorous fishes, such as drum and catfishes, are consistently abundant (Dettmers et al. 2001; Margraf and Knight 2002). In wetlands, ponds, and small streams, the absence or rarity of large fish predators may allow populations of opportunistic and periodic species to grow rapidly under favorable environmental conditions.

Mussel population dynamics and the factors that influence these processes remain poorly studied. In particular, population dynamics in small streams and lentic habitats are essentially unknown, but these habitats will provide an essential contrast to mid-sized and large rivers from which most of our information is currently derived. Nevertheless, life history traits appear to fundamentally influence population dynamics, predicting that species will differ markedly in their ability to persist under an array of physical and biotic challenges present in different aquatic habitats. In some cases, demographic and population responses may be less dependent on species identity than on the plasticity of life history traits. For example, the high plasticity of life history traits in *Amblema plicata* suggests that populations of this species function very differently in different habitats and may explain its wide distribution and ability to adapt to habitats from small streams to large rivers to lentic habitats. Other species, like the eastern elliptio, *Elliptio complanata*, that occur in a wide range of habitats are expected to show similar plasticity in life history traits and population dynamics. Species that show little life history plasticity are likely restricted to a narrower range of habitats and, consequently, may be more vulnerable to human alterations of aquatic ecosystems.

In addition to the factors I have discussed here, a wide variety of other factors are doubtless important in regulating mussel populations. Most obviously, abundance and availability of host fishes is expected to strongly regulate recruitment and population size. Few populations exist in isolation (at least historically), and metapopulation factors such as landscape connectivity and immigration also likely have important bearing on population growth and persistence and transcend local-scale processes. Immigration is expected to be higher in large rivers and for species with highly mobile host fishes than for small stream species that use sedentary fishes such as darters (Berg et al. 2007), but even small stream species are probably dependent to some extent on recolonization from other populations following disturbance (Chapters 8 and 10). Finally, competition for food and hosts as well as other species interactions are emerging as potentially overarching factors in regulating mussel populations. In the next chapter, I attempt to bring together these disparate facets of mussel ecology to propose a framework outlining the factors that structure mussel assemblages in a variety of habitats.

Chapter 8

Putting it all together

Explaining patterns of mussel assemblage structure

Explaining how mussel assemblages are structured and how so many species can coexist is the ultimate challenge in mussel ecology and has important implications for conservation. In this chapter, I describe patterns of assemblage structure and how they differ among habitats and regions across North America. I then evaluate separately the potential roles of habitat, host use, life history strategies, and biotic factors such as predation and competition in producing these patterns. Finally, I propose a conceptual framework that can explain how these factors interact to structure mussel assemblages.

8.1. Patterns of mussel assemblage structure

For this chapter, I compiled two data sets that I use throughout to examine patterns of assemblage structure at different scales and in relation to different factors. The first data set consists of 98 stream sites (80 different streams) across eastern North America (Appendix B), referred to hereinafter as the "broad-scale" data set. Most sites were in the Mississippian region (82 sites) because fewer data were available for other areas. I attempted to restrict this data set to sites that had not experienced severe human impacts and supported relatively healthy mussel assemblages. However, because few unimpounded large rivers exist today, and few quantitative historical data are available, it was necessary to include several large rivers that are impounded by navigation dams. These sites remain riverine in character (Section 4.1.D.2) and continue to support diverse and abundant faunas. For Mississippian region streams, I classified each site as small stream, mid-sized stream, or large river. Small streams were generally fourth order or smaller, and large rivers were the main stem channels of major watersheds; mid-sized streams were intermediate between these categories (Appendix B). I did not classify streams by size in other regions where strong stream-size assemblage gradients do not exist (Section 4.1.D.4). Data on species relative abundance (proportion of assemblage) were available for all sites, and data on absolute abundance (number/m^2) were available for 52 sites (38 streams). I also compiled host use and life history data for species in this data set based on sources and information presented in Chapters 5 and 6.

The second data set is from remarkably intensive surveys of the Ouachita and Saline rivers in Arkansas (Posey 1997; Davidson and Clem 2004). These data consist of estimates of species abundance in dense, main channel mussel beds throughout sections of these rivers (number of beds and stream length surveyed: Ouachita, 50, 146 km; Saline, 82, 81 km). Total abundance (all species, number/m^2) ranged among beds from 9 to 53 (Ouachita, mean = 24.7) and 8 to 105 (Saline, mean = 31.4). I used this data set to examine local patterns of assemblage structure that are influenced to a minimal extent by biogeographical factors or major differences in habitat among rivers.

Mussel faunas in North America are species rich, but how is this diversity distributed within assemblages? The most obvious characteristic of mussel assemblages – one that is evident to anyone who has sampled for mussels – is that most species are rare (Vaughn 1997a). This pattern is a pervasive characteristic of nearly all ecological assemblages (Magurran 2004). For mussels, the pattern is evident at scales from a single mussel bed to across North America: few species reach high abundance (say, more than 5/m^2), and most typically occur at far lower abundance (less than 0.5/m^2; Figure 8.1). This is influenced by differences in total mussel abundance across habitats (e.g., typically low abundance in small streams; Section 4.1.D.4), but a similar log-normal pattern exists in the proportional representation of species in assemblages. The vast majority of species (about 80%) make up less than 10 percent of the assemblages in which they occur, a substantial number (about 35%) make up less than 1 percent, but a single species rarely composes more than 50 percent of an assemblage (Figure 8.1).

The general absence of a single dominant species highlights another characteristic of most North American mussel assemblages: high evenness (Figure 8.2). Evenness is a measure of diversity and is the converse of dominance; the index of evenness I used (Hurlbert's probability of interspecific encounters, PIE) is the probability that two individuals drawn randomly from an assemblage will be two different species (Gotelli and Entsminger 2004). This probability is uniformly high across stream sizes in the Mississippian and Eastern Gulf regions, showing again that these assemblages are rarely dominated by a single species. Small streams in the Mississippian region have slightly lower median evenness and a greater range of values. In contrast, assemblages in the Atlantic region have characteristically low evenness and typically are dominated by a single species, the eastern elliptio, *Elliptio complanata*, especially in the Northern Atlantic province (Chapter 3). Assessing patterns of diversity in the Pacific region is difficult because of the low species richness and a lack of assemblage data. However, based on available information, evenness appears to be low because species co-occur to only a limited extent, typically resulting in local dominance by a single species (Howard and Cuffey 2003; Brim Box et al. 2006).

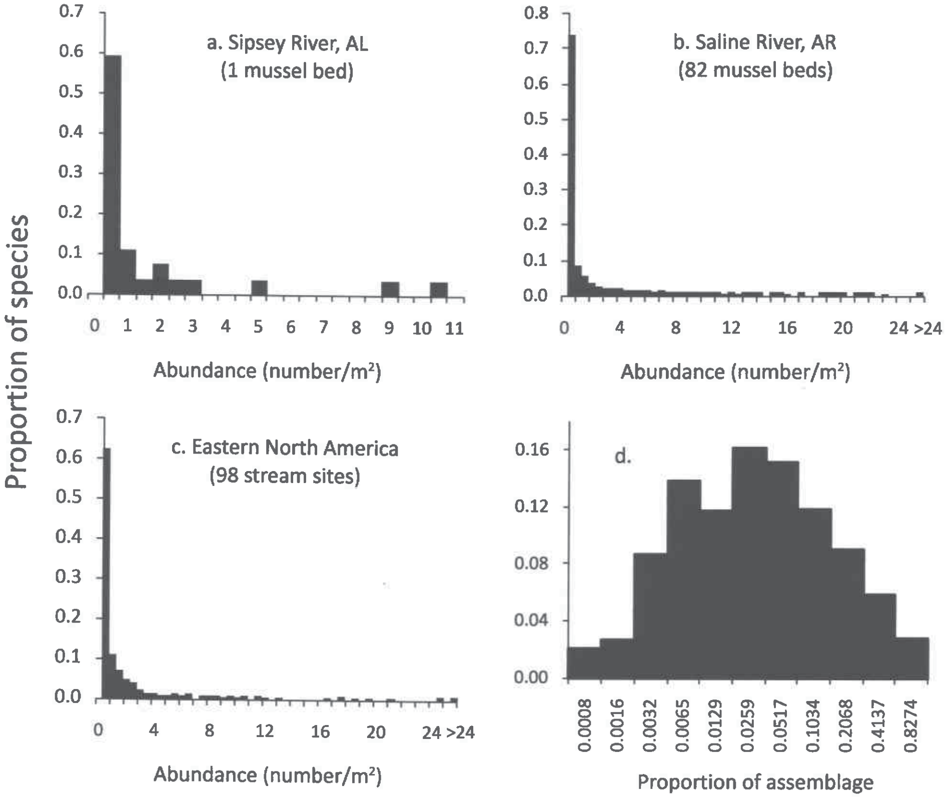

Figure 8.1. Proportional representation of species in abundance classes for North American mussel assemblages at different scales. (d) Data for eastern North America with proportional occurrence of species plotted in octaves corresponding to $\log_2$ classes.

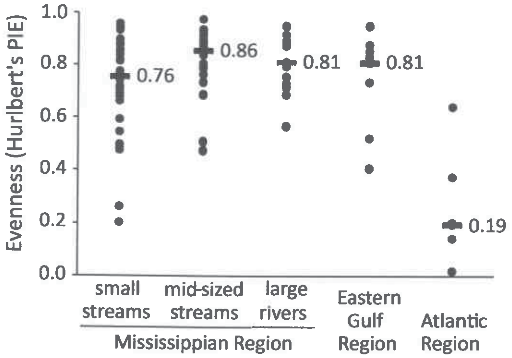

Figure 8.2. Evenness of mussel assemblages across stream sizes and biogeographical regions. PIE is the probability of an interspecific encounter (see text). Horizontal bars are median values.

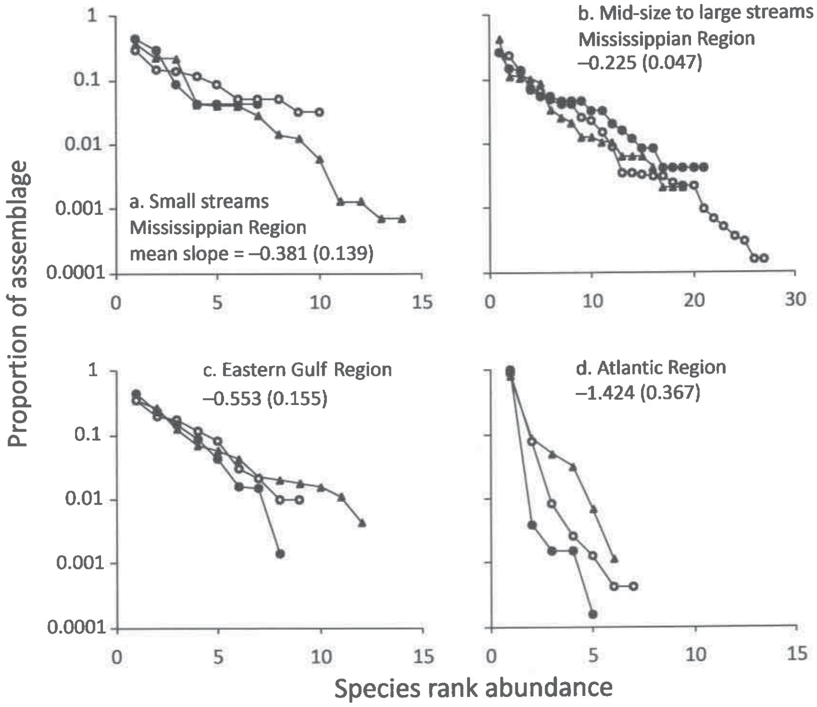

Figure 8.3. Rank–abundance plots for representative mussel assemblages across stream sizes and biogeographical regions. The *x* axis is the rank of species in the assemblage from most (1) to least abundant. Note different scale of *x* axis in panel (b) and log scale for *y* axis. The number in parentheses after the mean slope is the standard deviation. In each panel, different symbols represent different streams: (a) Copper Creek, Virginia, Horse Lick Creek, Kentucky, and Rush Creek, Alabama; (b) Clinch River, Virginia, Sipsey River, Alabama, and St. Croix River, Minnesota; (c) Cowart's Creek, Eightmile Creek, and West Fork Choctawhatchee River (all Alabama); (d) Ashuelot River, New Hampshire, Little River, North Carolina, and Neversink River, New York (see Appendix B for data sources).

Despite their high evenness, mussel assemblages show predictable structure in which dominance is shared by a small group of co-dominant species, and a larger number of subordinate species occur at lower abundance. For example, species abundance in mussel beds in the Kiamichi River, Oklahoma, was log-normally distributed, with the four most abundant species composing more than 70 percent of the biomass (Spooner and Vaughn 2009), and similar patterns are repeated across much of North America. These patterns are illustrated by rank–abundance plots for representative streams (Figure 8.3). Across stream sizes in the Mississippian and Eastern Gulf regions, three to five species typically make up about 60–75 percent of individuals, and the proportional representation of subordinate species is 1–3 orders of magnitude lower than co-dominants. The shallow slopes of these plots indicate high evenness consistent with a log-normal species abundance model. Slopes for small Mississippian

Table 8.1. *Dominant mussel species in assemblages in the Mississippian region*

Small streams	% of sites	Mid-sized streams	% of sites	Large rivers	% of sites
Villosa	69	*Actinonaias*[b]	47	*Reginaia ebena*	38
Lampsilis	50	*Amblema plicata*	34	*Quadrula pustulosa*	38
Elliptio dilatata	28	*Elliptio dilatata*[c]	31	*Amblema plicata*	31
Strophitus	22	*Ptychobranchus*	28	*Truncilla*	31
Pyganodon grandis	19	*Quadrula pustulosa*[d]	25	*Pleurobema*[g]	23
Lasmigona	16	*Pleurobema*[e]	22	*Ellipsaria lineolata*	15
Amblema plicata	13	*Fusconaia*[a]	19	*Fusconaia flava*	15
Alasmidonta	9	*Villosa*	13	*Obliquaria reflexa*	15
Toxolasma	9	*Megalonaias nervosa*	9	*Actinonaias ligamentina*	8
Anodontoides	6	*Cyclonaias tuberculata*	6	*Elliptio crassidens*	8
Fusconaia[a]	6	*Epioblasma*	6	*E. dilatata*	8
Ptychobranchus	3	*Leptodea fragilis*	6	*Megalonaias nervosa*	8
		Quadrula quadrula[f]	6	*Potamilus*	8
		Cyprogenia	3		
		Lampsilis	3		
		Lasmigona	3		
		Obliquaria reflexa	3		
		Pyganodon grandis	3		
		Quadrula verrucosa	3		

Note: Cell entries are the percentage of sites in each stream size category at which a species composed 10% or more of the assemblage. Genera with restricted distributions are excluded from this analysis (e.g., *Medionidus, Pleuronaia, Plectomerus*). See text for details about data set.

[a] Excludes *Reginaia ebena*.
[b] Includes *A. ligamentina* and *A. pectorosa*.
[c] Includes *E. arca*.
[d] Includes *Q. asperata*.
[e] Excludes *P. cordatum* and *P. rubrum*.
[f] Includes *Q. rumphiana*.
[g] *P. cordatum* and *P. rubrum* only.

streams and eastern Gulf Coast streams are similar, but slopes tend to be shallowest for mid-sized and large Mississippian streams. Rank–abundance plots for Atlantic region streams are steep, concordant with their low evenness and domination by a single species, and are suggestive of a geometric or log-series distribution.

Co-dominant species in mussel assemblages are a predictable subset of the regional fauna, but these species vary among biogeographical regions and stream sizes. Despite their high species richness, large rivers of the Mississippian region are consistently dominated by only a small group of species, including large-river specialists (e.g., ebonyshell, *Reginaia ebena*; Ohio pigtoe, *Pleurobema cordatum*) and stream-size generalists (e.g., threeridge, *Amblema plicata*; pimpleback, *Quadrula pustulosa*; deertoe and fawnsfoot, *Truncilla*) (Table 8.1). The hickorynut, *Obovaria olivaria*;

bankclimber, *Plectomerus dombeyanus*; and mapleleaf, *Quadrula quadrula*, also can be among the dominant species in some large rivers. These species often occur at high densities, forming well-defined mussel beds. Other large-river specialists (e.g., *Arcidens confragosus, Lampsilis abrupta/higginsi, Plethobasus, Quadrula metanevra, Q. nodulata*) as well as many stream-size generalists are regular components of these assemblages but are nearly always limited to a subordinate role.

Small streams in the Mississippian region are dominated by an entirely different and much larger group of species that overlap minimally with large-river dominants (Table 8.1); most of the genera listed in this table include multiple species. Other genera that can dominate in small streams in some areas include *Hamiota* and *Medionidus*. Even though they dominate assemblages proportionally, these species do not typically occur at high density in small streams and do not form well-defined mussel beds (Section 4.1.D.4). Mid-sized streams also have a wide array of dominant species, but these overlap broadly with small streams and large rivers. However, several species are regular dominants typically only in mid-sized streams (e.g., *Actinonaias, Ptychobranchus*, and *Pleurobema* but not *P. cordatum* or *P. rubrum*). Other dominants in mid-sized streams in some areas include *Lemiox, Medionidus, Plectomerus*, and *Pleuronaia*. Streams in the Eastern Gulf region are dominated by an array of species similar to those in mid-sized streams in the Mississippian region, especially *Amblema, Elliptio, Elliptoideus, Pleurobema, Quadrula*, and *Villosa*. Streams in the Atlantic region are overwhelmingly dominated by *Elliptio complanata*, but other dominants in some situations can include the alewife floater, *Anodonta implicata*; eastern floater, *Pyganodon cataracta*; and eastern pearlshell, *Margaritifera margaritifera*, in the Northern Atlantic province, and an array of other *Elliptio* in the Southern Atlantic.

Patterns of dominance can shift markedly along environmental gradients. A common pattern seen throughout the Mississippi River system is dominance by the mucket, *Actinonaias ligamentina*, and spike, *Elliptio dilatata*, in mid-sized streams but a gradual replacement of these species by threeridge, *Amblema plicata*, and other species in larger rivers (Ahlstedt and Jenkinson 1991; Posey 1997; Hornbach 2001; Davidson and Clem 2004). This could be due to some extent to loss of shoal habitats in impounded large rivers (Chapter 10), but historical evidence suggests that this pattern existed prior to impoundment (e.g., Wilson and Clark 1914), and similar patterns exist throughout the region. In the Tennessee River system, the pheasantshell, *Actinonaias pectorosa*, dominated historically only in smaller mid-sized streams where *A. ligamentina* was rare (Ortmann 1925). In the Ohio River, only six species make up nearly 80 percent of the mussel assemblage, out of a total of more than 30 species, but dominance shifts in a downstream direction from *Elliptio crassidens* and *Quadrula quadrula* to *Pleurobema cordatum* to *Reginaia ebena*, while abundances of *A. plicata* and *Quadrula pustulosa* remain relatively constant throughout (Figure 8.4). In the Ouachita River, abundance of co-dominant species varies among mussel beds, but dominance shifts from the pyramid pigtoe, *Pleurobema rubrum*, in the middle reaches of the river to

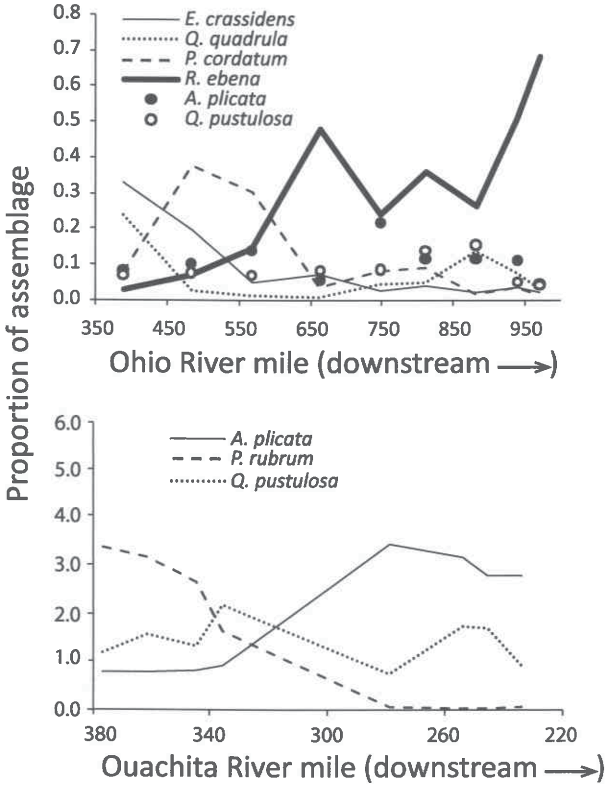

Figure 8.4. Shifting patterns of species dominance in the Ohio River, Kentucky, and the Ouachita River, Arkansas (data from Williams and Schuster 1989; Posey 1997).

Amblema plicata in the lower river, while abundance of *Quadrula pustulosa* remains relatively constant (Figure 8.4).

The log-normal distribution of species abundance is a pervasive pattern in freshwater fish assemblages and among many other organisms (Sheldon 1987; Magurran 2004). Interpretation of these distributions is contentious, but a biological explanation for the log-normal distribution is hierarchical niche partitioning and resource specialization, and it typically characterizes large, stable assemblages near equilibrium (Gotelli and Graves 1996). For example, old-growth mesophytic forests are characterized by high evenness, with shared dominance by a predictable subset of tree species that predominate according to small-scale variation in moisture, exposure, and other habitat factors, whereas early successional forests are more uniformly dominated by one or a few species (Braun 1950; Clebsch and Busing 1989). Alternatively, the log-normal distribution is seen as a null, statistical outcome of random variation in a large number of factors that determine species abundance (Caswell 1976). Geometric or log-series distributions are seen less frequently but are generally considered characteristic of small, stressed, or pioneer assemblages in which species abundance is determined by fewer factors or by dynamics of colonization in unsaturated habitats (Gotelli and Graves 1996; Magurran 2004).

Differences in species abundance distributions provide hypotheses about how mussel assemblages are structured in different habitats. The shallow slope of rank–abundance plots for mid-sized streams and large rivers in the Mississippian region suggests that these assemblages are near saturation and approach equilibrium conditions in which biotic interactions play a large role in determining species abundance. The relatively steeper slope for small Mississippian streams and the Eastern Gulf region may be indicative of assemblages that are limited to a greater extent by disturbance and dispersal, precluding saturation and lessening the effects of biotic interactions. The steep slope and high dominance in the Atlantic region are concordant with the presence of strong dispersal barriers that restrict movement of species within this region and preclude colonization from other regions (Chapter 3).

The degree to which mussel assemblages may be saturated and the potential role of biotic interactions in structuring these assemblages have received little attention (Section 8.5). Diverse stream fish assemblages in eastern North America appear to be saturated locally, resulting in strong competitive interactions that shape these assemblages and override effects of regional species richness to varying extents (Taylor 1996; Angermeier and Winston 1998; Matthews and Robison 1998). On the basis of an increase in species richness with increasing total mussel abundance among sites in the Kiamichi and Little rivers, Oklahoma, Vaughn (1997) concluded that there was no evidence of saturation or competition within these assemblages. However, this result could be explained as easily by a sampling artifact. Estimates of species richness are dependent primarily on the number of individuals encountered rather than the area sampled (Gotelli and Graves 1996). Because the same number of samples was taken at each site in the Oklahoma study (see Vaughn et al. 1996), higher richness is expected at sites with higher abundance simply because more individuals were encountered. In other rivers, the relationship between richness and total abundance is variable (Figure 8.5), but the problem of unequal numbers of individuals remains. In the Ouachita River, the lack of a relationship could be evidence of saturation or density compensation (Wright 1980). In many streams, the introduced bivalve, *Corbicula*, appears unable to reach high abundance in intact native mussel assemblages and dominates only in habitats with few mussels (Strayer 1999b; Vaughn and Spooner 2006b), providing additional evidence for saturation. Like for many organisms, local species richness of mussel assemblages is a strong function of regional richness, and local faunas are nested subsets of regional faunas (Vaughn 1997a; Rashleigh 2008). However, these relationships are based only on species presence or absence and do not go far in explaining patterns of dominance and assemblage structure. For example, a species could persist at a site but be held at low abundance by biotic interactions with other species.

A more informative approach to the question of saturation and potential competitive interactions is to examine across multiple sites the relationship between the

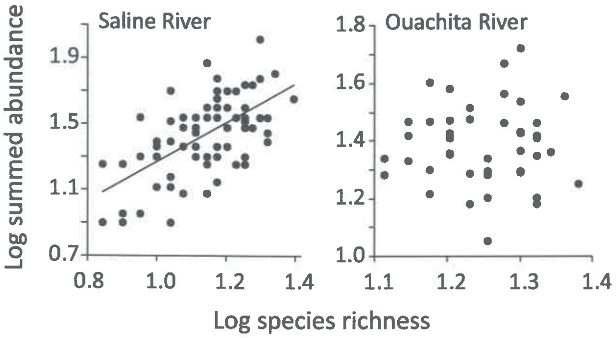

Figure 8.5. Relationship between species richness and total abundance among mussel beds in the Ouachita and Saline rivers, Arkansas. Relationship is significant for Saline River ($R^2 = 0.605$, $p < 0.0001$) but not for Ouachita ($p > 0.80$) (data from Posey 1997; Davidson and Clem 2004).

abundance of individual species and the summed abundance of all other co-occurring species. In the absence of saturation or competition, these relationships should be positive if species respond similarly to environmental factors. In addition, a positive relationship could indicate the existence of facilitative interactions whereby increased total abundance creates conditions more favorable for mussel growth (Spooner and Vaughn 2009, 2012; Section 8.5). A negative relationship would indicate that a species achieves its maximal abundance only when abundance of other species is low. Mechanisms that could produce this pattern include competitive exclusion or differences in habitat affinities among species. However, many mussel species show little difference in habitat use (Chapter 4). For species that do have distinct habitat affinities, the mechanisms that determine these affinities are typically unspecified but could include competitive interactions that limit them to marginal habitats (Sections 8.3 and 8.5).

I examined these relationships in the Ouachita and Saline river data set for 16 species in each river, including all co-dominant species and a representative set of subordinate species. Data were log-transformed, and significance of correlations for each river was adjusted for multiple testing (Benjamini and Yekutieli 2001). Few species showed a strong relationship to the summed abundance of all other species (Figure 8.6). In the Saline River, abundance of seven species (including two of three dominant species) was correlated positively with assemblage abundance ($p < 0.001$), but these relationships explained little variation in abundance ($R^2 = 0.09$–0.26). In the Ouachita River, only *Fusconaia flava* had a positive correlation ($R^2 = 0.10$, $p < 0.022$). For several species, patterns were suggestive of a negative boundary relationship in which maximum abundance is limited by increasing abundance of other species, but below this boundary, other factors influence the species' abundance. However, Monte Carlo simulations did not support these relationships (Gotelli and Entsminger 2004), and correlations were not significant. Other species showed evidence of a modal boundary relationship in which abundance peaked at an intermediate level of assemblage

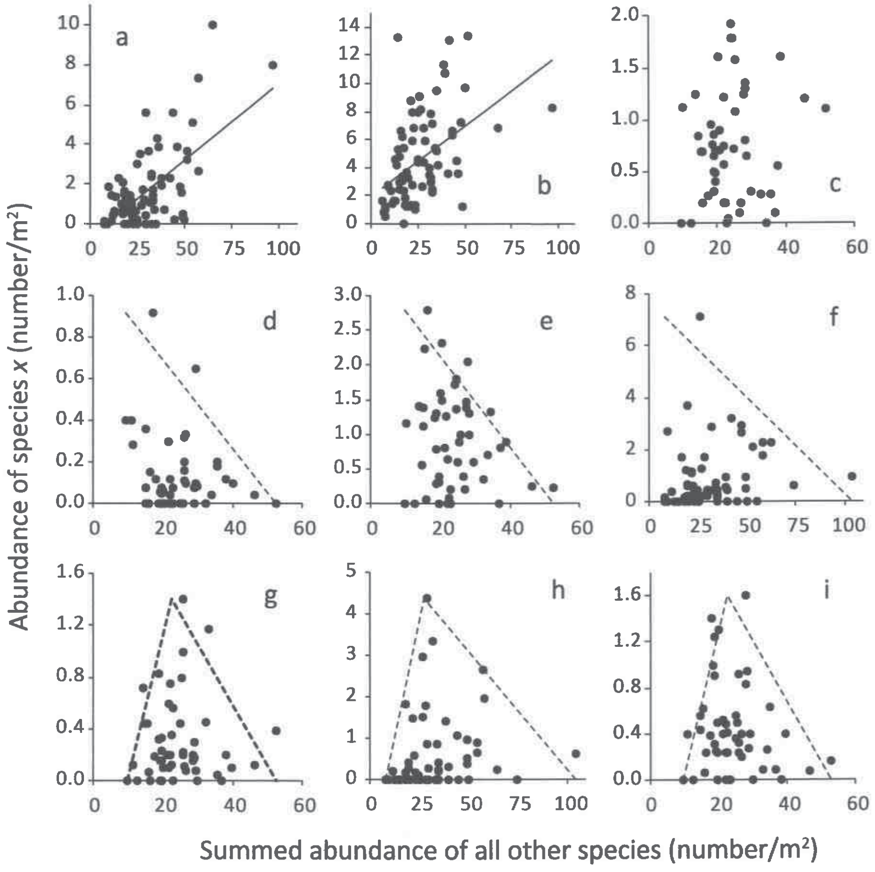

Figure 8.6. Relationships between individual species abundance and summed abundance of all other co-occurring species among mussel beds in the Ouachita and Saline rivers, Arkansas (data from Posey 1997; Davidson and Clem 2004). (a) Positive correlation ($r = 0.476$, $p < 0.0001$), *Fusconaia flava*, Saline. (b) Positive correlation ($r = 0.504$, $p < 0.0001$), *Quadrula pustulosa*, Saline. (c) No apparent relationship, *Megalonaias nervosa* (no significant correlation), Ouachita. (d–f) Hypothetical negative boundary relationships: (d) *Leptodea fragilis*, Ouachita; (e) *Quadrula quadrula*, Ouachita; (f) *Obovaria jacksoniana*, Saline. (g–i) Hypothetical modal boundary relationships: (g) *Quadrula verrucosa*, Ouachita; (h) *Plectomerus dombeyanus*, Saline; (i) *Lampsilis cardium*, Ouachita. Correlations are based on log-transformed data. Boundaries created as: negative (min x, max y), (max x, min y); modal (min x, min y), (median x, max y), (max x, min y) (Gotelli and Entsminger 2004).

abundance, but again, these relationships were not supported by Monte Carlo simulations. The possibility of a modal pattern is especially intriguing because it suggests that a species' abundance might increase initially because of facilitative interactions but could be limited by competition above some level of assemblage abundance. Many species showed no discernible pattern, suggesting that their abundance is independent of the abundance of co-occurring species.

In this data set, evidence of species interactions could be obscured by spatial variation in habitat conditions or other physical factors that also influence abundance, and my approach does not account for potential intraspecies effects. A further weakness of the data set for this purpose is that it represents a narrow range of habitats (i.e., only high-density, main-channel mussel beds in large rivers). Other data sets that also include lentic microhabitats and other habitats with lower total mussel density, as well as measurements of habitat variables, would allow more exhaustive exploration of patterns of co-occurrence (e.g., Taylor 1996). Abundance relationships between pairs of species that potentially compete for a specific shared resource (e.g., host fishes) also could shed light on whether these types of interactions are likely to play a role in structuring assemblages (Section 8.3). Nevertheless, comparison of these patterns with other streams highlights their significance. In a smaller, fourth-order stream, abundance of all species showed strong, positive relationships with total mussel abundance, suggesting that these assemblages were unsaturated and limited primarily by abiotic factors (Layzer and Madison 1995). The lack of strong positive relationships in the much larger Ouachita and Saline rivers leaves open the possibility that biotic interactions could play a role in structuring mid-sized- and large-stream assemblages; at the least, these patterns indicate that species respond differently to an array of factors.

In addition to differences in species composition and dominance, variability in assemblage structure differs widely according to stream size. Although large-river assemblages in the Mississippian region may vary from site to site, in general, these assemblages are highly distinctive and cluster tightly in a discrete area of species space (Figure 8.7). The distinctiveness of large-river assemblages is due to the presence of a suite of obligate large-river species, including co-dominant and subordinate species, as well as the rarity or absence of small-stream species (e.g., *Alasmidonta viridis, Anodontoides, Toxolasma, Villosa*; Section 4.1.D.4). In sharp contrast, structure of small-stream assemblages is highly variable. These assemblages are distinct from those of large rivers but otherwise show little consistent pattern. Species that defined this group on the ordination axes included a large number of species whose abundances varied widely among small-stream sites. This great heterogeneity is similar to that seen for the composition of mussel assemblages in isolated lentic habitats (Section 4.1.D.2). Assemblages in mid-sized streams overlap broadly with both small streams and large rivers. To an extent, this is an artifact of my stream classification scheme because mid-sized streams span a greater range of physical conditions than the other categories. Mid-sized sites range from the lower reaches of large tributaries to sites that more closely resemble small streams. Nevertheless, the placement of these sites in species assemblage space (Figure 8.7), along with dominance of some species only in mid-sized streams (Table 8.1), illustrates the transitional nature of these assemblages.

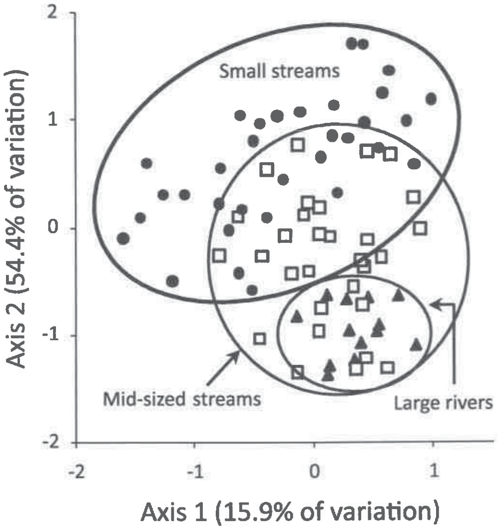

Figure 8.7. Ordination of 76 mussel assemblages in the Mississippian region based on proportional species representation in each assemblage (nonmetric multidimensional scaling based on Sørensen distance, PC-ORD; McCune and Mefford, 1999). Proportions were arcsine-transformed. To minimize biogeographical differences among assemblages, species were combined into generic-level groupings following Campbell et al. (2005); generic groups present in less than 5% of assemblages were omitted. The best solution was two-dimensional (70% of variation among assemblages explained, final stress = 21.33, instability = 0.0001). Note that axis 2 explains the most variation.

The fundamental differences in assemblage structure between habitats and biogeographical regions described in this section are likely caused by an array of factors operating at multiple scales. In North American fish assemblages, the influence of disturbance and competition varies at different scales (Power et al. 1988; Angermeier and Schlosser 1989; Taylor 1996). The great variability in small-stream and lentic mussel assemblages and their lower evenness suggest that stochastic processes such as disturbance or dispersal are of primary importance in these habitats. In contrast, the high evenness and predictable nature of large-river assemblages suggest that deterministic processes such as competition play a large role in structuring these assemblages. These divergent selective forces have resulted in an array of life history strategies and other ecological attributes in mussels. Ecological differences among species, including variation in niche requirements and niche width, are expected to result in predictably large differences in abundance (Nee et al. 1992). The consistent patterns of species dominance and the differences in these patterns among habitats beg the questions, why do some species dominate in some habitats but not in others? and why are some species always rare? In the following sections, I examine how ecological differences among species influence the structure of mussel assemblages across a range of aquatic habitats.

8.2. The role of habitat and disturbance

Niche partitioning of available habitat is a fundamental explanation of how multiple species can coexist. For mussels, partitioning of physical habitat among species can partially explain one of the most pervasive patterns in assemblage structure in the Mississippian region: higher species richness in larger streams (Section 4.1.D.4). In general, habitat diversity increases in larger streams, and increased habitat diversity is associated with increased fish species richness (Schlosser 1982a). Large, unimpounded rivers present a variety of habitats, including deep, stable runs; shallow riffles; and extensive lentic microhabitats. These habitats provide niches for a wider variety of mussel species than the narrower array of microhabitats available in small streams and lakes. However, this explanation can explain coexistence for only a small percentage of the fauna because most species appear to have broad niche width for habitat (Section 4.2.C). In small streams, few strong patterns of microhabitat specialization are apparent among species at all. Even limited habitat partitioning does not explain *why* species are limited to certain habitats or why, among species with similar "habitat preference," some species predictably dominate assemblages but others are consistently rare.

To explore the habitat factors that potentially determine mussel assemblage structure, we need to begin by discussing fundamental physical differences in aquatic habitats and how these factors influence organisms in general. In addition to a lower diversity of habitats, small streams have higher temporal variability in habitat diversity (Schlosser 1982a). Temporal stability, particularly the frequency and intensity of disturbance, is considered one of the primary physical factors that structure ecological communities (e.g., Resh et al. 1988; Lake 2000). Streams with differing disturbance regimes are associated with distinctive groups of fish and aquatic insect species that have characteristic suites of life history traits adapted for their particular habitats (Schlosser 1982b; Death 1995; Poff and Allan 1995).

Small streams are viewed as temporally unstable habitats because they experience frequent disturbance from drought, oxygen stress, and floods, which have relatively greater effects on small streams than on large ones (Section 4.1.D.1). These types of disturbance are typically periodic and correspond to long-term drought or flood cycles with return periods of about 2–15 years (Dickerson and Dethier 1970; Poff and Ward 1989; Seager et al. 2009). Although lentic systems are often considered stable habitats (Resh et al. 1988), they also experience temporal variability and this variation may occur annually or even more frequently. Stratification of large lakes results in anoxia and cold temperatures in the hypolimnion, which can reduce available mussel habitat to a small percentage of the lake area (e.g., Paterson and

Cameron 1985). In small lakes and wetlands, warm summer temperatures can severely deplete oxygen levels, and lakes also may experience sharply depressed oxygen levels at night during suspension of photosynthesis (Matthews 1998). In northern lakes, ice cover can result in depleted oxygen and extensive scouring of the littoral zone (Lewis 1984; Section 4.1.A). These types of disturbance may be especially challenging to mussels because they are sedentary, and many species have relatively high oxygen requirements (Section 4.1.C). In contrast, large rivers represent more stable habitats that are less affected by drought and floods. The downside to life in a stable habitat is that organisms have greater potential to reach the carrying capacity of the system, at which point competition for resources can become strong, limiting population growth (Pianka 1970). In unstable habitats, disturbance prevents populations from reaching carrying capacity, and populations are controlled primarily by their intrinsic growth capacity.

Like other aquatic organisms, mussel life history strategies and other ecological traits surely have been shaped by these divergent selective forces. We expect that patterns of assemblage structure will correspond to the ways that these strategies allow species to adapt to an array of challenges in aquatic habitats. In addition to adaptations common to other aquatic organisms, the host relationship of freshwater mussels represents another way in which specialization for resource use allows the coexistence of species, and it plays a large role in shaping assemblages.

8.3. The role of the host relationship

The diverse North American fish fauna presents a unique niche dimension that is considered a major factor in the spectacular radiation of the co-occurring mussel fauna (Haag and Warren 1998; Rashleigh 2008). Because of the great degree of host specialization (Chapter 5), the host niche appears to be partitioned much more finely than habitat or food resources. Consequently, host relationships likely play an important role in structuring mussel assemblages at several levels. For example, mussel species richness should be related to the diversity of available hosts (Watters 1992; Vaughn and Taylor 2000), the abundance of a particular mussel species should be influenced by the abundance of its host (Rashleigh and D'Angelis 2007; Strayer 2008), and some types of host infection strategies may be more effective than others in certain habitats, resulting in shifting patterns of dominance.

The role of the host relationship has been acknowledged for many years. Ortmann (1920, 311) wrote that "the distribution of the fish-host, and the ecological peculiarities of it, must largely influence the distribution of the Naiades." Similarly, "a better understanding of fish host relationship has been an unfortunate omission in most studies involving the ecology and distribution of mussels" (van der Schalie and van der Schalie 1950, 460). In recent years, recognition of the important role of the host relationship has grown, along with our knowledge of the intricacies of this relationship.

However, there has heretofore been no attempt to exhaustively review how the host relationship influences mussel assemblages at multiple scales.

8.3.A. Hosts and the distribution of mussel species

Obviously, mussels cannot exist where their hosts are absent. At the broadest scale, the geographical distribution of hosts dictates the potential distribution of a mussel species. As expected, some of the most widely distributed mussels are host generalists (e.g., *Alasmidonta undulata, Amblema plicata, Lasmigona complanata, Megalonaias nervosa, Pyganodon cataracta, P. grandis, Strophitus undulatus, Utterbackia imbecillis*). Similarly, many specialists that use widespread host fishes, such as black basses, sunfishes, or catfishes, have broad distributions (e.g., *Lampsilis cardium, L. siliquoidea, Quadrula pustulosa, Q. quadrula, Q. verrucosa, Toxolasma parva, Villosa iris*). Other specialists achieve wide distribution by their ability to parasitize an array of fish species within a widely distributed phylogenetic group such as darters or minnows (e.g., *Epioblasma triquetra, Pleurobema sintoxia*).

There are several examples of close correspondence between the geographical distributions of mussels and their hosts. The distribution of the alewife floater, *Anodonta implicata*, matches closely that of its host, the alewife, *Alosa pseudoharengus*, and within this area, it occurs only in river systems that have alewife runs (Johnson 1946; Nedeau et al. 2000). The distribution of the fragile papershell, *Leptodea fragilis*, also corresponds remarkably well to its host, the freshwater drum, *Aplodinotus grunniens*. In the southeastern United States, both species are generally distributed in larger streams from Texas east to the Mobile Basin, but *L. fragilis* is conspicuously absent in the intervening Pascagoula River system and other river systems east of the Mobile Basin, where drum are also absent (Figure 8.8). Similar distributional patterns are seen in this region between drum and the fawnsfoot, *Truncilla donaciformis*, and between the black sandshell, *Ligumia recta*, and its hosts sauger and walleye (*Sander*) (Ross 2001; Jones et al. 2005). In the upper Mississippi River system, the distribution of the pistolgrip, *Quadrula verrucosa*, is nearly identical to that of its primary host, the flathead catfish, *Pylodictis olivaris* (Hove et al. 2011).

Despite these examples, host breadth or host distribution is not a good general predictor of mussel distribution because of confounding biogeographical or habitat factors (see Rashleigh 2008). The distribution of many species that evolved apparently by vicariance in isolated river systems is limited primarily by dispersal barriers rather than by the distribution of their host fishes. The Cumberland monkeyface, *Quadrula intermedia*, occurs only in upland portions of the Tennessee River drainage, despite the much broader distribution of its host fishes, *Erimystax dissimilis* and *E. insignis* (Yeager and Saylor 1995; Figure 8.8). Many other narrowly endemic mussel species occupy only a fraction of the range of their host fishes; these species include specialists (e.g., *Fusconaia burkei, Hamiota, Lampsilis virescens,*

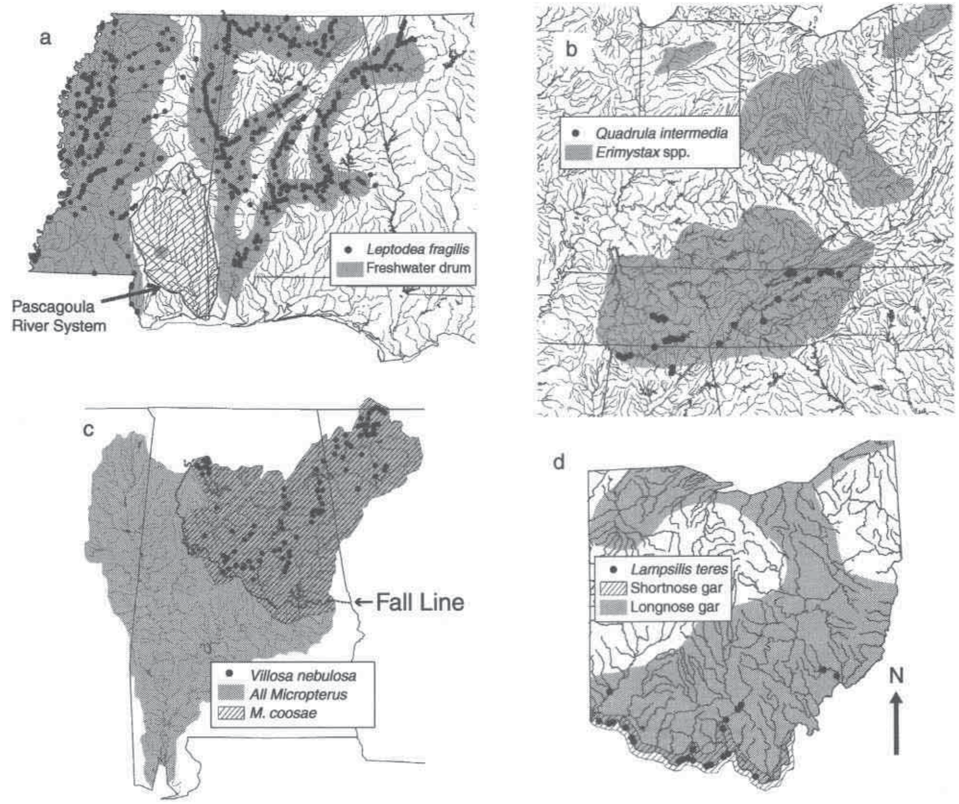

Figure 8.8. Distribution of four mussel species relative to the distribution of their host fishes. (a) Fragile papershell, *Leptodea fragilis*, and freshwater drum (*Aplodinotus grunniens*) in Alabama, Florida, Georgia, and Mississippi. Isolated occurrences of both species in the Pascagoula River system are based on single, historical records (data from Mettee et al. 1996; Ross 2001; Boschung and Mayden 2004; Williams et al. 2008; Mississippi Museum of Natural Science, Jackson). (b) Cumberland monkeyface, *Quadrula intermedia*, and the minnows, *Erimystax dissimilis* and *E. insignis* (data from Lee et al. 1980; Parmalee and Bogan 1998; Williams et al. 2008). (c) Alabama rainbow, *Villosa nebulosa*, and the black basses, *Micropterus coosae*, *M. henshalli*, and *M. salmoides* (data from Mettee et al. 1996; Boschung and Mayden 2004; Williams et al. 2008). (d) Yellow sandshell, *Lampsilis teres*, and shortnose gar (*Lepisosteus platyrhincus*) and longnose gar (*L. osseus*) in Ohio (data from Trautman 1981; Watters et al. 2009).

Lemiox rimosus, Medionidus, Pleurobema strodeanum, Villosa) and generalists (e.g., *Amblema neislerii, Lasmigona etowaensis, L. holstonia, Strophitus connasaugaensis*). For other species, habitat factors may limit distribution, despite their generalist host use (e.g., *Anodonta suborbiculata, Anodontoides ferrusacianus*; Chapter 4) or, for specialists, the wide distribution of their hosts (e.g., *Ligumia subrostrata, Toxolasma texasiensis*).

The second level at which the host relationship can influence mussel distribution is among habitats within the range of a species. Habitat requirements of hosts may determine the occurrence of mussels rather than requirements of the mussels themselves. The most conspicuous examples of this are species that are specialists on obligate large-river fishes (e.g., *Elliptio crassidens, Leptodea fragilis, Ligumia recta, Obovaria olivaria, Reginaia ebena, Truncilla*). These mussel species are not generally distributed within a river system but occur primarily in large streams inhabited by their hosts (Figure 8.8). In small midwestern streams, specialists on freshwater drum (*Leptodea, Truncilla, Potamilus*) occurred only in the lower reaches of tributaries near their confluence with large rivers or in stream reaches where drum access was not restricted by dams (Watters 1996; Myers-Kinzie et al. 2001). However, some large-river mussel species are host generalists (e.g., *Megalonaias nervosa*) or use widespread fishes (e.g., *Lampsilis higginsi, Pleurobema rubrum*; Waller and Holland-Bartels 1988; Culp et al. 2009), indicating that other factors limit their distribution. Habitat use by hosts also may influence the distribution of mussels at a smaller scale. Most mussel species that occur frequently under large, flat rocks are specialists on darters, sculpins, or the mudpuppy (*Necturus*), all of which share this specialized habitat (Section 4.2.A). Other small-scale features of mussel distributions potentially related to host movements or behaviors have not been studied.

Separating the influence of host distribution from mussel habitat requirements or other factors is often difficult. The Alabama rainbow, *Villosa nebulosa*, is restricted to upland streams, despite the general distribution of its host fishes, black basses (*Micropterus*), but its distribution follows closely that of redeye bass (*M. coosae*; Figure 8.8). Although *V. nebulosa* glochidia can metamorphose robustly on several species of *Micropterus* in the laboratory (Haag and Warren 2003), immunological compatibility in the wild or mechanisms of host infection may favor redeye bass. However, this pattern could also be explained simply by a similar preference of both species for upland streams. The yellow sandshell, *Lampsilis teres*, is a specialist on gars (Howard 1914; Keller and Ruessler 1997) and occurs mainly in large, lowland streams (Williams et al. 2008; Watters et al. 2009). The longnose gar (*Lepisosteus osseus*) is distributed widely throughout eastern North America, including clear, upland streams, but the combined distribution of shortnose (*L. platostomus*) and spotted gar (*L. oculatus*) parallels that of *L. teres* much more closely (Figure 8.8). Longnose gar are primarily piscivores that feed in open water, but other gar species, especially shortnose gar, feed on the bottom to a greater extent, and crayfish can make up a large percentage of their diet (Ross 2001). Consequently, benthic feeding gar species may be more likely to encounter mantle lures of *L. teres*. The concordance between the distribution of *L. teres* and these gar species also could be explained by similar habitat requirements. However, *L. teres* has declined dramatically in the upper Ohio River system in Kentucky and Ohio in the last 50 years, coincident with the disappearance of shortnose gar from the region during the same time period but despite the continued presence of longnose gar (Trautman 1981; Watters et al. 2009; W. R. Haag, observation).

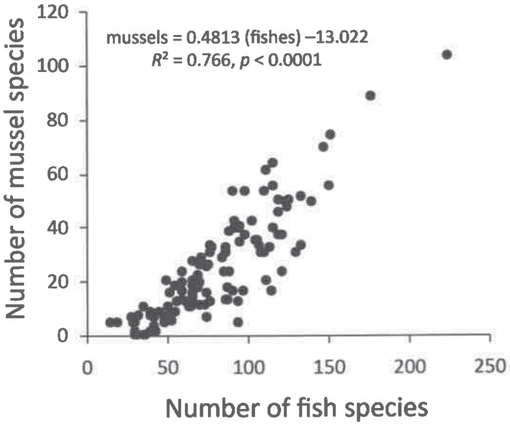

Figure 8.9. Relationship between fish and mussel species richness in 113 North American river systems (mussel data from Haag 2010; fish data from Hocutt and Wiley 1986; Benke and Cushing 2005).

8.3.B. Hosts and assemblage structure

In addition to influencing species distributions, host relationships likely play an important role in structuring mussel assemblages. At the most fundamental level, the number of fish species in a watershed or at a site is a strong predictor of mussel species richness (Watters 1992; Vaughn and Taylor 2000; Myers-Kinzie et al. 2001; Mulcrone 2004) and, unlike stream size, explains a high percentage of variation in mussel richness even at the continental scale (Figure 8.9; see Section 4.1.D.4). These patterns suggest a strong linkage between fishes and mussels, but they could be simply a result of biogeographical or other unmeasured factors that influence these two groups in similar ways. For example, river systems with high fish and mussel richness tend to also have high richness of other aquatic groups, such as crayfish and turtles, but this does not imply a direct ecological linkage between these groups. However, in the Red River system of Oklahoma and Texas, fish richness alone explained 15 percent of the variation in mussel richness among sites, and fish effects potentially confounded with habitat or spatial factors accounted for another 37 percent (Vaughn and Taylor 2000). Furthermore, variation in mussel richness increased with increasing fish richness, suggesting that host diversity sets an upper limit for mussel diversity but that other factors can reduce diversity below this threshold.

Although fish richness predicts mussel richness continent-wide, the form of this relationship varies among biogeographical regions. Throughout most of the Mississippian and Eastern Gulf regions, the slope of the relationship representing the rate at which mussel richness increases with fish richness is similar, and the average number of fish species per mussel species ranges from only 1.9 to 3.7 (Table 8.2), suggesting that about one-third to one-half of the fish fauna is used as hosts. The number of fish per mussel species also is remarkably consistent across spatial

Table 8.2. *Relationships between mussel and fish species richness among 113 river systems in North America according to biogeographical affinity*

Biogeographical affinity	Slope	Number of fish per mussel species: Mean	Min	Max
Mississippian region	0.499			
Ohioan province	0.413	1.9	1.7	2.3
Tennessee-Cumberland province	–	2.1	2.0	2.2
Mobile Basin province	–	2.3	2.0	2.5
Sabine–Trinity province	–	2.6	2.3	2.8
Pontchartrain–Pearl–Pascagoula province	–	2.7	2.2	2.9
Upper Mississippi province	–	2.8	2.1	4.6
Interior Highlands province	0.399	2.8	2.4	3.5
Mississippi Embayment province	–	3.4	3.1	3.9
Western Gulf province	–	3.4	2.3	6.1
St. Lawrence–Great Lakes province	0.467	5.7	3.2	10.6
Great Plains province	0.166	11.9	2.4	36.0
Eastern Gulf region	0.479			
Escambia–Choctawhatchee province	–	3.3	2.8	4.1
Apalachicolan province	–	3.7	2.7	4.9
Peninsular Florida province	–	10.1	4.0	31.0
Atlantic region	0.260			
Southern Atlantic province	0.103	3.8	2.4	5.8
Northern Atlantic province	0.140	5.5	3.9	6.9
Pacific region	ns	13.7	2.8	36.0

Note: Slope is for the linear regression of mussel richness on fish richness; ns denotes that the relationship was not significant. Provinces without entries for slope had too few streams to conduct a regression. Min and max are the minimum and maximum numbers of fish per mussel species in each area. See Figure 8.9 for data sources.

scales within the Ohio River system (ranging from 2.1 to 2.6; Watters 1992). In the Great Plains, St. Lawrence–Great Lakes, and Peninsular Florida provinces and the Atlantic region, the slope of the fish to mussel relationship is lower, or the number of fish species per mussel species is higher and more variable (Table 8.2). The Pacific region has the highest number of fish species per mussel species, and there was no relationship between fish and mussel richness. This suggests that the host resource in these areas is less saturated than in the Mississippian and Eastern Gulf regions and that mussel diversity is limited less by fish diversity than by dispersal barriers (e.g., Atlantic and Pacific regions), historical disturbance (e.g., glaciation in the Northern Atlantic and Great Lakes provinces or sea level rise in Peninsular Florida), or current habitat conditions that limit mussel species to a greater extent than fishes (e.g., Great Plains province).

The degree to which the host resource is saturated and competition for hosts limits populations is fundamental to understanding how mussel assemblages are structured.

Table 8.3. *Host partitioning by specialists in a freshwater mussel assemblage in the Sipsey River, Alabama*

Mussel species	Gar	Skipjack	Minnows						Suckers	Catfishes			Sunfishes	Black Basses	Darters								Walleye	Drum
Lampsilis teres	X																							
Elliptio crassidens		X																						
Reginaia ebena		X																						
F. cerina			X	X	X	X	X	X																
Pleurobema decisum					X																			
Quadrula asperata										X														
Q. rumphiana										X	X	X												
Q. verrucosa												X												
Villosa lienosa													X											
Lampsilis ornata														X										
L. straminea														X										
Villosa vibex														X										
Elliptio arca															X	X								
Medionidus acutissimus															X	X	X	X	X	X	X	X		
Obovaria unicolor																X	X	X						
Ligumia recta																							X	
Leptodea fragilis																								X
Potamilus purpuratus																								X
Truncilla donaciformis																								X

Note: Within host categories (e.g., minnows), columns represent different fish species. Most fish species not used as hosts by specialists are not shown (host use assessed from sources in Cummings and Watters 2010). Host use of *Quadrula rumphiana* was inferred from hosts of closely related species. *Obliquaria reflexa* is a common member of this assemblage (approximately 2%–7% of total; Haag and Warren 2010), but host use is unknown.

Niche theory predicts that species that use the same resource in the same way cannot coexist because one species will eventually outcompete the others, but partitioning of a resource allows coexistence of multiple species (Schoener 1989). Modeling of mussel–host dynamics showed that species with similar host use could compete strongly for hosts, often to the exclusion of one species (Rashleigh and DeAngelis 2007). Whether host competition occurs in the wild is unknown and is difficult to study. However, peak glochidial infestation rates of host fishes are often 50–100 percent, and combined with acquired resistance of these fishes to further infections, this suggests that host competition could limit both mussel diversity and abundance (Strayer 2008). The great diversification and specialization of host use and elaborate host attraction strategies are hard to fathom without host competition as a strong selective force in their evolution.

As predicted by theory, there is striking partitioning of the host resource by mussel assemblages (Table 8.3), suggesting that strong selective pressure has reduced host competition. In addition to the pattern shown for the Sipsey River, similar patterns exist in other streams where host use is known fairly completely for the entire mussel

Table 8.4. *Overlap in host use among host specialists in four streams in the Mississippian Region*

Stream	Number of mussel species	Number of fish species	Number of fishes used as hosts by specialists	Observed overlap (expected)	Observed variance in overlap (Expected)
Sipsey River, Alabama	25	72	30 (42%)	0.092 (0.031)*	0.073 (0.013)
Tributaries of Black Warrior River, Alabama	15	41	19 (46%)	0.156 (0.073)**	0.115 (0.021)**
North Fork Holston River, Virginia	15	66	28 (42%)	0.089 (0.040)*	0.081 (0.015)*
Puskus Creek, Mississippi	10	25	10 (40%)	0.320 (0.033)**	0.269 (0.012)*

Note: Overlap was calculated using Pianka's method with 1,000 randomly generated host use matrices with number of hosts and species constrained (Gotelli and Entsminger 2004). Probability of observed > expected $^{*}p < 0.01$, $^{**}p < 0.001$. Data sources are as follows. Sipsey River: mussels, Haag and Warren (2010); fishes, Boschung and Mayden (2004). Black Warrior River system: mussels, Haag and Warren (2008); fishes, Boschung and Mayden (2004). North Fork Holston River: mussels, Neves and Widlak (1988); fishes, Jenkins and Burkhead (1994). Puskus Creek: mussels and fishes, M. L. Warren and W. R. Haag (unpublished data). Host use assessed from sources in Cummings and Watters (2010).

assemblage (Table 8.4). In all these streams, about half of available fish species are used as hosts by specialists, and the degree of overlap in host use is relatively low (Table 8.4). Despite this apparently tidy partitioning of the host resource, the degree of overlap is greater than expected by chance in all of these streams (Table 8.4), showing that partitioning of the host resource is imperfect; including generalists would further increase overlap in host use. The high variance in overlap indicates that there is internal structure in these patterns representing host-use guilds with high overlap within but low overlap among guilds (Gotelli and Entsminger 2004). These results have at least two interpretations. The higher than expected overlap in host use could mean that competition is not important within host guilds, and there is no selective pressure to partition the resource more finely. Alternatively, even though over half of fish species are not used by specialists and represent vacant niches, immunological or other constraints may prevent further diversification in host use. In this scenario, competition within host guilds could be an important factor in structuring assemblages.

These examples are based on imperfectly known host relationships, and differences in host use in the wild or transformation success among mussels on apparently shared hosts could lessen competition. Nevertheless, overlap must exist to some extent, and there are several ways species with similar host use could coexist. First, host use is likely identical for few species. In the Sipsey River, species that share minnows or darters differ in host breadth (Table 8.3). The gulf pigtoe, *Fusconaia* *cerina*, and southern clubshell, *Pleurobema decisum*, both use *Cyprinella venusta* as a primary host, but *F. cerina* also uses several other minnow species (Haag and Warren 2003), which could allow coexistence of these two species even if *P. decisum* is a superior host competitor (see Rashleigh and DeAngelis 2007). Even species that have identical host use may partition their shared resource. Black basses (*Micropterus*) are primary hosts for most *Lampsilis* (Keller and Ruessler 1997; Haag and Warren 2003). In the Sipsey River, the southern pocketbook, *L. ornata*, occurs in main-channel shoals, but the southern fatmucket, *L. straminea*, occurs almost exclusively in lentic microhabitats (Section 4.2.B); because they rarely co-occur, these species may be exposed to different subsets of the bass population. Differences in host attraction strategies also may reduce host competition. *Villosa nebulosa* and *V. vibex* also both use bass and often co-occur in similar habitats, but *V. nebulosa* displays lures only at night, and *V. vibex* displays primarily in the day, potentially targeting distinct ecological subsets of a shared host resource (Haag and Warren 2000). Finally, models showing competitive exclusion between species assume a constant environment such that these interactions proceed to equilibrium; disturbance or other factors that cause temporal variation in mussel and host abundance could promote coexistence of species with shared hosts (Rashleigh and DeAngelis 2007). Watters (1997) suggested that differences in timing of glochidial release (i.e., short-term vs. long-term brooding) could reduce competition for shared hosts; however, all species with shared host use in the previous examples release glochidia at about the same time (see Haag and Warren 2003).

The abundance of hosts is expected to limit mussel abundance either by rarity of hosts below some threshold or by rarity of susceptible fishes due to acquired resistance (Watters 1997; Strayer 2008). In experiments in hatchery ponds, recruitment of *Ligumia subrostrata* and *Pyganodon grandis* was positively related to host fish abundance, as expected (W. R. Haag and J. Stoeckel, unpublished data). However, recruitment appeared to reach an asymptote at host densities greater than 20 fish per mussel suggesting that host abundance limited population growth only below this level. Few data exist on the relationship between mussel and host abundance in the wild because such studies pose several difficulties. First, comprehensive host use data for entire fish assemblages are available for few streams. Second, representative estimates of fish abundance are difficult to obtain, especially in larger streams, and are often biased against some fish species, depending on the sampling methods used (e.g., catfishes, suckers, drum, and other large fishes are often missed by seining or backpack electrofishing). Third, human alterations to streams have disrupted mussel assemblages so widely that it is difficult to find an array of comparable study sites that have escaped these impacts. In European streams, adult density and strength of recent recruitment of *Margaritifera margaritifera* were not related to density of the host fish (brown trout, *Salmo trutta*), but these results were confounded by widespread trout stocking and the reduction of *M. margaritifera* in many streams by eutrophication or other impacts unrelated to host abundance (Geist et al. 2006). In tributaries of western Lake Erie, abundance of several mussel species was correlated positively with abundance of individual host species (Mulcrone 2004). However, that study did not attempt to relate mussel abundance to the summed abundance of all host species present at a site (in part because of incomplete host data), and these streams have also experienced a wide range of human impacts that potentially obscure relationships with host fishes.

Haag and Warren (1998) examined the relationship between mussel and host abundance in six unaltered tributaries of the Black Warrior River in Alabama using relatively comprehensive host information. I reanalyzed these data to include host information for additional species and to include the potential effect of stream size (Figure 8.10). Mussel abundance was positively correlated with host abundance for four specialists that infect hosts using conglutinates (Warrior pigtoe, *Pleurobema rubellum*, and triangular kidneyshell, *Ptychobranchus greenii*), mucus webs (Alabama spike, *Elliptio arca*), or mantle magazines (Alabama orb, *Quadrula asperata*, and pistolgrip, *Q. verrucosa*, combined). *Quadrula asperata* was present at one site where its host was not recorded, but capture success for catfishes was low. All these species tended to be increasingly common in larger streams, but correlations of abundance with stream size were not significant. However, these species are common constituents of mid-sized- and large-stream mussel assemblages in the Mobile Basin and are rare or absent in small streams (Williams et al. 2008; W. R. Haag, observation). In contrast, abundances of three specialists that infect hosts with mantle lures (orange-nacre mucket, *Hamiota perovalis*; Alabama moccasinshell, *Medionidus acutissimus*; and southern rainbow, *Villosa vibex*) and a host-generalist (southern creekmussel, *Strophitus subvexus*) were not correlated with host abundance, but the correlation for *M. acutissimus* was marginally significant and negative ($p < 0.064$). These species tended to be more common in smaller streams, and abundance was negatively correlated with stream size for two species.

These patterns suggest that host attraction strategies mediate relationships between mussel and host abundance and influence assemblage structure in different-sized streams. Host generalists or specialists that infect hosts with mantle lures appear able to persist at much lower host abundances than the other species, which appear to have a minimum host abundance threshold below which they are rare or absent. Fish abundance in small streams is often more variable temporally than in larger streams (e.g., Schlosser 1990). Because mantle lures are displayed for long periods even in the absence of fish, they may be effective in small streams or other situations where hosts are present at low or variable densities (Haag and Warren 1998, 2000). Use of a taxonomically broad range of fish species by generalists also may release these species to some extent from a density-dependent relationship with hosts. In contrast, the probability of host infection for specialists that release glochidia in conglutinates or mucus webs during a short time may be more strongly dependent on high abundance of hosts, limiting them to larger streams with more predictable fish assemblages.

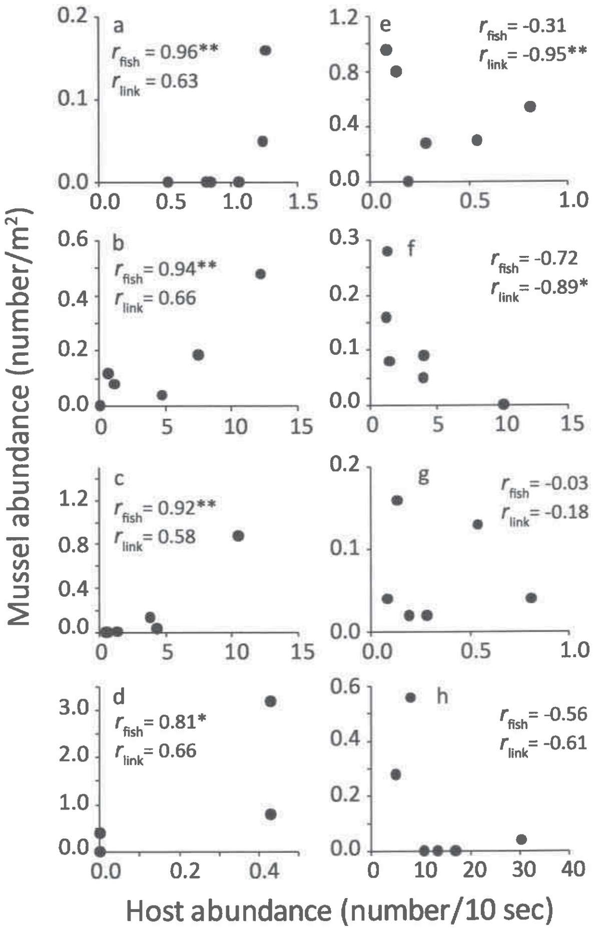

Figure 8.10. Pearson correlations between mussel abundance, host fish abundance, and stream size in tributaries of the Black Warrior River, Bankhead National Forest, Alabama. (a) *Elliptio arca*, (b) *Pleurobema rubellum*, (c) *Ptychobranchus greeni*, (d) *Quadrula asperata and Q. verrucosa*, (e) *Hamiota perovalis*, (f) *Medionidus acutissimus*, (g) *Villosa vibex*, (h) *Strophitus subvexus*; $^{*}p < 0.05$, $^{**}p < 0.01$; data points for stream size (link magnitude) not shown. Host abundance is the summed abundance of all known host species for each mussel species and is based on timed electrofishing samples (reanalysis of data from Haag and Warren 1998; host relationships based on Haag and Warren 1997, 2003).

Large-scale patterns in the broad-scale data set reveal similar differences in assemblage composition in different-sized streams based on host use (Figure 8.11). Small streams are dominated by specialist mussel species that use as hosts black basses or darters and sculpins and by generalists in the tribe Anodontini; individually, each of these host use guilds can make up nearly 100 percent of assemblages in some streams. Other host guilds are either absent in small streams or rarely compose more than 10 percent of assemblages. Mid-sized streams include all host guilds, but assemblages are

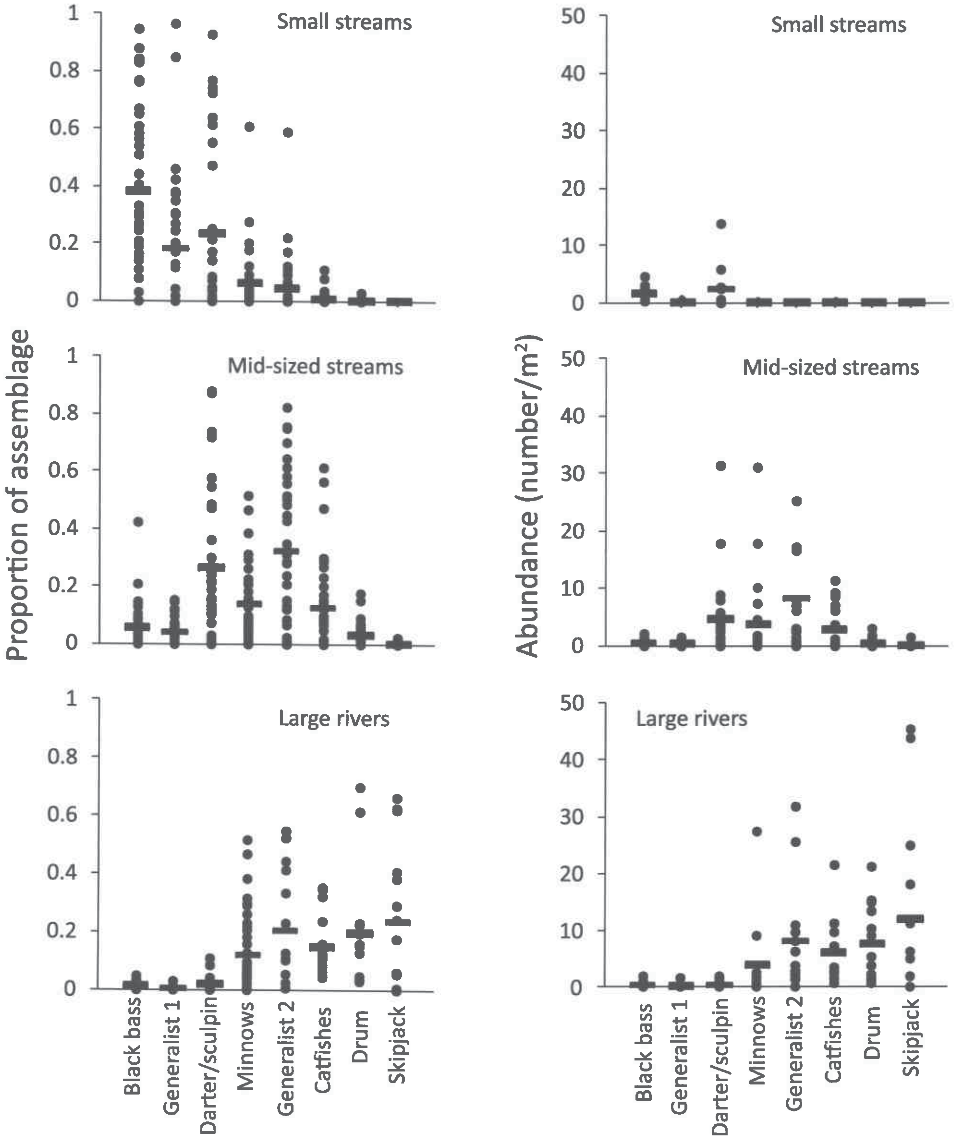

Figure 8.11. Composition of mussel assemblages in the Mississippian region related to host use. Points are summed proportions and abundances for all species within each host guild at each site. Horizontal bars are average values. Host category "black bass" also includes rock bass (*Ambloplites*) and sauger and walleye (*Sander*). Host category "generalist 1" includes generalists in the tribe Anodontini; "generalist 2" includes *Actinonaias* spp., *Amblema plicata*, and *Megalonaias nervosa*. Abundance plot for mid-sized streams does not show one high value beyond the scale (*Amblema plicata*, 70.9/m^2, Big Sunflower River, Mississippi). Sample sizes: proportion, 82 sites (34 small, 34 mid-sized, 15 large river); abundance, 45 sites (10 small, 22 mid-sized, 13 large river).

dominated by species that use darters and sculpins, minnows, and catfishes and by the host generalists *Actinonaias* and *Amblema plicata*. Large-river assemblages are similar to mid-sized streams, with the exception that species that use darters and sculpins are rare, and there is increased dominance by species that use drum and skipjack herring.

Patterns based on species abundance are similar, with one important exception (Figure 8.11). Although specialists on bass, darters and sculpins, and anodontine generalists dominate small-stream assemblages proportionally, these species rarely achieve high abundance in these habitats. Mean abundance for all three of these guilds is less than $2.4/m^2$, and their abundance rarely exceeds $5/m^2$ in small streams. Furthermore, bass specialists and anodontine generalists rarely – if ever – achieve high numerical abundance in *any* stream type. Specialists on sunfishes (*Lepomis*) also are uniformly rare; this host guild is not depicted in Figure 8.11, but their maximum abundance in my data set was $1.3/m^2$. In contrast, all other host guilds frequently reach abundances an order of magnitude higher.

Because there is high concordance between host use and host infection strategies, patterns of assemblage composition based on infection strategies are similar to those for host use. For example, all species in my data set that are specialists on black bass infect hosts using large mantle lures, most minnow specialists release pelagic conglutinates, and all catfish specialists use mantle magazines (Chapter 5). Differences in host attraction strategies among species that specialize on darters and sculpins are not reflected in Figure 8.11. Darter and sculpin specialists infect hosts either with cryptic mantle lures, demersal conglutinates, or possibly mucus webs (see Table 5.1). Similar to the patterns shown in Figure 8.10, species that use mantle lures can be dominants and achieve high abundance (up to $13/m^2$) in both small and large streams. In contrast, darter specialists that use conglutinates or mucus webs achieve high abundance in mid-sized streams but not in small streams, where abundance averaged only $0.1/m^2$ and did not exceed $0.7/m^2$.

These broad-scale patterns build on the idea that availability and abundance of suitable hosts play an important role in structuring mussel assemblages. Small and mid-sized streams in much of North America are dominated numerically by minnows, darters, and sculpins (Matthews 1998), allowing mussel species that use these fishes as hosts, as well as host generalists, to proportionally dominate assemblages in these habitats. However, in small streams, low or temporally variable fish abundance, combined with variable physical conditions, may limit absolute mussel abundance regardless of host strategy. In mid-sized streams, more stable fish assemblages and physical habitat allow these species to reach high abundances. In large rivers, increased abundance of fishes, such as drum and catfishes (e.g., Dettmers et al. 2001; Margraf and Knight 2002), allows specialists on these fishes to dominate mussel assemblages and reach high abundances. The rarity of darter specialists in large rivers may in part be an artifact of widespread impoundment, which has eliminated riffle habitats inhabited by these fishes (Chapter 10; Section 8.4). Mussel species that are specialists on numerically rare fish species appear to be limited throughout by host availability. Top predators, such as black basses, are conspicuous members of fish faunas in a wide range of aquatic habitats but represent only a small percentage of individuals compared to numerically dominant fishes, such as minnows, darters, and drum (Matthews 1998). Mantle lures may allow specialists on black basses to persist in small streams or other habitats where other species are limited by low host abundance, but these species never achieve high abundance in any habitat. Similarly, *Lampsilis teres* and *Ligumia recta*, specialists on gar and on sauger and walleye, respectively, are typical components of mid-sized- and large-stream faunas but are never abundant; in my data set, maximum abundance was 0.2/m^2, but most values were much lower.

8.3.C. Evaluating evidence for host competition

At this time, no direct evidence addresses whether host competition further limits mussel abundance, but patterns of co-occurrence between species with overlapping host use can allow examination of the potential for this type of interaction. I examined correlations between abundance of species with shared host use among high-density, main-channel mussel beds in the Ouachita and Saline rivers (Section 8.1). Associations between species pairs in these rivers were of five types: (1) weak negative association, (2) negative association with symmetrical boundary, (3) strongly negative association with an asymmetrical boundary, (4) weak positive association, and (5) positive association with a modal boundary (Figure 8.12). Negative association with a symmetrical boundary shows that two species can coexist when each is at low to moderate abundance, but an upper abundance threshold exists such that when one species becomes more abundant, the other is successively rarer. Negative association with an asymmetrical boundary indicates a stronger relationship in which each species reaches high abundance only when abundance of the other species is low. Positive association with a modal boundary shows that maximum abundance of one species occurs when abundance of the other species is intermediate.

Overall, abundance of only 11 percent of species pairs showed a negative relationship of any kind, and most of these were weak correlations ($r < 0.5$) with no evidence of a boundary threshold (Table 8.5). Six species pairs showed evidence of stronger negative relationships with asymmetrical or symmetrical boundaries, and all involved the generalists *Actinonaias ligamentina*, *Amblema plicata*, and *Megalonaias nervosa*. Only two pairs of specialists had negative correlations, and both were weak ($r = 0.26$–0.28). Surprisingly, abundances of many specialists that share fish hosts were positively correlated. In both rivers, abundances of most catfish specialists (*Quadrula pustulosa, Q. quadrula*, and *Q. verrucosa*) and minnow specialists (*Fusconaia flava, Pleurobema rubrum*, and *Q. metanevra*) were positively correlated within guilds, including several pairs with $r > 0.5$. Abundances of drum specialists (*Ellipsaria lineolata, Leptodea fragilis, Potamilus purpuratus, Truncilla*

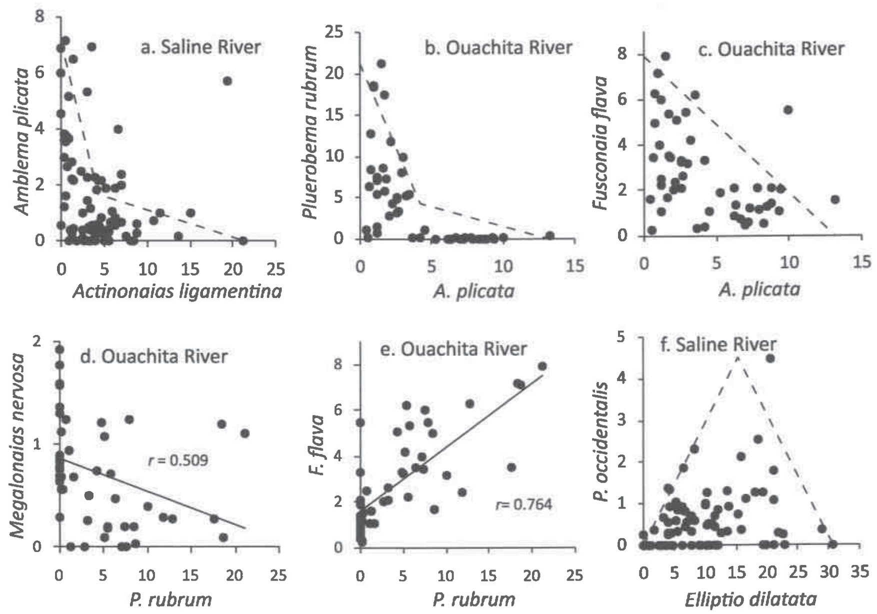

Figure 8.12. Five patterns of co-occurrence between mussel species with overlapping host use among mussel beds in the Ouachita and Saline rivers, Arkansas. (a,b) Strongly negative association with asymmetrical boundary. (c) Negative association with symmetrical boundary. (d) Weak negative association. (e) Weak positive association. (f) Positive association with modal boundary. Both axes are species abundance (number/m^2). Correlation coefficients are based on log-transformed abundance (data from Posey 1997; Davidson and Clem 2004).

donaciformis, and *T. truncata*) showed few significant relationships of any kind. In both rivers combined, the numbers of positive, negative, and nonsignificant correlations for species with shared host use did not differ from the results of comparisons between species with nonshared hosts ($G = 2.61$, 2 df, $p > 0.10$).

These results provide little evidence for host competition among mussel species with overlapping host use. The positive relationships between abundance of many specialists suggest that these species respond similarly to local habitat factors or perhaps to abundance of host fishes, but interspecific host competition is not strong. The boundary relationships involving *A. ligamentina*, *A. plicata*, and *M. nervosa* suggest that high abundance of these species may limit abundance of other generalists and some specialists. In both rivers, *A. ligamentina* was more abundant in upstream beds but was gradually supplanted by *A. plicata* downstream, reflecting a longitudinal shift in species dominance (Section 8.1). Habitat factors therefore may explain the limited co-occurrence between these species. However, abundance of the washboard, *M. nervosa*, did not show a strong longitudinal pattern in the Ouachita River. Furthermore, host competition could provide a partial mechanism for longitudinal shifts in dominance among different habitats. If species A has narrower habitat requirements

Table 8.5. *Relationships between abundance (number/m^2) of species with shared host use among main channel mussel beds in the Ouachita and Saline rivers, Arkansas*

Species pairs	Shape of relationship (sign)	*p* (Obs > Exp)
	Ouachita River	
Generalists vs. generalists		
Amblema plicata vs. *Actinonaias ligamentina*	asymmetrical boundary (–)	0.000
Megalonaias nervosa vs. *A. ligamentina*	asymmetrical boundary (–)	0.010
Generalists vs. specialists		
A. plicata vs. *Fusconaia flava*	symmetrical boundary (–)	0.019
A. plicata vs. *Pleurobema rubrum*	asymmetrical boundary (–)	0.002
M. nervosa vs. *P. rubrum*	asymmetrical boundary (–)	0.029
	Saline River	
Generalists vs. generalists		
A. plicata vs. *A. ligamentina*	asymmetrical boundary (–)	0.039
Generalists vs. specialists		
A. ligamentina vs. *Elliptio dilatata*	modal boundary (+)	0.016
Specialists vs. specialists		
E. dilatata vs. *Ptychobranchus occidentalis*	modal boundary (+)	0.003

	Number of correlations (Proportion within host class)		
	Not significant	Positive	Negative
	Both Rivers		
Generalists vs. generalists	2 (0.33)	1 (0.17)	3 (0.50)
Generalists vs. specialists	44 (0.54)	22 (0.27)	15 (0.19)
Specialists vs. specialists			
Species with shared host resource	22 (0.58)	14 (0.37)	2 (0.05)
Species with nonshared host resource	92 (0.69)	32 (0.24)	9 (0.07)

Note: *p* (obs > exp) is the probability that the observed number of points within the specified shape is greater than expected from 1,000 randomizations with data-defined constraints (Gotelli and Entsminger 2004). See Figure 8.12 for description of shapes. All pairwise correlations were tested (log-abundance, significance at $p < 0.05$) for the most abundant species in each river (Ouachita, 15 species; Saline, 18 species). *Obliquaria reflexa* and *Plectomerus dombeyanus* were common in both rivers (0.2–1.1/m^2) but were excluded from this analysis because their host use is unknown. Shapes were tested only for species with significant correlations. Data from Posey (1997) and Davidson and Clem (2004).

than species B, the inability of species A to persist or function optimally in unsuitable habitats may release species B from host limitation in those habitats. The modal boundary between *Elliptio dilatata*, *A. ligamentina*, and *Ptychobranchus occidentalis* could be caused by a combination of habitat requirements and competition for hosts or other resources. If these species have similar habitat requirements unrelated to host use, they all may be excluded from unsuitable habitats, but in suitable habitats, high abundance of *E. dilatata* may limit abundance of the other species.

All of the species in this example use numerically abundant hosts (e.g., minnows, darters, drum, catfishes), which may lessen the potential for host competition in streams with large, stable fish populations. As in the broad-scale data set, species that use top predators such as black basses, gar, and sauger/walleye (*Lampsilis*, *Ligumia recta*) were uniformly rare, with an average collective abundance across mussel beds in both streams of less than 0.5/m^2. If these species are limited by low host abundance, competition should be intense among species with similar host use. In main-channel mussel beds of the Ouachita and Saline rivers, the plain pocketbook, *Lampsilis cardium*, composed 84–95 percent of bass specialists. As in the Sipsey River (see previous discussion), other co-occurring bass specialists (*L. powelli*, *L. siliquoidea*) may avoid host competition with *L. cardium* by their occurrence primarily in lentic microhabitats or stream margins (Harris and Gordon 1988). In contrast, *Lampsilis abrupta* is restricted to main-channel habitats, and its general rarity may be due to host competition with *L. cardium*.

Unlike bass specialists, whose rarity in all habitats can be explained by host limitation, the general rarity of anodontine generalists is puzzling because broad host use should reduce the potential for host competition with other species or conspecifics. Similarly, the rarity of species that use sunfishes, which are abundant in many aquatic habitats, is unexplained. Many anodontine generalists are restricted to lentic habitats, and their rarity could be explained by the rarity of this habitat type in many streams. However, even in impounded streams and lakes, abundance of these species is typically low, even though they may proportionally dominate these assemblages (Ahlstedt and McDonough 1993; Haag and Warren 2007). As discussed in Section 8.2, the important question here is, *why* are anodontine generalists restricted to lentic habitats? One possibility is that anodontine generalists are poorer competitors for hosts in stream habitats with higher mussel diversity and overall abundance, perhaps because their broadcasting infection strategy is less efficient than other strategies.

The relative efficiency of host attraction strategies is unknown, but it is reasonable to expect that highly developed mantle lures or conglutinates are more efficient than haphazard release of glochidia, either freely or in mucus webs. In experiments in hatchery ponds, recruitment of the pond mussel, *Ligumia subrostrata*, a specialist that uses mantle lures, was nearly equal to or slightly lower than recruitment of the giant floater, *Pyganodon grandis*, a generalist that uses mucus webs, in ponds where the two species co-occurred. However, this does not necessarily show that mucus webs are equivalent to or more efficient than mantle lures because *P. grandis* releases glochidia in late winter, earlier than *L. subrostrata* (J. Stoeckel and W. R. Haag, unpublished data). Early glochidial release is reported in other populations of *P. grandis* (Watters and O'Dee 2000) and in other anodontine generalists (Roberts and Barnhart 1999) and may in part be an adaptation to reduce competition with other species that have potentially more effective infection strategies. The relative effectiveness of infection strategies and the degree of overlap in host use between generalists and specialists in the wild also is important for understanding the reasons for the negative relationship between abundance of *Actinonaias*, *Amblema*, and *Megalonaias* and several specialists (Table 8.5). The high abundance of these species in many streams indicates that their host infection strategy must be reasonably efficient and, despite their classification as generalists, the true breadth of host use for *Actinonaias*, *Amblema*, and *Megalonaias* remains poorly known. My analyses of patterns of co-occurrence in the Ouachita and Saline rivers provide little evidence of host competition, but this discussion illustrates the types of potential interactions that need to be examined in greater detail. The potential for host competition may be greater in smaller streams with lower or more variable host abundance. Even in large streams, evidence of host competition may be obscured in simple comparisons of abundance of species with shared host use. In addition to differences in efficiency of host attraction strategies, outcomes of potential host competition between species may be determined to a great extent by historical or stochastic factors. A species that has recently colonized an area may be unable to achieve high abundance because of competition for hosts with previously established species (see Rashleigh and DeAngelis 2007). Similarly, if mussel abundance in a stream is reduced by drought or other stochastic factors, a species that repopulates the area rapidly may hold an advantage over other species with similar host use for some time to come. Similar to competition for food (Section 8.5), the outcomes of host competition may not be determined solely by which species is most efficient in infecting hosts but by which species can produce the greatest excess of recruits relative to juvenile mortality. For example, in two species that compete for hosts, a species with higher juvenile survival could prevail even though its infection rate is lower than that of a competing species with higher mortality. This is an example of how host strategies could interact directly with other life history traits.

8.4. The role of life history strategies

I used the broad-scale data set (Section 8.1) combined with information presented in Chapter 6 to investigate patterns of mussel assemblage structure related to life history strategies and specific life history traits. Species that achieve high abundance are mostly limited to those with long life spans and late maturity. Abundance is positively correlated with life span, but this relationship is best described by an evolutionary boundary representing an increasing upper limit to abundance with increasing life span (Figure 8.13). Nearly all species that reach abundances of more than $5/m^2$ have maximum life spans greater than 30 years. This pattern also is seen in other species not represented in this data set. The eastern pearlshell, *Margaritifera margaritifera*, frequently reaches ages of more than 100 years and occurs at abundances of at least $30–80/m^2$ (Hastie et al. 2000a, 2000b; Geist et al. 2006). Maximum age of the

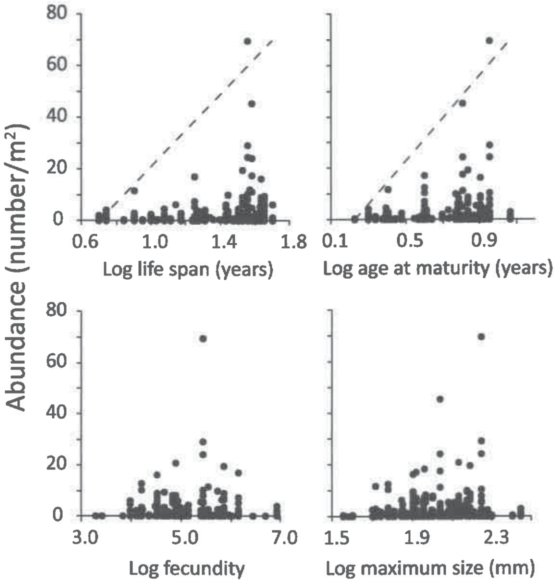

Figure 8.13. Relationships of mussel species abundance to life history variables. Evolutionary boundaries indicated are supported by Monte Carlo simulations showing that the probability of the observed number of points within the boundary is greater than expected from 1,000 randomly generated data sets (Gotelli and Entsminger 2004); life span, p observed > expected = 0.003; age at maturity, p observed > expected = 0.001. Correlations are not significant, and evolutionary boundaries are not supported for fecundity or maximum size.

spectaclecase, *Cumberlandia monodonta*, exceeds 50 years, and it can occur in locally dense aggregations of more than $120/m^2$ (Stansbery 1966; Baird 2000). Few species with maximum life spans less than 20 years reach abundances greater than $5/m^2$, and most occur at far lower abundance. The only exceptions in my data set were *Truncilla*, which have short life spans but can be abundant in large rivers. Similarly, the short-lived oyster mussel, *Epioblasma capsaeformis*, can reach high abundance in some streams (Jones and Neves 2011). Abundance is related similarly to age at maturity (Figure 8.13). The slope of this boundary is steeper than for life span such that species that mature at age 3 frequently reach intermediate abundances and maximum abundance increases rapidly with increasing age at maturity. Similar to life span, *Truncilla* were the only species with early maturity (less than 3 years) that reached high abundance.

Abundance showed no relationship to fecundity or body size (Figure 8.13). Neither variable was positively correlated with abundance or showed evidence of an evolutionary boundary. A modal relationship is suggested for fecundity but was not supported by Monte Carlo simulations, and this apparent pattern is due to only a few large values. Similarly, the pattern for body size suggests a boundary relationship of increasing abundance for larger species, but this is due primarily to two high

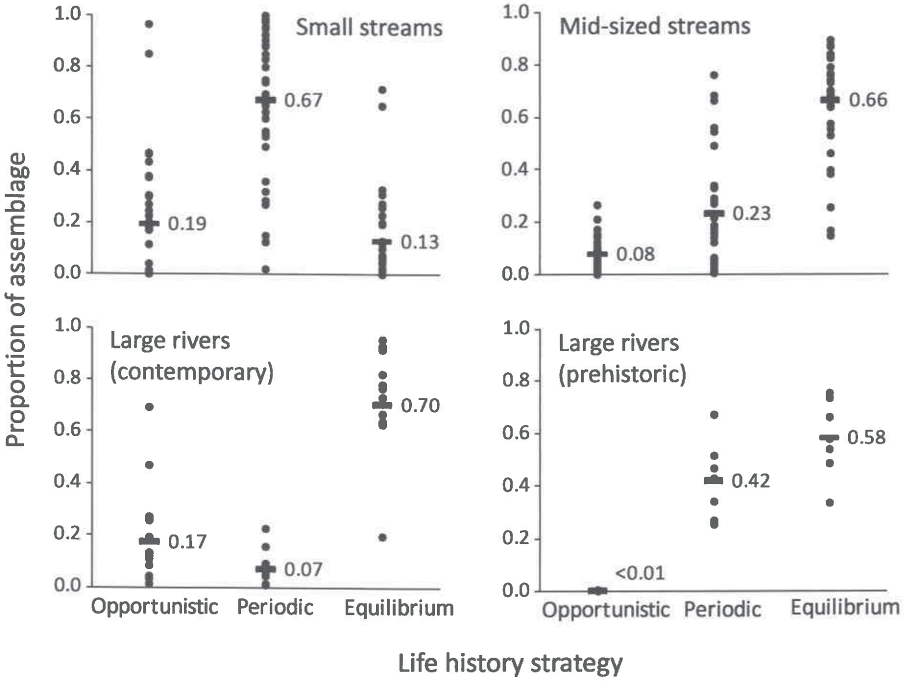

Figure 8.14. Composition of mussel assemblages in the Mississippian region relative to life history strategies. Horizontal bars are mean values. All panels are based on contemporary assemblages, except for large rivers (prehistoric) (for prehistoric data sources, see Haag 2009b).

abundance values for large-bodied species (*Amblema plicata* and *Reginaia ebena*), and species across a wide range of sizes frequently reach abundances of more than $10/\text{m}^2$. Average abundance of short-term brooders ($2.2/\text{m}^2 \pm 0.34$ SE) is significantly higher than for long-term brooders (0.9 ± 0.11; ANOVA, $F = 35.5$, $p < 0.0001$, log abundance), which could be interpreted to mean that high investment in brooding reduces the ability to achieve high abundance. However, brooding period has a strong phylogenetic basis (Chapter 1) and is highly correlated with life span (Chapter 6), suggesting that, similar to fecundity, it is of little direct significance in determining abundance. Furthermore, there are several notable exceptions of long-lived, long-term brooders that can reach high abundance in an array of stream types (especially *Actinonaias* and *Ptychobranchus*).

I classified species in the broad-scale data set into the life history strategies according to Table 6.3. The occurrence of these strategies across habitat types differs greatly. Small streams are dominated by periodic strategists and, to a lesser extent, by opportunists, but equilibrium strategists rarely make up more than 25 percent of these assemblages (Figure 8.14). Mid-sized streams are transitional in composition, including an increasing proportion of equilibrium strategists and a decreasing presence of periodic and opportunistic species. Contemporary large rivers are overwhelmingly

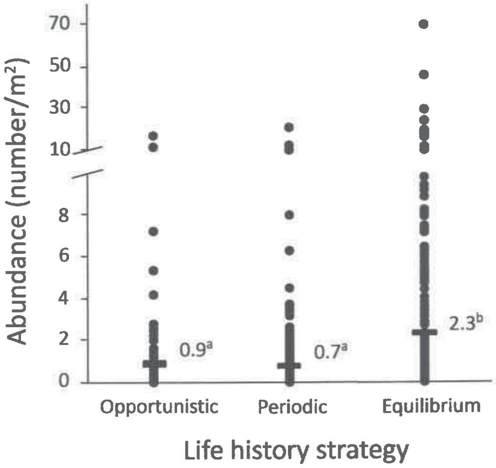

Figure 8.15. Mussel species abundance relative to life history strategies. Horizontal bars are mean values. Abundance differs significantly among strategies (ANOVA, $F = 16.6$, 2 df, $p < 0.0001$, log-transformed abundance). Means with different superscripted letters are significantly different ($p < 0.01$); note break in y axis scale.

dominated by equilibrium strategists, and periodic and opportunistic species are minor components of these assemblages. The only exceptions were the opportunists, *Truncilla*, which composed up to 65 percent of some large-river assemblages. In contrast, all other opportunists combined never made up more than 3 percent of any large-river assemblage. Lentic habitats were not represented in this data set, but these assemblages (excluding those in riverine lakes) are dominated by a characteristic group of mostly opportunistic species (e.g., *Anodonta, Ligumia subrostrata, Pyganodon, Toxolasma parva, Utterbackia*), and equilibrium strategists are rare or absent in these habitats (Section 4.1.D.2).

Across stream sizes, equilibrium strategists reach higher abundance than the other strategies (Figure 8.15). Periodic and opportunistic strategists are uniformly rare, with few exceptions. The only opportunistic species that reach abundances more than 5/m^2 are *Truncilla*, and abundances of most other species are typically much less than 1/m^2. The periodic strategists *Elliptio dilatata* and *E. arca* can reach high abundance, but these species lie in a position in life history space intermediate between the periodic and equilibrium strategies (see Figure 6.12). The only other periodic strategist in my data set to reach high abundance was the Cumberland moccasinshell, *Medionidus conradicus* (10–13/m^2), and another periodic species, *Epioblasma capsaeformis*, can achieve local abundances as high as 40/m^2 (Jones and Neves 2011).

It is likely that the representation of life history strategies and host guilds in mussel assemblages has changed in response to human alteration of streams, particularly in impounded large rivers. Many types of chronic and acute impacts to streams affect mussel species similarly, regardless of life history strategy or host use (Sections 10.5.B and 10.5.C). However, loss of shallow, shoal habitat by impoundment results in a predictable decline in periodic strategists and specialists on darters and minnows, even in rivers that remain riverine in character and continue to support diverse assemblages (Section 10.5.A). In prehistoric shell middens at seven large-river sites in the Cumberland, Green, and Tennessee river systems, periodic strategists composed a much higher percentage of assemblages than in contemporary large rivers, and these assemblages were more similar to those in contemporary mid-sized rivers (Figure 8.14). Equilibrium species dominated most sites, and dominant periodic species (composing more than 10% of the assemblage) were restricted to relatively long-lived species, all of which were probably darter specialists (*Elliptio dilatata*, *Epioblasma torulosa*, and *Obovaria retusa*). Opportunistic strategists were extremely rare at all sites. Prehistoric humans apparently harvested mussels primarily from easily accessible shoal habitats, and preservation of thin-shelled species – characteristic of most opportunistic species – is often poor (Haag 2009b). Consequently, equilibrium species characteristic of more stable, deeper habitats and opportunistic species found in lentic backwaters are probably underrepresented in these samples. Nevertheless, these data suggest that large rivers provided habitats more similar to mid-sized streams at least locally, but even so, large-river mussel assemblages were fundamentally different from those in small streams.

Although life history traits and host use explain patterns of assemblage structure at broad scales, these relationships cannot provide finer predictions of species abundance or assemblage composition. For example, the form of the relationships between life span, age at maturity, and abundance suggests that these traits set an evolutionary boundary on abundance, but within these constraints, abundance is influenced by other factors. Furthermore, life history or host strategies alone do not explain why only some equilibrium species dominate assemblages and why patterns of dominance within strategies shift predictably in different streams.

8.5. The role of competition for food and space

Competition for food or space is an important factor that structures ecological communities. Until recently, many researchers doubted that food limitation could occur in mussel assemblages (e.g., Coker et al. 1921; Haag and Warren 1998). Indeed, at low density, mussels likely have little impact on suspended or deposited food concentration. Similarly, phytoplankton production in lakes can exceed grazing rates of mussels, even when mussels occur at relatively high density (Cahoon and Owen 1996; McMahon and Bogan 2001, citing Kasprzak 1986), and positive feedback between bivalve grazing and phytoplankton may reduce further the potential for bivalves to limit phytoplankton (Strayer 1999b). However, density-dependent limitation involving both food and space is documented widely in marine bivalve assemblages (Mackie 1984; Dame 1996). There has been little research on competition for space among mussels, but a growing body of literature shows that competition for food may be important in structuring mussel assemblages in some situations.

Bivalves can remove a large percentage of the seston or phytoplankton in streams in part because phytoplankton production is typically low (Cohen et al. 1984; Lauritsen 1986; Caraco et al. 1997, 2006). These strong effects are reported primarily for invasive bivalves (*Corbicula* and *Dreissena*) that reach extremely high abundance. For example, the population of *Dreissena* in the Hudson River during initial colonization filtered essentially the entire water column in one day, and mussel assimilation exceeded phytoplankton production (Strayer et al. 1996b). Similar effects may have been widespread in rivers before historical declines in native mussel abundance (Caraco et al. 2006) and are suggested in contemporary studies with unionids. Food limitation appears especially likely in streams under low-flow conditions in summer, when mussel filtering rates and hydrologic residence times are high. Even at moderate densities ($7/m^2$), mussels may filter a substantial percentage of the water in a stream reach, and the percentage can be nearly 100 percent at densities of $50/m^2$ (Vaughn et al. 2004). The freshwater mussel assemblage in the Hudson River (prior to zebra mussels) occurring at a density of only $8/m^2$ was estimated to filter daily a volume of water roughly equal to the daily summer discharge of the river (Strayer et al. 1994). In the Mississippi River, mussel assemblages occurring at a maximum density of only $4.5/m^2$ were estimated to filter up to 12 percent of river discharge at low flow (Newton et al. 2011). Within high-density mussel beds, food limitation could be even more severe because of local zones of resource depletion. If this is the case, we should see a gradual decrease in abundance or body condition in the downstream sections of mussel beds.

These observations suggest that food limitation may occur at least seasonally, especially in high-density, large-river mussel assemblages and may limit overall mussel abundance. Food competition with invasive zebra mussels (*Dreissena*) is thought to strongly limit populations of native mussels (Strayer and Smith 1996; Baker and Levinton 2003). Model predictions for native mussel population size under food limitation (Morales et al. 2006b) show oscillations over time similar to those seen in natural populations (Haag and Warren, in preparation; see Chapter 7). Furthermore, models that did not incorporate food competition provided realistic depictions of population growth only at low mussel density (less than $1/m^2$). In addition to limiting overall mussel abundance, food competition may be important in structuring assemblages.

A number of studies have provided evidence that competition for food among and within mussel species can result in declines in growth and body condition (reviewed in Vaughn et al. 2008). Most convincingly, in a manipulative experiment in a river conducted at high mussel density ($32/m^2$), body condition of other species decreased in the presence of the mucket, *Actinonaias ligamentina*, and condition of *Actinonaias* decreased with increasing density of that species (Vaughn et al. 2007). This result was explained potentially by depletion of food resources by *Actinonaias*, which has higher total filtration rates than the other species, or by physical interference from burrowing and movement. Feeding interactions can also have positive facilitative effects within mussel assemblages. Mussel species had higher biomass and body condition in more species-rich assemblages, and increased abundance of species such as *Actinonaias* was associated with higher body condition of subordinate species (Spooner and Vaughn 2009; 2012). However, condition of subordinate species declined at sites with greater dominance of *Actinonaias* (Spooner and Vaughn 2009). These results suggest that dominant species such as *Actinonaias* and *Amblema* are keystone members of mussel assemblages that have a range of important positive and negative effects on other species.

Feeding interactions appear to vary across environmental conditions according to physiological differences among species. Resource acquisition and assimilation of *Actinonaias* peaked at about 25°C, but at higher temperatures, filtering rate decreased, and energetic stores were depleted through anaerobic metabolism (Spooner and Vaughn 2008). In contrast, *Amblema* was thermally tolerant; its filtration rate was highest at 35°, and it continued to assimilate energy. Similarly, in the St. Croix River, Minnesota, where temperatures never exceeded 25°C, *Actinonaias* had higher weight-specific metabolic and filtering rates than *Amblema* (Baker and Hornbach 2001). Differences in thermal optima also were seen among *Lampsilis cardium, Quadrula pustulosa*, and *Truncilla truncata* (thermally sensitive) and *Fusconaia flava, Megalonaias nervosa*, and *Obliquaria reflexa* (thermally tolerant). Differences among species in feeding and metabolic efficiency under different conditions may play a major role in assemblage structure. For example, species may partition available habitat along even slight thermal gradients, corresponding to differences in physiological optima (Spooner and Vaughn 2009). However, the outcome of competitive interactions for food among species is not determined simply by which species can acquire resources most rapidly or efficiently; rather, the superior competitor may be the species with the lowest equilibrium resource requirements such that metabolism and reproduction can be sustained at a given temperature and food concentration without catabolism of stored energy reserves (Tilman 1982; Grace 1991; Strayer 1999b). Because food limitation can limit mussel growth and gamete production (Jokela and Mutikainen 1995a; Bauer 1998; Kesler et al. 2007; Galbraith and Vaughn 2009), even slight competitive reduction of food supply below equilibrium thresholds may limit the ability of a species to persist or dominate in a habitat. The inability of invasive *Corbicula* to reach high abundance in dense native mussel assemblages has been explained potentially by its high metabolic demands, which make it a poorer competitor for food, despite having filtration rates higher than native mussels (Vaughn and Spooner 2006b).

Life history theory predicts that in stable habitats, dominant species should be superior competitors that exclude or limit other species (Pianka 1970; Grime 2001). In late successional plant communities, ruderal and stress-tolerant species are limited to a subordinate role by resource competition from dominant competitor species

(Grace 1991). Similar competitive interactions could explain the dominance of equilibrium strategists in large river mussel assemblages. Although data on food requirements of mussels are lacking, it is reasonable to expect that long-lived, slow-growing equilibrium species have lower resource requirements and may dominate over fast-growing opportunists and periodic species when food is limiting. *Actinonaias* and *Amblema* had lower mass-specific filtering rates but lower oxygen consumption than subordinate species (Spooner and Vaughn 2008) suggesting that they have lower equilibrium resource requirements. The low metabolic rate and energy requirements of *Margaritifera margaritifera* were invoked to explain the dominance of this species in nutrient-poor streams where *Unio crassus* and *Anodonta piscinalis* – species with higher metabolic rates – were rare (Bauer et al. 1991). The metabolic rate of mussels is thought to be closely and positively related to the growth constant *K* (Bauer 1992). Given the great variation in *K* among species (Haag and Rypel 2011), we should expect similarly wide variation in metabolic rate and energy requirements. Two rapidly growing species, *Pyganodon grandis* (opportunistic strategy) and *Lampsilis siliquoidea* (periodic strategy), have little capacity for metabolic acclimation at high temperatures (McMahon and Bogan 2001), suggesting that they may be particularly sensitive to reduction in food availability under these conditions. Furthermore, *P. grandis* regulates oxygen consumption at low concentration by increasing its heart rate (and presumably metabolic demands), but riverine species regulated oxygen less efficiently (Chen et al. 2001). These metabolic differences among species may represent trade-offs allowing some species to colonize stressful habitats but limiting their occurrence in habitats where food competition occurs.

In large rivers with diverse mussel faunas, many opportunistic and periodic species are restricted to lentic microhabitats (Section 4.2.B). Because equilibrium species are typically absent in these marginal habitats – perhaps because of frequent disturbance – they may be refuges in which species with high energy requirements escape competition for food in high-density, main-channel mussel beds. There are at least two alternatives to this hypothesis. First, species with high growth rates may be limited in main-channel mussel beds not by competition but by low overall food concentration, and organic sediments in lentic microhabitats may be a richer food source necessary to sustain fast growth. Second, the thin shells of many fast-growing species may be poorly adapted for anchoring or burrowing in coarse, densely packed sediments of mussel beds or may reduce their ability to compete for space with heavy-shelled species. A few opportunistic or periodic species more commonly reach high abundance in dense mussel beds, especially *Epioblasma, Medionidus*, and *Truncilla* (Section 8.4). Because they are small species, they may have lower total energy demands (despite potentially high metabolic rates) and are less limited by space. In addition, spatial and temporal heterogeneity in physical conditions in rivers may provide localized niches in which these species reach physiological and competitive optima (Spooner and Vaughn 2009).

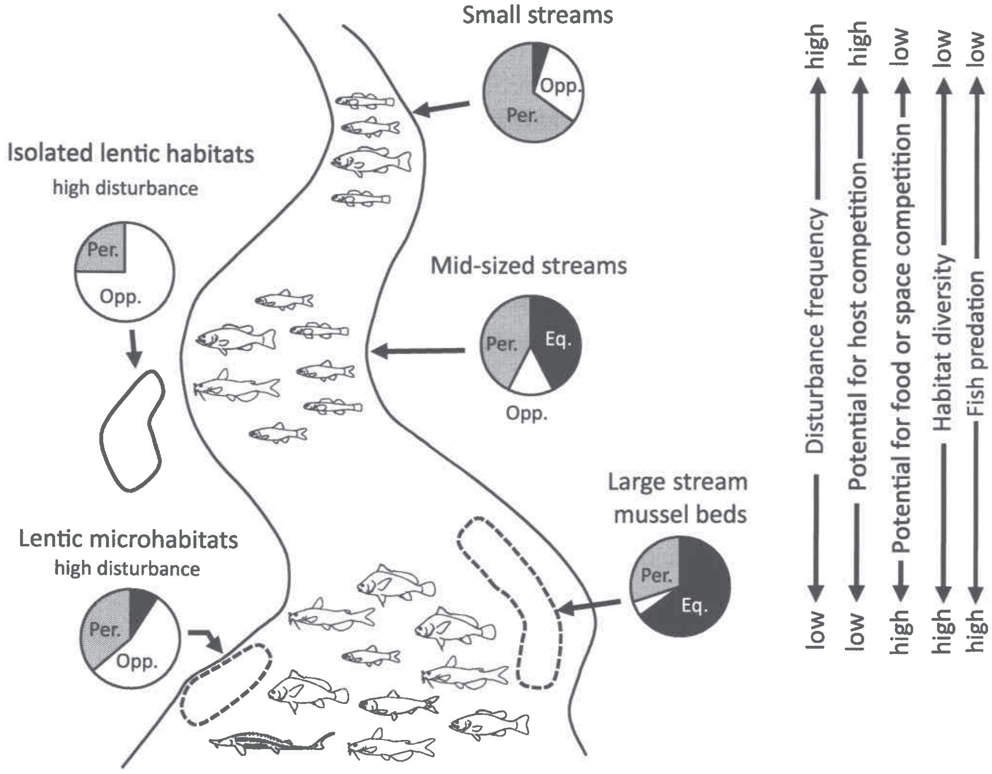

Figure 8.16. Schematic of the host-habitat continuum showing physical and biotic factors proposed to structure mussel assemblages in different habitats. Assemblages change from those dominated by periodic (Per.) and opportunistic (Opp.) life history strategists in small streams to assemblages dominated by equilibrium (Eq.) strategists in large-stream mussel beds. Gradients depicted at the right of the figure apply to main channel habitats and assemblages. Marginal habitats with high disturbance frequency are depicted at the left. Fish symbols depict a gradient in host fish assemblages from low-diversity, sparse assemblages dominated by minnows and darters in small streams to diverse, high-abundance assemblages dominated by large-river fishes (e.g., catfishes, freshwater drum, skipjack herring, sturgeon) in large streams but with low abundance of black bass and other top predators throughout (fish symbols from Burr and Warren 1986).

how these divergent strategies interact with other factors to determine the composition of assemblages in different habitats (Figure 8.16).

8.6.A. Opportunistic strategy

The opportunistic strategy is characterized by fast growth, early maturity, short life span (and thus, fast turnover times), and high reproductive output, all of which allow rapid population growth (Winemiller and Rose 1992; Chapter 7). Early and high investment in growth and reproduction is selected for in situations of high extrinsic mortality (Chichon 1997), and these traits allow opportunists to rapidly colonize and dominate highly disturbed or stressful habitats such as isolated lentic systems, anthropogenically degraded habitats (e.g., unstable channelized streams), and, to a lesser extent, small streams (Figure 8.16). Other adaptations of these species to stressful or unstable habitats include tolerance of low oxygen concentration (Section 4.1.C); production of multiple broods in a season (*Utterbackia*); hermaphroditism (*Toxolasma, Utterbackia*); thin, inflated, or winged shells that increase buoyancy in soft or unstable substrates (Section 1.3.C); and generalist host use. In addition, specialists in this strategy use fishes that also are tolerant of disturbed habitats (e.g., gar, sunfishes), and many have mantle lures that allow them to infect hosts even when host abundance is low or variable.

Although opportunists may dominate proportionally in some habitats, their total abundance is limited by high mortality, including extrinsic mortality from predation and frequent adverse conditions (Chapter 7) and intrinsic mortality as a physiological consequence of high growth rates and early reproduction (Bauer 2001; Haag and Rypel 2011). Predation is expected to be especially intense in large rivers with an abundance of molluscivorous fishes. High growth rates and other adaptations to stressful habitats may come as a trade-off of higher energy requirements, which makes them poor competitors for food, limiting their abundance in dense mussel beds or restricting them to marginal, lentic microhabitats in streams (Figure 8.16). Because of their typically thin shells, opportunists, especially large species, also may be poor competitors for space. For generalists, broadcasting of glochidia may be a relatively inefficient strategy that further limits abundance. *Truncilla* are the only opportunists that can be prominent and abundant components of large-river assemblages. This exception may be a result of the difficulty of classifying some species cleanly into life history strategies. *Truncilla* lie in a position in life history space near the periodic strategy (Figure 6.12), suggesting that these species may become locally abundant for the same reasons as other small-bodied periodic species (see subsequent section). However, similar to other opportunists, *Truncilla* can persist in highly altered streams where other periodic and most equilibrium species have been extirpated (Chapter 10).

8.6.B. Periodic strategy

The periodic strategy lies intermediate between the opportunistic and equilibrium strategies. Periodic species dominate primarily in small streams, which may lie in an intermediate position along a gradient of disturbance frequency and intensity (from high frequency in lentic habitats to low frequency in large streams). This strategy also favors rapid but periodic population growth. In addition to relatively early maturity, periodic strategists have highly variable annual recruitment, which may be synchronous among periodic species, suggesting that they maximize population growth during periods of favorable conditions (Chapter 7). Similarly, large variation in annual recruitment appears to be the rule among periodic fishes (Winemiller and Rose 1992). Many periodic mussels have low fecundity, but in many species, this is offset by highly efficient mantle lures. Other species are host generalists, a trait that may similarly reduce dependency on high host numbers. At least one periodic species (*Lasmigona subviridis*) has direct development of glochidia, which obviates entirely dependence on host fishes (Chapter 5). Body size tends to be small, but the adaptive significance of this trait is unclear. In stream fishes and other invertebrates, intermittent flow and frequent floods both select for small body size (Poff and Ward 1989). For mussels, large species may be especially prone to displacement during floods and may have difficulty penetrating coarse, small-stream substrates after dislodgement (Section 1.3.C). Small size also may allow some species to compete for food (because of lower total energy requirements) or space in dense mussel beds composed primarily of large, heavy-shelled species.

Similar to opportunists, abundance of periodic species may be limited by high mortality and short life span. Some species also are limited by the general rarity of their host fishes (e.g., *Lampsilis* and black basses) or by limited or variable host abundance in some habitats. Because of their relatively high growth rates, periodic species may compete poorly for food with equilibrium species. Consequently, they are typically subordinate species in large-river mussel beds or are limited to lentic microhabitats. Some periodic species occasionally achieve high abundance and dominance in mid-sized or large streams perhaps because temporal and spatial variation in physical conditions creates localized niches where they reach physiological and competitive optima (Spooner and Vaughn 2009). However, in these situations abundance and recruitment may be highly variable over short time periods (Chapter 7) because of the periodic nature of favorable conditions. For *Epioblasma* and *Medionidus*, high abundance may be further facilitated by their small size and use of abundant hosts (darters). Other species, such as *Elliptio*, may be intermediate between the periodic and equilibrium strategies and dominate only where equilibrium species are limited by hosts, biogeography (*E. complanata*), or other factors. Some periodic species, particularly darter specialists, were apparently more abundant in large rivers prior to impoundment because extensive shallow riffles provided habitats similar to smaller streams where host abundance was high and equilibrium species were limited by disturbance.

8.6.C. Equilibrium strategy

The equilibrium strategy is characterized by slow growth, late maturity, long life, and generally low investment in reproduction. Annual recruitment of these species is often low but relatively constant among years (Chapter 7). These traits are favored in stable habitats (e.g., Pianka 1970). Slower growth rates and greater metabolic efficiency likely make equilibrium species superior competitors for food relative to other strategies, and allow them to dominate in large rivers and mid-sized streams. Because of their long life spans and low adult mortality, these species frequently accumulate at high abundance in stable habitats.

Unlike opportunists and periodic species, which can occur in any habitat type, life history traits limit the occurrence of equilibrium strategists in frequently disturbed or stressful habitats such as small streams, isolated lentic systems, and channelized streams. Abundance may be limited further in small streams by rarity or absence of host fishes and by host attraction strategies that depend on predictably high host abundance. Even in stable habitats, abundance may be limited by competition with other equilibrium species that have lower equilibrium resource requirements and therefore dominate assemblages (e.g., *Actinonaias*, *Amblema*). Patterns of dominance among and within rivers can vary widely according to variation in physical conditions that favor species with different physiological optima (Vaughn et al. 2007; Spooner and Vaughn 2008). Whether host competition occurs between equilibrium species is unknown. At present, there is little evidence for competition between specialists that use similar hosts, but competition between generalists (e.g., *Actinonaias* and *Amblema*) could play a role in shifting patterns of dominance (Section 8.3); however, evidence of competition could be obscured by historical factors and, in general, host competition has received little study.

Margaritifera margaritifera and perhaps other margaritiferids are interesting exceptions in this framework. On the basis of its very long life span and late maturity, *M. margaritifera* appears to represent one of the most extreme examples of an equilibrium strategist (Chapter 6), yet it reaches maximum dominance and abundance in small streams. This species occurs primarily in nutrient-poor, high-gradient streams but is limited to boulder-strewn reaches, which provide shelter from scouring flows (Vannote and Minshall 1982; Hastie et al. 2001). These specialized habitats may be unusually stable for small streams; major floods sufficient to cause high mortality of mussels are rare in some *Margaritifera* streams, but their frequency may have increased because of human modification of watersheds (Hastie et al. 2001). In addition, the life history of *M. margaritifera* has evolved to cope with entirely different challenges (primarily low productivity of its habitat) than other equilibrium species. This species may therefore represent a unique outlier among mussel life history strategies, which corresponds more closely to the stress-tolerator strategy for plants (Grime 2001). Like *Margaritifera*, stress-tolerant plants grow under extreme conditions (e.g., lichens, bristlecone pine) and are long-lived and late maturing, and devote little energy to reproduction annually. Although *Margaritifera* has very high fecundity, the energetic cost of the brood is low because of its small glochidia (Bauer 1998). Other margaritiferids also occur in nutrient-poor streams (*M. falcata*, *M. hembeli*, *M. marrianae*) or other highly specialized habitats (*Cumberlandia monodonta*), often in the absence of other mussel species, suggesting that their unique life history allows them to exploit otherwise vacant niches.

Naturally, this framework must be viewed with several caveats. Host use and life history data for most species remain incomplete at this time. The degree of overlap in host use among mussel species in the wild, especially between generalists, is a fundamental question that must be answered to evaluate the extent to which host competition may occur. Data on age at maturity are estimated for most species in my analyses (Chapter 6), and direct observations for a large number of species are needed. Furthermore, the life history data I compiled to analyze patterns of assemblage structure are based on average values or values from single populations, which in many cases do not correspond to the streams for which assemblage data were available. Species life history traits can vary substantially among populations, especially growth rate, life span, and probably age at maturity (Kesler et al. 2007; Haag and Rypel 2011). For example, *Amblema plicata* may be considered either an equilibrium or periodic strategist based on differences in life span among populations (Chapter 6). Phenotypic plasticity in life history traits and feeding ecology is expected to be manifested predictably in assemblage composition. Finally, even though I restricted the data sets used in this chapter to relatively unaltered streams to the extent possible, mussel assemblage structure has doubtlessly been changed by human impacts, particularly in impounded streams. Nevertheless, ecological processes continue to shape these assemblages, and in Chapter 10, I show how this framework also can be used to explain the effects of different types of human impacts on mussel assemblages.

Despite the potential challenges that mussels face in lentic systems (Section 8.2), it is unclear whether these represent unstable or stressful habitats and, consequently, why these habitats are dominated by opportunistic species. Fine sediments characteristic of lentic habitats have been viewed traditionally as unsuitable habitats for mussels, but diverse and dense assemblages often are found in these substrates in riverine habitats (Chapter 4). Across a range of stream sizes, fish assemblages in hydrologically variable streams had a high proportion of species in common with lentic habitats (Poff and Allan 1995). Although life history characteristics of these species were not specified, this suggests that lentic fishes also are adapted to variable or unstable conditions. Nevertheless, the effect of disturbance and other potential limiting factors on mussel populations in lentic systems needs study. Similarly, specific limiting factors in small streams need to be evaluated more extensively.

Research on competition in mussels has only just begun. The role of competition for space is largely uninvestigated, and the nature and extent of food limitation remains unclear. Other alternatives to competition need to be evaluated. The possibility that some species may avoid competition for food by specialization on a particular food resource is an important topic about which little is known. Some species may be limited in certain habitats not by competition with other species but by low availability of the food resource on which they specialize. Filtering of gametes in dense mussel beds has also been proposed as a limiting factor. Finally, there probably are large random and historical components to the structure of assemblages that must be accounted for. For example, random fluctuations in dispersal and colonization may interact with or even supersede other factors that structure assemblages. Similarly, to some extent, present-day patterns of assemblage composition may be artifacts of previous competition or other selection pressures in different assemblages or habitats.

Even when these caveats are considered, the patterns described in this chapter give compelling evidence for the important and predictable role of life history and host strategies in structuring mussel assemblages. The life history classification I presented in Chapter 6 was developed independent of information about assemblage structure, but the strong differences in life history composition among assemblages in different habitats are remarkable. The framework I propose provides specific hypotheses that can be tested with more detailed and population-specific life history information as well as with additional findings about food and space competition. Furthermore, as we will see in subsequent chapters, mechanisms that structure mussel assemblages may help us explain patterns of imperilment and develop more effective conservation strategies for these animals.

Chapter 9

Human exploitation of mussels

People have been drawn to shells for a very long time. Like their marine counterparts, freshwater mussels produce pearls that have been admired by humans for thousands of years. Gossip in Rome in the first century B.C. speculated that Julius Caesar invaded England in part to search for pearls in the freshwater pearlshell, *Margaritifera margaritifera* ("Brittanium petisse spe margaritarum"), and he returned with a ceremonial cuirass (a piece of armor protecting the torso) made of British pearls, which he dedicated to the temple of Venus Genetrix (Flory 1988:498). Christopher Columbus purportedly presented Queen Isabella with a necklace of freshwater pearls on returning from his first voyage to North America (Vertrees 1913), and when Hernando De Soto failed to find gold in the southeastern United States during his expedition in the 1500s, he turned his attention to stealing freshwater pearls from native people, who also held pearls in high esteem. There's no other substance quite like mother-of-pearl, and shells are a perfect natural history curio: they're beautiful, portable, and don't need to be processed or kept in noxious preservatives. My children love to hunt for mussel or snail shells at the river (they've had a little coaching on this), and so did I, well before mussels paid my bills. People also love to eat shellfish, again in part because they're an ideal quarry: they're not dangerous, and you don't have to stalk them, shoot them, or skin them; they just sit there waiting to be eaten.

Humans have come up with a multitude of uses for mussels. In addition to eating prodigious quantities of mussels, prehistoric people used the shells as ornaments, tools, and utensils and collected great quantities of pearls. In historic and recent times, humans continue to seek freshwater pearls and used shells extensively to make buttons and shell novelties. Although to a lesser extent than marine species, freshwater shells have been sought by collectors for many years, especially during the 1800s (Chapter 2). Mussels also have been used for more plebian purposes. Mussel meat has been used for fishing bait, fertilizer, hog and poultry feed, and in pet food (Kunz 1898; Coker 1919; Tudorancea 1972; Howells et al. 1996). Shells or crushed shells have been used as road fill; to produce lime; as a constituent in polishes, soaps, and cleansing powders; in the manufacture of tile and artificial marble; and as poultry grit or other livestock feed supplements (Rafinesque 1820; Kunz 1898; Coker 1919).

One of the most unique and creative uses of mussels I've seen occurs in a few counties in south central Kentucky, where shells have been used to adorn graves in rural cemeteries since at least the 1920s (Crawford 1994; Plate 21). The largest cemetery following this tradition is at the Hill Grove Missionary Baptist Church in Edmonson County, Kentucky, which I visited in 2009. Mussels were gathered from the nearby Nolin River and other local streams and were sometimes collected from piles left behind by pearlers (Heege 1998; Section 9.3). The shells are boiled in lye to remove the periostracum and arranged on the mounded earth of the grave; it is believed that shells placed during a waning moon remain on the graves better than those placed during a new moon (Heege 1998). Each grave requires about 200–300 individual shell valves. Hill Grove has over 100 graves adorned with shells, representing approximately 25,000 valves of at least 26 freshwater mussel species as well as a few marine shells. A large percentage of shells on most graves were the mucket, *Actinonaias ligamentina*, which dominates mussel assemblages in this region. However, some people evidently had a specific aesthetic preference as several graves were decorated primarily with large specimens of washboard, *Megalonaias nervosa*. This tradition continues to the present day but is declining due to the difficulty of obtaining shells subsequent to the impoundment of the Nolin River and because of legal restrictions on collecting mussel shells in other streams. Nevertheless, many existing graves are maintained fastidiously. At Hill Grove, the shells are cleaned and rearranged annually in preparation for the church's summer homecoming, and this huge chore also has played a large role in the decline of the tradition.

The tradition of shell-decorated graves is developed to an exceptionally high degree and has been especially durable at Hill Grove church, but this practice is widespread in various forms. Graves decorated with freshwater mussel shells have been documented throughout the southeastern and central United States, including other parts of Kentucky, Alabama, Arkansas, Illinois, Missouri, and Texas, and encompass European, African, Hispanic, and Native American heritages (Long 1981; Heege 1998; Eans 2007). In addition, use of freshwater and marine shells in grave decoration and as motifs on funerary monuments occurs throughout Africa and was common in classical Greek and Roman times, extending as far as Britain (Heege 1998), illustrating the reverence people worldwide have had for shells.

9.1. "Can you eat 'em?"

I suspect that nearly everyone who studies freshwater mussels has fielded this question from curious onlookers along a riverbank or while discussing their profession at a cocktail party. The answer is not straightforward. Prehistoric people around the world used mussels extensively as a food source (Section 9.2), and this traditional practice continues to a limited extent in the U.S. Pacific Northwest, where mussel harvest is a reserved treaty right for some tribes (Brim Box et al. 2006). Otherwise, consumption of mussels by humans is rare today. When one orders "mussels" in a restaurant, without exception, these are marine mussels (e.g., *Mytilus edulis*, *Perna canaliculus*) and not freshwater mussels. A contemporary issue is that, as filter feeders, freshwater mussels can accumulate many of the undesirable compounds that now wind up in rivers and lakes. Another possible reason for the rarity of freshwater mussels on menus today is that they contain unusually high levels of putrescine, an intermediate compound in amino acid metabolism that is responsible for the foul odor of decaying flesh (J. Hurley-Sanders, personal communication). Putrescine occurs naturally in both living and dead tissues and is toxic in large doses, but it is present in lower amounts in marine mollusks like oysters (Gould and Cottrell 1974). Whatever the reason, in Western culture, there is a strong, long-standing stigma associated with eating freshwater mussels:

> I'll manacle thy neck and feet together:
> Sea-water shalt thou drink; thy food shall be
> The fresh-brook muscles . . .
>
> *(William Shakespeare,* The Tempest, *Act I, ca. 1610–1611)*

The magician Prospero issued this threat to Ferdinand, who was attempting to court his daughter and whose father robbed Prospero of his birthright as the Duke of Milan; in other words, he was very angry. The potency of Prospero's threat is illustrated in the diary of a Confederate soldier from the American Civil War who, along with three other hungry companions, collected a sackful of mussels from the Duck River, in Tennessee, with the expectation of an imminent feast:

> We tried frying them, but the longer they fried the tougher they got. . . . Then we stewed them, and after a while we boiled them, and then we baked them, but every flank movement we would make on those mussels the more invulnerable they would get. We tried cutting them up with a hatchet, but they were so slick and tough the hatchet would not cut them. Well, we cooked them, and buttered them, and salted them, and peppered them. They looked good, and smelt good, and tasted good; at least the fixings we put on them did, and we ate the mussels. I went to sleep that night. I dreamed that my stomach was four grindstones, and that they turned in four directions, according to the four corners of the earth. I awoke to hear four men yell out, "O save, O save me from eating any more mussels!"
>
> *(Sam R. Watkins,* Co. Atych, *in Parmalee and Bogan 1998, 35)*

The early naturalist Constantine Rafinesque provides another less than glowing report of the edibility of mussels: "The animals contained in these shells are scarcely fit for food, the taste being extremely flat and insipid, and consequently but little used for that purpose. Some of the large species, however, have an enticing appearance, but the only mode by which they are rendered fit for the table, consists, in soaking them for a time in vinegar, they may then be fried or soused" (Rafinesque 1820, 12).

A modern treatise on self-sufficient living gives a recipe for mussels but warns, "Don't bother with mussels if you don't have a good set of teeth" (Freed 1978, 46).

Out of curiosity, my wife, a coworker, and I once ate some mussels, and we had about the same results as other reports, but fortunately without the gastric distress experienced by Sam Watkins. The smaller native mussels and Asian clams, *Corbicula fluminea*, were actually quite tender, but we were struck by their almost complete lack of flavor. The larger mussels were a different story: they were very tough and had an odd and disagreeable taste – maybe this was the putrescine. If you've ever cut open a mussel, you've noticed their peculiar, pungent smell. They tasted just like that smell, and the unpleasant memory of the flavor stayed with me for several days.

Not surprisingly, use of mussels as food in Western cultures is rare. Accounts of early settlers in North America – who were often on the brink of starvation – eating mussels are virtually absent (Parmalee and Bogan 1998), and the folk traditions of our self-sufficient ancestors, who utilized nearly every edible part of their environment, are conspicuous in their lack of information about preparing and eating mussels. The French botanist François Michaux traveled throughout the Ohio River valley in 1802 and noted the abundance of mussels in rivers but stated that they were not eaten by the settlers (Michaux 1805). The Lewis and Clark expedition of 1803–1806 subsisted largely on what could be foraged from the environment; the journals of the expedition report piles of mussel shells at campsites recently abandoned by Plains Indians along the Missouri River, but there is no mention of the expedition itself making use of this readily available food source (Moulton 2002).

In a very few instances, respondents of surveys of pearl or shell harvesters in the 1890s and again in the 1990s reported using mussels for food (Kunz 1898; Howells et al. 1996). Canadian lumberman reportedly harvested and ate mussels while rafting logs to market (Kunz 1898). In Romania, where mussel shells were used extensively for button production and as poultry and hog feed, "only here and there cases are known that mussel flesh is consumed by man" (Tudorancea 1972, 527). I've found only one explicitly favorable account of the edibility of mussels: "formerly the people about the lake [Cedar Lake, Indiana] were accustomed to cook and eat the *Anodontas* with much relish, but had gotten out of the habit in late years" (Wilson and Clark 1912, 27). When I'm in the field I frequently ask local residents whether they have ever eaten mussels and, in about 25 years, have received only one positive response, from a grizzled old-timer way out in the woods who assured me that he eats them "all the time."

Given the deserved disdain with which Western culture regards mussels as food, the extent to which other peoples around the world ate mussels is puzzling. Mussel shells in many prehistoric middens are noteworthy for their uniformly small size, and if larger shells are present, they are usually modified as implements (Section 9.2). Apparently these people avoided larger, tougher mussels, and they may have had other methods for rendering mussels palatable. Alternatively, mussels may have been important primarily as an emergency food during lean times. If so, the answer to the question, “Can you eat ’em?” may be, “Yes, but only if you have to.” Ironically, their dubious food quality may be one of the few things mussels have going for them from a conservation perspective. If they were choice eating, mussels would likely be in even more trouble today.

9.2. Prehistoric Americans

Prehistoric people did not share our modern aversion to eating mussels. In North America, humans harvested mussels as early as 10,000 years ago and left behind extensive deposits of discarded shells at village sites. These shell middens occur throughout North America alongside water bodies ranging from small creeks to large rivers to lakes (Klippel et al. 1978; Lyman 1980; Theler 1987). Shell middens are particularly numerous and extensive along the large rivers of the central and southeastern United States. Hundreds of middens are found along the 1,050 km length of the Tennessee River (Parmalee et al. 1982; Hughes and Parmalee 1999). In the middle portion of the river near Muscle Shoals, Alabama (Chapter 10), middens up to 6 m deep extend nearly continuously along the banks (Webb and DeJarnette 1942; Figure 9.1). At least 48 shell middens occur within a four-county area along the Green River in Kentucky; several middens each cover nearly 1 ha and were deposited over a period of about 560 years (Morey and Crothers 1998). The largest of these middens contain an estimated 45 million mussels (Haag 2009b).

The vast majority of shells in middens are unworked, suggesting that mussels were harvested primarily for food. In a midden near Muscle Shoals, only 6 in about 100,000 shell valves had been modified as ornaments or utensils (Morrison 1942). In the Columbia River basin in the Pacific Northwest, mussels were harvested extensively for food by Native Americans well into the twentieth century (Brim Box et al. 2006). In that area, mussels were harvested during much of the year, by hand when water conditions were favorable or with forked sticks through holes in the ice (Lyman 1984, citing Spinden 1908 and Post 1938). On the basis of the timing of formation of winter growth rests (Section 1.3.A), shells in prehistoric middens in the central United States were harvested primarily from about June to September, coinciding with low-water periods and seasonal occupation of riverbank villages (Claassen 1986). Mussel species characteristic of lentic microhabitats are consistently and conspicuously absent in aboriginal middens, suggesting that harvest focused on dense, main channel mussel beds where returns per unit time were greatest (Vannote and Minshall 1982; Haag 2009b).

Mussels were evidently prepared for consumption by steaming. Native people of Nootka Sound, British Columbia, steamed marine bivalves by layering green leaves or pine boughs over heated rocks, placing bivalves on the leaves, then pouring water over the pile and covering it with mats to retain the steam (Parmalee and

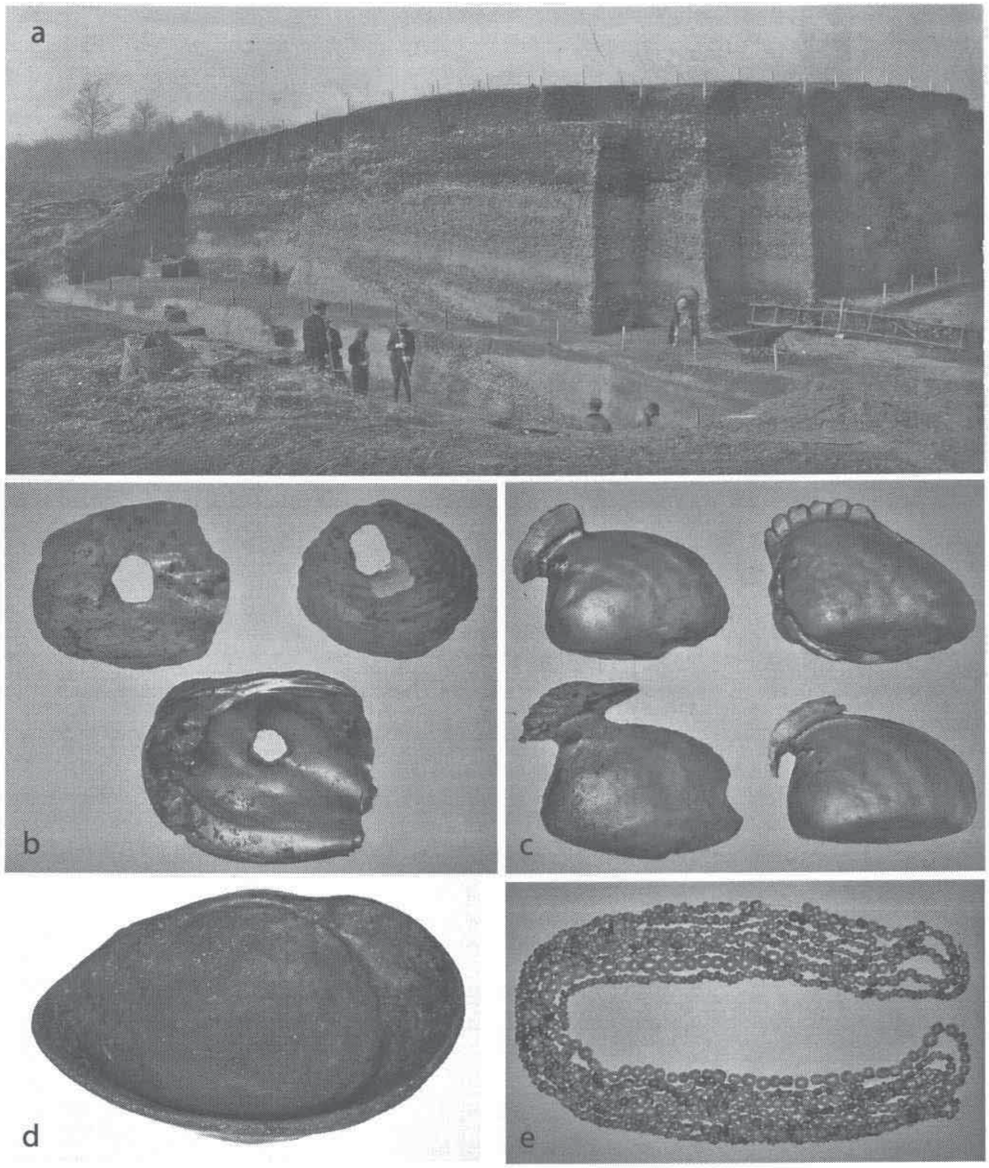

Figure 9.1. (a) Prehistoric Native American shell mound along the Tennessee River, Colbert County, Alabama. Light-colored layers in the center of the excavated cross section are mussel shells (courtesy Tennessee Valley Authority and University of Alabama Museums). (b) Drilled shells thought to have been hafted to a wooden handle and used as hoes. (c) Carved shell utensils thought to have been used as spoons. (d) Ceramic shell effigy bowl resembling *Lampsilis ovata*. (e) Necklace of 1,300 freshwater pearls recovered from a prehistoric burial along the Tennessee River (b–e from Parmalee and Bogan 1998).

Klippel 1974, citing Hough 1926). Similar hearths consisting of river cobbles that had been heated repeatedly, and in some cases containing uneaten mussels, have been found at prehistoric village sites in the central and southeastern United States (Baker 1941; Morrison 1942; Webb and DeJarnette 1942). In the Columbia River basin, Native Americans also prepared mussels by boiling, baking, broiling, and drying (Lyman 1984, citing Spinden 1908 and Post 1938).

The relative importance of mussels in the diet of prehistoric people is unknown. Despite their abundance, shell middens accumulated over long time periods and are preserved better than other plant and animal food sources, possibly exaggerating their apparent importance. Mussel meat contains about 40 percent of the caloric and protein content of fish, mammals, and birds but is higher in carbohydrates and fiber (Parmalee and Klippel 1974). Their low caloric content is offset by the ease with which mussels are procured. In habitats with moderate mussel abundance, at least 200 mussels/hr can be harvested by one person, representing about 1,200 calories, or about half the minimum daily requirement, assuming only small mussels (10 g tissue mass) are collected (Theler 1991). However, the difficulty of actually eating more than 200 mussels a day suggests that mussels were a supplemental food item. The pattern of accumulation of shells in some middens supports frequent but low-intensity utilization (Theler 1991). Ethnographic evidence from the Pacific Northwest indicates that mussels were of minor importance during much of the year but were relied on heavily in late winter, when stored foods were depleted (Lyman 1984, citing Post 1938). The prevalence of mussels in middens also varies over longer time periods, suggesting that they were relied on heavily during more extended periods of food shortage (Lyman 1980). Dependence on mussels may have changed according to subsistence patterns, with preagricultural hunter-gatherer societies relying on mussels to a lesser extent than later agricultural societies (Claassen 1986). Regardless, the vast quantities of shells in middens and their presence over great temporal and spatial scales show that mussels were an important component of a diversified and seasonally variable diet.

Prehistoric people used mussels in a variety of other ways. During the late Woodland and Mississippian periods (beginning about 1,500 years ago), ground mussel shells became the primary material used to temper clay for pottery production throughout much of eastern North America (Theler 1990; Weinstein and Dumas 2008). Although direct evidence is lacking, shells also may have been used as a source of alkali for removing hair from hides or for nixtamalization of corn (Van Dyke et al. 1980), the process by which the pericarp is removed and the nutritional value is improved. Shells were used widely for utilitarian purposes, including as spoons, dippers, scrapers, and hoes, and as material from which to fashion fishing lures (Parmalee and Bogan 1998; Cartwright 2003; Figure 9.1). Shell implements were sometimes embellished and included in grave offerings, but otherwise shells were rarely used for purely ceremonial or decorative purposes. In rare cases, ear pendants, gorgets, and other ornaments or ceremonial objects were made from freshwater mussel shells (Lyman 1984; Parmalee and Bogan 1998). Instead, most finely worked or modified shell objects were made from marine mollusks, especially whelks (*Busycon* spp.; Parmalee and Bogan 1998). In contrast, freshwater pearls were widely sought and coveted. Historical accounts of early European explorers and settlers across North America are replete with descriptions of pearls possessed by native people (Kunz 1898), and De Soto acquired a single 159 kg cache of pearls from a chief in South Carolina (Clayton et al. 1994). A necklace composed of about 1,300 pearls was found in a burial along the Tennessee River (Parmalee and Bogan 1998; Figure 9.1), and two bushels of freshwater pearls were found in a series of burial mounds in Ohio (Kunz 1898). Faithfully reproduced mussel shell effigy bowls were found in burials along the Cumberland River in Tennessee (Parmalee and Bogan 1998; Figure 9.1), attesting to the prominent role of mussels in these societies.

9.3. The first pearl rush

Despite the great importance attached to freshwater pearls by Native Americans and early European explorers, large-scale pearl harvest in historical times began relatively late but abruptly. In 1857, a 93-grain pearl found by a carpenter in Notch Brook, near Paterson, New Jersey, was purchased by Tiffany and Co. of New York and ultimately sold for $67,000 (2009 $US) to the Empress Eugenie of France (the wife of Napoleon III). At the same time, a much larger 400-grain pearl was found in a dish of fried mussels collected from another nearby stream, but its value was destroyed by cooking (Kunz and Stevenson 1908). These finds sparked the "first great pearl excitement," which led to almost complete elimination of mussels from Notch Brook and nearby streams (Kunz 1898). Pearls are not uncommon in mussels, but most are small and irregularly shaped (called baroques) and have little value (Figure 9.2). Because marketable pearls occur in only a small percentage of mussels (less than 0.01%; Shira 1913), pearl harvest was a wildly unsustainable endeavor characterized by boom and bust cycles resulting from rapid depletion of local populations (Anthony and Downing 2001). Consequently, pearl harvest moved rapidly west and south beginning in about 1860, as northeastern streams were depleted.

The lure of quick riches prompted widespread pearl prospecting across North America. New discoveries resulted in pearl rushes in nearly all U.S. states with sizeable mussel populations. During these pearl rushes, hordes of people descended on local streams. Extensive tent communities sprang up along the Black River, Arkansas, during a rush beginning in 1897, and over 500 people were seen pearling on one sandbar in a single day (Stockard 1904; Claassen 1994). In summer 1911, more than 400 pearl hunters were working on Caddo Lake in Louisiana and Texas (Shira 1913). Similarly, "great crowds" searched for pearls during a pearl rush on the Clinch River, Tennessee (Kunz 1898). During three months in 1889, pearls worth more than

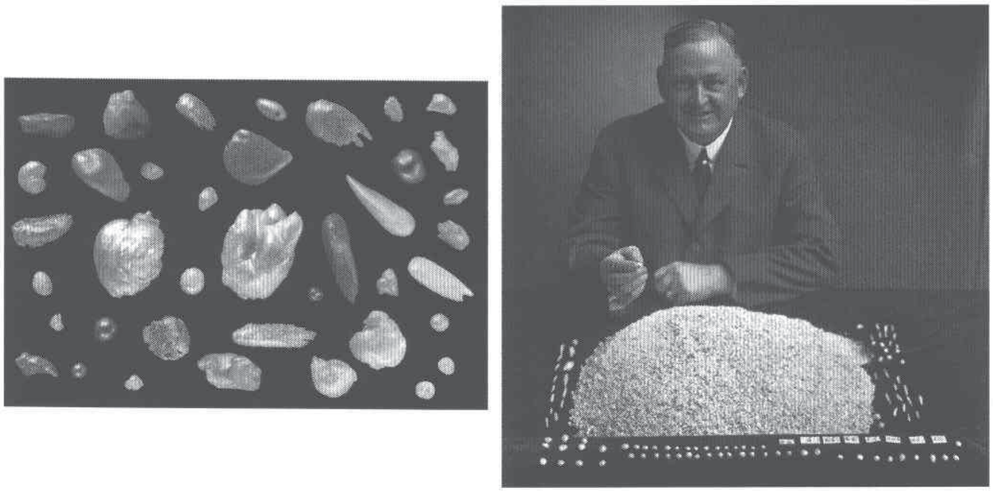

Figure 9.2. (left) Natural freshwater pearls (Richard T. Bryant, photo). (right) Pearl buyer with pearls harvested from the upper Mississippi River (courtesy Davenport Public Library, Davenport, Iowa).

$267,000 (2009 $US) were collected from streams in Wisconsin (Kunz 1898), and in nine weeks in 1911, pearl buyers purchased at least $2,420,000 worth of pearls from Caddo Lake (2009 $US; Shira 1913). Pearl buyers canvassed the pearling grounds and later resold the pearls to gem dealers in large cities (Figure 9.2). These transient speculators followed pearl rushes; at one time, there were 27 buyers registered at a hotel in Prairie du Chien, Wisconsin, on the upper Mississippi River (Madson 1985). Pearl rushes were encouraged by sensational newspaper accounts such as reference to the Black River area as the "Arkansas Klondike" (Kunz 1898). Speculation and excitement ran high during these times; in Arkansas, an entire lake was leased, fenced, and guarded for its pearl contents, and local farmers had difficulty finding field hands at harvest time (Kunz 1898).

At the time of the pearl rushes, mussels were abundant in many areas because streams were relatively unimpacted by human activities, and mussels had not been harvested in significant numbers since earlier exploitation by Native Americans. Consequently, mussels could be collected by hand with little or no specialized equipment, especially in small streams. Similar to gold and silver rushes, pearl fever lured people from many walks of life, including farmers, factory workers, laborers, tradesmen, riverboat roustabouts, Maryland oystermen, and even bankers, lawyers, and doctors (Kunz 1898; Stockard 1904). Many of these people remained in an area after a rush played out, resulting in significant demographic changes in some areas, and pearl rushes may have been a primary reason for the founding of some communities (Claassen 1994).

Pearl fever subsided in most areas by the early 1900s due to rapid depletion of mussel populations, generally low returns from pearling, and increased competition

AMERICAN PEARL FISHERIES GIVE OUT

Large Shipments of Clam Shells to Button Factories Ruin Chances of Big Finds—Arkansas Specimens Better Than Oriental.

PEARL-BEARING clams are disappearing from the sandbars of Arkansas and the Mississippi River at a rate that threatens to make the species extinct in less than two years. The beginning of the end has commenced, and unless new fields are discovered soon the pearl-fishing industry of the United States will be a thing of the past.

The reasons for this are manifold. Of late years the demands on the clam have been more than it could stand. In addition to its "prize package" manner of yielding up pearls, the shell of the bivalve itself is of a practical commercial value. During the past year twenty-five factories for the conversion of clam shells into pearl buttons have been erected at Muscatine, Iowa. This now makes fifty-five factories in this

hunters that nearly every clam was removed from its bottom in less than nine months. Flushed with their success, these hunters then swarmed out on to the Mississippi. In this river the pearls are scarce and not so valuable, and not much was done in the way of getting rich until a very valuable pearl field was found in the White River, in Arkansas.

Thither hurried the pearl fishers. All the past season they have been grappling for clams there, until now, as the season closes, few clams are left on the sandbars. A month or six weeks more on this river will clean it out entirely, and perhaps forever, of pearl-bearing bivalves.

The next most promising field is the Cumberland River in Kentucky. Here

Figure 9.3. *New York Times*, September 28, 1902.

for the resource from the button industry (Figure 9.3; Section 9.4). However, pearling continued to be practiced widely by local people, especially boys and farmers, during lulls between crops or by people "without regular occupation" (Kunz 1898). In the early 1900s, large piles of shells collected by pearlers were a common sight along rivers throughout the central United States (e.g., Boepple and Coker 1912; Clark and Wilson 1912; Wilson and Clark 1912, 1914; Coker and Southall 1915; Clench 1925). With the rise of the button industry, mussels were harvested primarily for their shells, but as late as 1920, pearls obtained as a by-product of this fishery continued to represent from one-half to one-third of the average sheller's income or, in some cases, even surpassed the value of the shells (Coker 1919; Anthony and Downing 2001). Pearl buyers continued to operate near shelling grounds for the button industry at least into the 1950s (Madson 1985). Even today, pearls may contribute supplemental income in the harvest of mussel shells for the cultured pearl industry (Section 9.5), and a few people still harvest mussels specifically for pearls (Kennedy 1985). In Europe, poaching by pearl hunters remains a major problem in the conservation of the pearl mussel, *Margaritifera margaritifera* (e.g., Helama et al. 2007).

9.4. Buttons

During the first few decades of pearl harvest, mussel shells were usually discarded as having no value. This changed rapidly with the advent of the freshwater shell button industry in the 1890s.[1] The American shell button industry began largely through the efforts of a German immigrant, Johann Boepple (also spelled "Böpple" or "Böepple")

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[1] Splendid, vintage film footage of nearly all aspects of the button industry (c. early 1950s), including harvest, shell processing and buying, and button manufacture, is available at http://www.fws.gov/midwest/mussel/multimedia/one_button_clam.html, courtesy of the Muscatine Arts Center, Muscatine, Iowa.

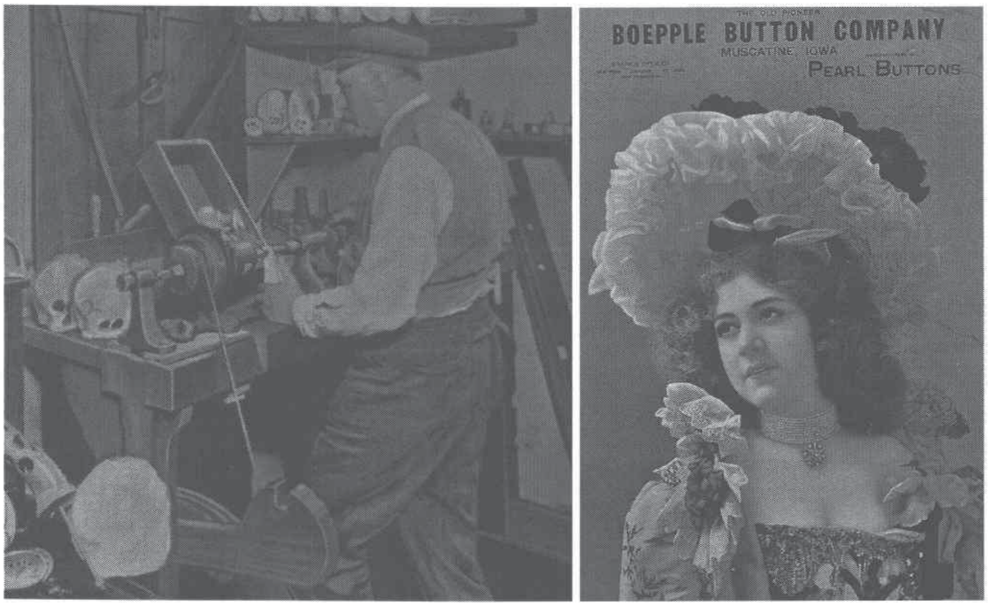


Figure 9.4. (left) Johann Boepple at his foot-powered button cutting lathe, c. 1891. Surrounding him is a variety of materials used to manufacture buttons and other items, including animal horns, marine shells, and freshwater mussel shells (on shelves in background). (right) Advertisement for Boepple Button Company, c. 1900 (both courtesy Muscatine Arts Center, Muscatine, Iowa).

(Figure 9.4). Legend has it that Boepple got the idea for using shells to make buttons after cutting his foot on a mussel while bathing in the Sangamon River in Illinois (Parmalee and Bogan 1998; Pritchard 2001). In reality, Boepple's was a calculated venture representing the culmination of previous attempts to utilize North American mussel shells. As early as 1802, a report from Kentucky stated that "the mother o' pearl [of freshwater mussels], which is very thick, in it is used in making buttons" (Michaux 1805, 189). Similarly, Say (1830–1838) reported, "Many of them [freshwater mussel shells] are of a beautiful perlaceous color and consistence, and we are informed that some of the very thick ones of the Ohio, have been, at Pittsburgh, successfully turned into buttons and ornaments." In 1872, a man from Peoria, Illinois, shipped mussel shells from the Illinois River to Germany to assess their potential value in manufacturing. In 1883, a manufacturing plant was established in Knoxville, Tennessee, to make buttons and novelties using shells from the Tennessee River but failed in part because of lack of suitable machinery. Another factor in the failure of these ventures was the availability of inexpensive imported buttons and raw materials prior to 1890. Shell button factories were in operation in Cincinnati, Ohio, and St. Paul, Minnesota, in the 1880s but used imported marine shells despite the fact that both cities are on rivers that later became among the most important sources of freshwater button shell (Coker 1919).

Boepple was an experienced button manufacturer and turner in Germany, utilizing marine shells, ivory, bone, and buffalo horn, but his business faced difficulties from high tariffs on imported shell and other materials. In 1886, Boepple examined American shells that had been shipped to Germany some years earlier, likely the shells sent from the Illinois River in 1872. Finding these suitable for button manufacture and lured by the prospect of abundant domestic raw materials, he sold his business the following year and immigrated to Illinois, bringing with him some of his trade tools. By his own account, Boepple indeed found his first mussel bed after cutting his foot in the Sangamon River and finding the bottom of the river "covered with mussel shells." Over the next few years, he began to produce shell buttons and novelties in his spare time from farm work and construction labor. In 1890, the McKinley Tariff, similar to the protectionist tariffs that drove Boepple from Germany, increased prices on imported buttons and marine shell. Seeing his opportunity, Boepple moved to Muscatine, Iowa, on the Mississippi River, and opened his first button factory in the basement of a cooper's shop in 1891 (Figure 9.4). Existing equipment designed to work marine shell proved unsuitable for freshwater shell, and Boepple pioneered the development of appropriate equipment and techniques. Despite his innovations, Boepple's resistance to mass-production techniques (he used a foot-powered lathe) forced him from button manufacturing. He became a freelance shell buyer and, in 1910, went to work for the U.S. Bureau of Fisheries' Fairport Biological Station (Section 2.2.B), serving as its expert on commercial shell and surveying mussel stocks in rivers throughout the central United States. In a cruel irony, he reportedly cut his foot again on a mussel shell while surveying a stream in Indiana and died from infection shortly after, in 1912 (Smith 1899; Coker 1919; Claassen 1994; Anthony and Downing 2001; Kurtz 2003).

Boepple's methods formed the basis of the button industry. Prior to processing, shells were soaked in water for a week or more to reduce chipping and wear on saws. Circular blanks were then cut from the shells using a lathe fitted with a tubular saw blade (Figures 9.5 and 9.6). Cutting blanks was considered a highly skilled occupation due to the economic necessity of maximizing the number and quality of blanks cut from each shell, and cutters were paid by the gross produced. Blanks were ground on an emery wheel to remove the periostracum and produce a uniform thickness (Figure 9.5). The faces of the ground blanks were carved to produce a central depression in various patterns and then drilled (Figure 9.6). The resulting buttons were tumbled and polished then sorted into grades based on quality and size. Grinding, facing, and drilling were first done by hand but became automated by about 1901; however, blank cutting remained a manual process (Smith 1899; Coker 1919).

Boepple's button factory was in full production by 1892. This demonstration of the feasibility of using freshwater shells, combined with a favorable trade environment, resulted in an explosion of the button industry (Figure 9.7). Three new factories were established in 1895, 9 in 1897, and 36 in the first 6 months of 1898. Most of

Figure 9.5. Button manufacturing. (a) Blank cutters at their lathes in a small cutting factory in Andalusia, Illinois, c. 1915. Man in foreground is holding a shell with special tongs while cutting blanks; additional shell tongs are hanging on the rack in the window. Drilled shells can be seen in the trough below the lathe (courtesy Augustana College Special Collections, Rock Island, Illinois). (b) Blank cutting room in a large button factory. (c) Automatic facing and drilling machines in the McKee-Bliven Button Company, Muscatine, Iowa. (d) Sorting and boxing buttons for shipment in the Hawkeye Pearl Button Company, Muscatine, Iowa, c. 1910 (b–d courtesy Oscar Grossheim Collection, Musser Public Library, Muscatine, Iowa).

these factories were in Muscatine or other towns directly on the Mississippi River in Iowa and Illinois, and the button industry represented an economic savior for a region struggling with the demise of the white pine lumber industry (Scarpino 1985). In 1897, the industry began to expand and shells were shipped to new factories as far away as Cincinnati and Cleveland, Ohio, and Omaha, Nebraska (Smith 1899). By 1900, there were 70 button factories in the Mississippi River valley (Anthony and Downing 2001). As the industry grew, many factories specialized in either cutting of blanks or finishing, but others carried out all phases of production. In 1912, 196 factories in 20 states were involved in button manufacture (Coker 1919). At the industry's peak in 1916, it produced 5.75 billion buttons valued at $230 million (2009 $US) and employed about 20,000 people (Scarpino 1985; Claassen 1994).

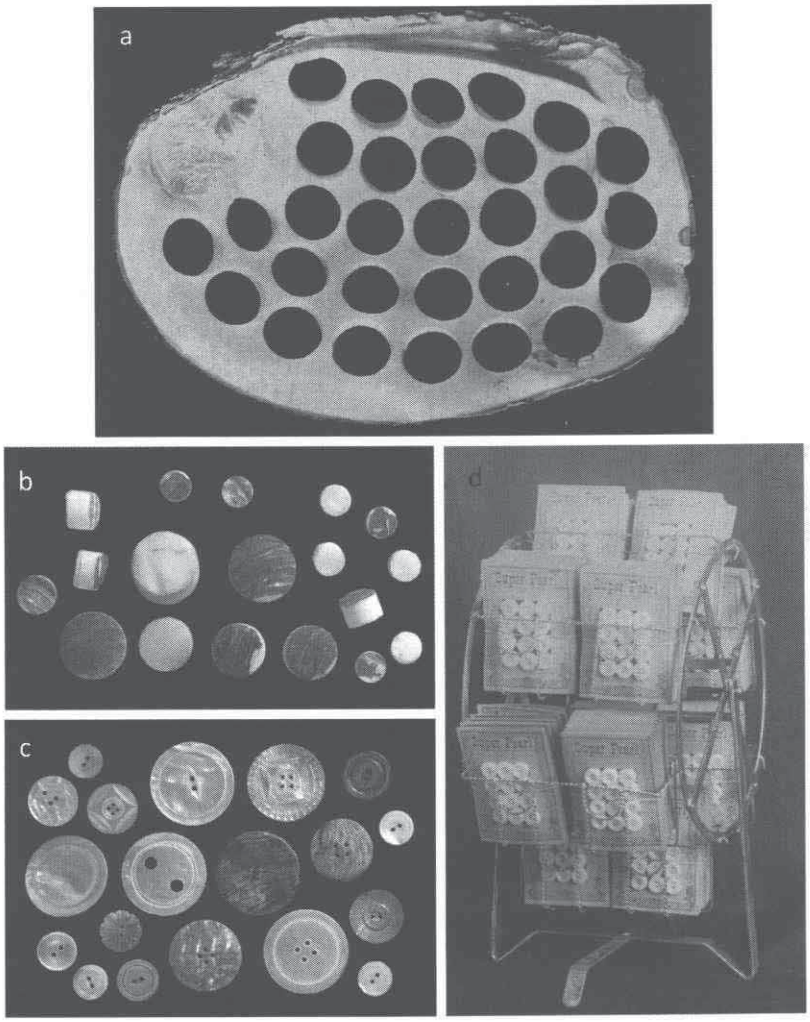


Figure 9.6. (a) *Megalonaias nervosa* shell drilled for button blanks (from Coker 1919). (b, c) Blanks and finished buttons (Richard T. Bryant, photos). (d) Button display from the Hawkeye Pearl Button Company, Muscatine, Iowa (courtesy Oscar Grossheim Collection, Musser Public Library, Muscatine, Iowa).

This industry created an overnight demand for large quantities of shells, resulting in a unique American subculture: the sheller. Button manufacture required thick-shelled species that are most abundant in large rivers, and thinner-shelled, small-stream species that often produced pearls had no value. Consequently, unlike pearling, which drew people from all walks of life, shellers were primarily fishermen or others associated with various river trades. Shellers and their families were often nomadic, moving to new shelling grounds as local stocks were depleted, and lived in temporary camps on riverbanks or in homemade houseboats (Smith 1899). In winter and spring, shellers typically fished, trapped, salvaged drift logs, or did odd jobs but moved to shelling

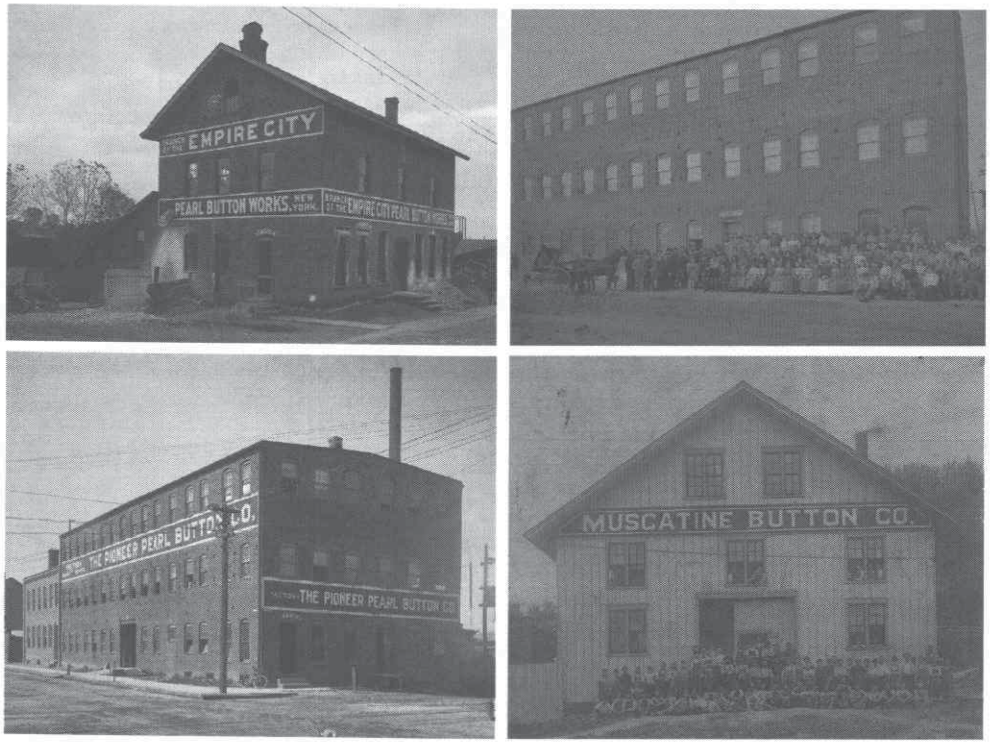


Figure 9.7. Just a few of the button factories in Muscatine, Iowa, in the early 1900s (courtesy Oscar Grossheim Collection, Musser Public Library, Muscatine, Iowa).

camps in summer and fall (Hubbard 1977). During shelling season, houseboat communities of 35–75 families existed at numerous locations on the Ohio, Mississippi, and other rivers in the early 1900s (Claassen 1994). Along the upper Mississippi River, packet boats plied the river in summer selling groceries and other supplies to shelling camps (Madson 1985). Shelling camps and their inhabitants were often viewed with disdain by permanent, local residents who objected to the smell of putrefying mussel meat and considered shellers shiftless and lawless (Scarpino 1985).

In addition to full-time shellers, farmers, loggers, and others shelled seasonally in late summer when mussel beds in smaller streams were accessible by wading. In the late 1890s, Iowa farmers complained that the number of people taking up shelling made it difficult to find field hands (Smith 1899). In the 1920s and 1930s, shelling camps of up to 150 local people were established for several weeks each summer on the Clinch River, Tennessee, and similar camps were common sights along many other rivers (Claassen 1994). The number of people engaged in shelling was difficult to count due to their transient or seasonal nature, but their numbers grew rapidly along with the proliferation of button factories. In 1897, 300 people were shelling on the Mississippi River in the vicinity of Muscatine, but one year later, this number swelled

Figure 9.8. (top) Harvesting mussels through the ice with shell tongs and rakes, upper Mississippi River, c. 1898–1899 (from Smith 1899). (bottom) Shell tongs (both from Coker 1919).

to an estimated 1,000 (Smith 1899). By 1914, over 10,000 people nationwide were thought to be engaged in shelling to some extent (Anfinson 2003).

Mussels were harvested by several methods. Prior to intense exploitation, mussels could be harvested in large numbers by hand at low water. However, the densest mussel beds were usually found in deeper water, and other methods were needed in the days before diving equipment. During the first few years of the button industry, mussels were harvested with long-handled rakes or scissor-like tongs similar to oyster tongs. Rakes and tongs were even used through holes in the ice (Figure 9.8); on one day in winter 1898–1899, 142 men were observed working on the ice over a mussel bed in the Mississippi River near LeClaire, Iowa (Smith 1899). These devices continued in use for many years, but in 1897, the brail, or crowfoot dredge, was developed near

Muscatine and became the most common harvest method well into the twentieth century (Figure 9.9). A brail consists of a steel pipe or wooden beam 2 m or more in length. From the beam dangle short cords or chains placed about 15 cm apart to which are attached a series of multipronged hooks (the crowfeet). The brail is lowered into the water on a stout line and allowed to drag over the bottom (Figure 9.10). When the hooks fall within the valves of a filtering mussel, the shell closes quickly and firmly on the hook, causing the mussel to be pulled from the substrate by the movement of the boat. An underwater sail, or mule, often was used to provide additional propulsion. Most boats employed two brails, one being picked of mussels while the other fished. This unlikely method has earlier antecedents. Native Americans, Canadian loggers, and Chinese fishermen reportedly dragged tree branches across streambeds to capture mussels in similar fashion (Claassen 1994), and the first brails may have been simply weighted cedar trees (Nelson 1983). Modern-day Chinese fishermen use a device similar to a brail consisting of a series of thin iron rods attached to a bamboo pole (Savazzi and Peiyi 1992). In addition to rakes, tongs, and brails, large mechanical dredges were used in some operations (Smith 1899; Coker 1919). After harvest, mussels were steamed from their shells in large vats at the shellers' camps that lined many rivers (Figure 9.11), and shells were delivered to button factories or purchased by buyers who traveled the rivers by boat (Figure 9.9). Shellers also searched steamed-out mussel tissues for pearls.

Button manufacturers had clear species preferences based on nacre quality and color. The most sought-after species were those with unstained, white, or iridescent nacre of moderate thickness and without exterior sculpture, which made shells difficult to cut. The yellow sandshell, *Lampsilis teres*, surpassed all other species in quality and was the first to be used widely. However, this species does not form dense beds, limiting its supply, and because of its exceptional quality, most were ultimately exported to Germany for specialty use. By 1894, the ebonyshell, *Reginaia ebena*, became the industry standard due to its abundance, wide distribution, and consistently high quality, and it retained this status throughout the history of the button industry. Initially, only medium-sized individuals were used. Small individuals yielded few blanks, and large shells had a higher percentage of waste in the blank-cutting process and necessitated extensive grinding to achieve button thickness. As mussel stocks became depleted, manufacturers were forced to use an increasingly greater range of species and sizes. In total, about 50 other mussel species were used to some extent (Anthony and Downing 2001), especially (roughly in order of preference) *Actinonaias ligamentina, Fusconaia subrotunda, Lampsilis siliquoidea, Ellipsaria lineolata, Ligumia recta, Quadrula pustulosa, Q. quadrula, Amblema plicata, Megalonaias nervosa*, and *Pleurobema* spp. These other species were less desirable because they were variable in quality, limited in distribution or abundance, or heavily sculptured. For example, the fatmucket, *Lampsilis siliquoidea*, was unsuitable for button manufacture in most streams due to its thin shell, but those from Lake Pepin, on the Mississippi River, were

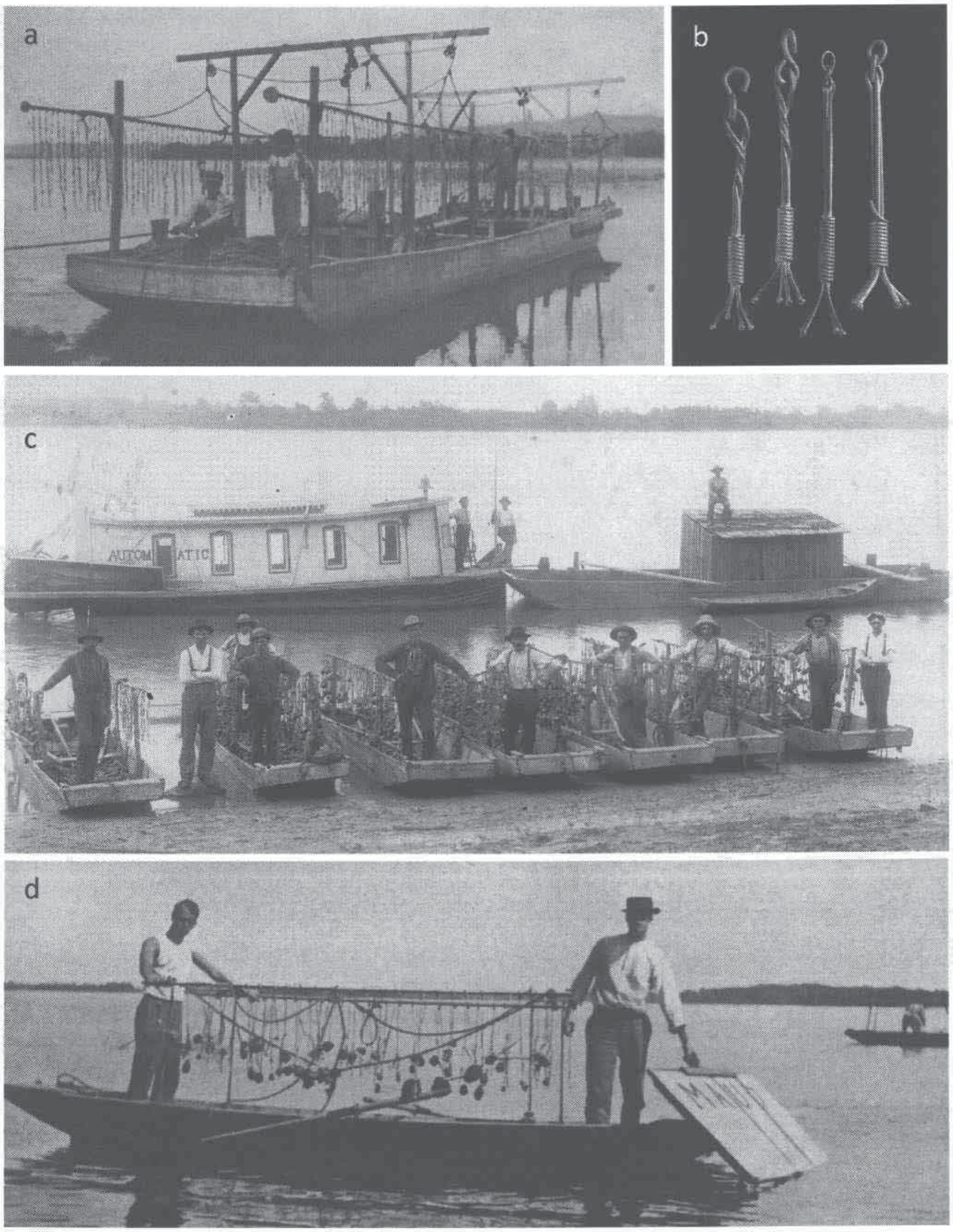


Figure 9.9. Brailing. (a) Large brail boat on the Ohio River, showing two brails and pulley systems for raising and lowering brails (from Coker 1919). (b) Crowfoot hooks used in brailing. Note small knobs at ends of hooks, which prevent hooks from pulling out of the shell (Richard T. Bryant, photo). (c) Brail boats on the upper Mississippi River. In the background is a scow of the Automatic Button Company used to buy shells from shoreline camps and transport them to the factory (courtesy Oscar Grossheim Collection, Musser Public Library, Muscatine, Iowa). (d) Brail boat showing mussels attached to crowfoot hooks and a "mule" (held by man at right; from Lefevre and Curtis 1912).

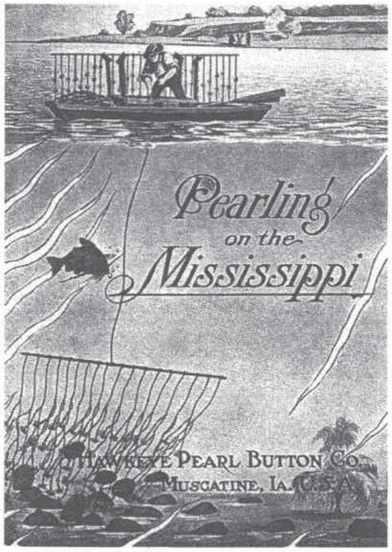


Figure 9.10. Illustration of use of brail (from pamphlet distributed by Hawkeye Pearl Button Company, Muscatine, Iowa, c. 1914).

thicker and greatly esteemed. Similarly, the butterfly, *E. lineolata*, and long-solid, *F. subrotunda*, yielded excellent button material but were generally uncommon. Despite their beauty, species with purple or pink nacre were used rarely and mostly for novelties because of market preference for uniform, white buttons and because these colors fade quickly. Small or thin-shelled species were used only in isolated cases (e.g., use of the sugarspoon, *Epioblasma arcaeformis*, for souvenirs or "fancy articles"; Boepple and Coker 1912). Commercially valuable species were largely restricted to the Mississippian region. Species in Atlantic or Pacific coast drainages were not used in button manufacture due to their thin or colored shells (Coker 1919, except where noted).

In the late 1890s, principal shelling grounds were restricted to about 270 km of the Mississippi River, centered on Muscatine, Iowa. Early harvests from these virgin mussel beds were staggering (Figure 9.11). Between 1894 and 1897, 9,000 tons of mussels were taken from a single bed 2.4 km long and 0.3 km wide near New Boston, Illinois, representing an estimated 100 million mussels (Smith 1899). In the first year, up to 1 ton (roughly 10,000 mussels) per day could be taken from this bed by a single sheller. From 1894 to 1899, annual harvest throughout the upper Mississippi River increased more than 200 times from 89 to 21,627 tons (Coker 1919; Anthony and Downing 2001).

Not surprisingly, such heavy exploitation resulted in rapid depletion of mussel beds in the vicinity of the button factories, and many beds were considered commercially exhausted by 1899 (Smith 1899). Harvest spread quickly into increasingly distant rivers, but button factories remained centered around Muscatine. After cutting blanks,

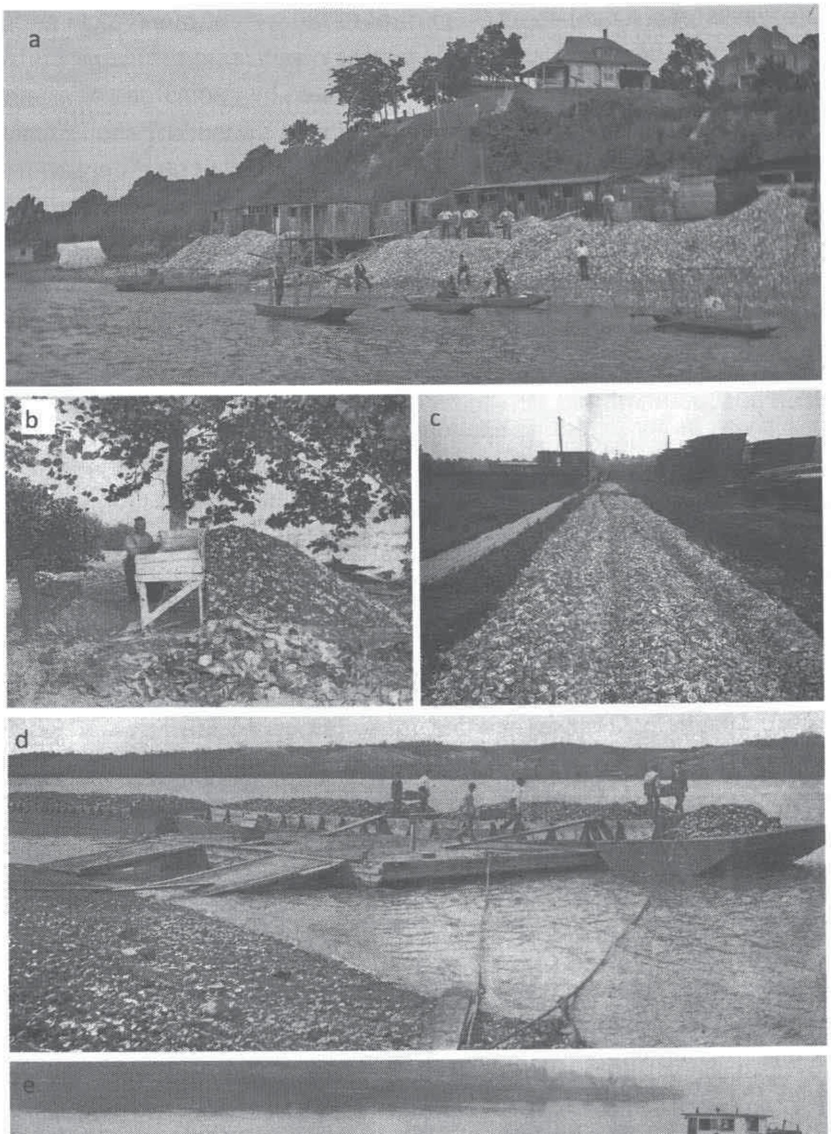


Figure 9.11. (a) Shellers' camps along the upper Mississippi River, c. 1910. (b) Steaming and sorting shells at a shoreline camp. The vat used to steam out mussel meats is on the ground at left. Man is sorting shells by size, with large shells in foreground. (c) Road paved with drilled-out shells, Muscatine, Iowa, c. 1910. (d, e) Barges transporting mussel shells on the upper Mississippi River. (a, c courtesy Oscar Grossheim Collection, Musser Public Library, Muscatine, Iowa; b, e from Coker 1919; d from Smith 1899).

colloquial names for mussel species, including many that are still used today (e.g., monkeyface, pigtoe, pimpleback, pistolgrip, rabbitsfoot, pocketbook) as well as others that were a bit too colorful and have necessarily fallen from use. Burt Lancaster used a brail to catch mussels in the 1955 film *The Kentuckian*; despite its historical inaccuracy (the film is set in the 1820s, about 70 years before the button industry and development of the modern brail), this portrayal by Hollywood shows the former prominence of shelling in American culture. Perhaps most important, the massive and unsustainable harvests of the button era prompted the first widespread recognition of the vulnerability of mussel populations to human impacts, the first coordinated efforts to study their ecology (Chapter 2), and the first concerted efforts to save them (Chapter 11).

9.5. The second pearl rush

Virtually any shelled mollusk – including snails – can produce pearls; the largest recorded pearl is a 6.4 kg specimen from a giant clam (*Tridacna* sp.) (Cobb 1939). However, most mollusks do not have nacreous shells (Watabe 1988), and pearls produced by these species are of low value because they lack luster and iridescence. Lustrous pearls are produced by relatively few species, notably freshwater mussels and the marine pearl oysters (*Pinctada* spp.). Because of this, and the irregular shape of most natural pearls, gem-quality pearls are exceedingly rare. In the early 1900s, Japanese fisheries scientists perfected techniques for producing cultured pearls using *Pinctada fucata*, ultimately making spherical, gem-quality pearls widely available. This technique involves implanting into a pearl oyster a spherical bead (nucleus) together with a piece of mantle tissue to stimulate nacre production. After several months to a few years, the oyster encapsulates the bead with its own nacre, producing a consistently spherical pearl in a fraction of the time required in the wild. After experimenting with clay, glass, lead, and wood nuclei, in the 1920s, it was discovered that polished beads cut from freshwater mussel shells made the ideal nucleus for cultured pearls due to their luster and similar chemical and structural composition (Claassen 1994; Fassler 1997).

Freshwater mussels in Japan and much of the world are relatively thin shelled, and species with shells of sufficient thickness for producing pearl nuclei occur predominantly in China and the United States. The Japanese began to import American shell for nuclei as early as the 1920s but initially used primarily Chinese shell from the Yangtze River (Claassen 1994). However, Chinese shells frequently have a Tolberg layer, an organic wax that interferes with adherence of pearl oyster nacre to the nucleus (Latendresse 1980); this layer occurs in some North American shells but is less prevalent (Sparks and Blodgett 1983). Because of the higher quality shell and the extensive supply network already in place for the button industry, Japanese imports of American shell increased beginning in the late 1940s as the cultured pearl industry was rebuilt after World War II. After suspension of trade between Japan and China in the late 1950s, the United States became the sole supplier of shell for the rapidly growing cultured pearl industry and remains the principal supplier today (Neves 1999). Few people who own cultured pearls produced in the last 50 years are aware that their gems consist of only a thin veneer of exotic pearl oyster nacre and are composed primarily of freshwater mussel shell most likely from Alabama, Arkansas, Kentucky, or Tennessee.

The Japanese export market led to a revival of shelling that occurred simultaneously with the demise of the button industry. Spatial and temporal patterns of these two fisheries show many similarities, but the history of shelling for pearl nuclei is more complex because of the volatility and global nature of the industry. Furthermore, harvest patterns were influenced by the legacy of exhaustive harvests of the button era and by accelerated degradation of stream habitats, both of which reduced the availability of profitable shelling grounds. Another major difference was that, unlike the rapid explosion of the button fishery, harvest for pearl nuclei increased gradually in its initial years. From the 1940s to the early 1960s, the principal shelling grounds in the heyday of the button industry were largely abandoned (Starrett 1971; Anthony and Downing 2001), and the Tennessee River provided the bulk of button material (Section 9.4). Tennessee River shells were exported to Japan for nuclei throughout this period, but until the mid-1950s, the majority of the harvest continued to supply the button industry (Scruggs 1960). As the button industry died, increased demand for nuclei kept Tennessee River harvests at relatively constant levels until the early 1960s. Harvests were dominated by *Pleurobema cordatum*, which, although inferior for button production, was ideal for nuclei and became the preferred species for Japanese buyers. The buyers also considered Tennessee River *P. cordatum* superior to those from other streams (Fassler 1997).

By 1944, the Tennessee River was impounded throughout its length, and it was widely assumed that mussel populations would be eliminated. However, many sections retained riverine characteristics, and shellers found extensive mussel beds remaining in submerged portions of the original river channel (Isom 1969). These beds were composed mainly of riverine species like *Pleurobema cordatum* that had recruited prior to dam construction, but there was little recruitment under the impounded conditions (Scruggs 1960; Section 10.5.A). Consequently, harvest began to decline rapidly in the mid-1950s. At this point, the fishery behaved exactly as the button fishery had earlier: as yield declined, prices rose sharply, leading to intensified effort and an acceleration of stock depletion. In 1961, there were at least 900 shellers working on the river (Williams 1969). This intense effort resulted in a brief spike in harvest followed quickly by a crash of the fishery by 1964.

Japanese pearl culturalists were forced to relax their stringent requirements for Tennessee River pigtoes and seek other sources. Again reflecting patterns of the button era, harvest shifted to a wider array of species and to other streams, many of which had seen little harvest for more than 30 years, allowing stocks to recover to some extent. Shelling was revived on the traditional button grounds of the Illinois, Wabash, and upper Mississippi rivers and peaked briefly in 1965 but at levels far lower than peak harvests of the button era. The harvest in 1965 from the Wabash River was about 900 tons, compared to nearly 2,500 tons in 1914 (Coker 1919; Anderson et al. 1993). Harvest also was revived to a moderate extent in other regions (e.g., Kansas, Busby and Horak 1993); however, this resurgence was short-lived. After 1966, there was little harvest on the Illinois River because of a lack of a market for the shells (Starrett 1971). By 1970, harvest had dropped to very low levels across the United States, and harvest and shell prices remained low for the next 15 years (Crowell and Kinman 1993; Anthony and Downing 2001).

The reasons for this lull are not clear. By the 1970s, mussel populations across the United States had been seriously reduced by impoundment, water pollution, and other habitat degradation, in addition to commercial harvest (Section 10.3). It is possible that mussel stocks were simply too low to sustain large harvests. This explanation seems unlikely because, as seen in previous and following examples, scarcity of shell would have driven up prices, resulting in intensified harvest despite low stocks. Given the small size of the cultured pearl industry at the time, expansion of harvest may have satisfied market demand and stabilized prices at low levels. Regardless of the cause, once again, shelling faded into the background of American culture.

This changed dramatically in the late 1980s. By the 1960s, mussel species that can adapt to lentic conditions had begun to colonize overbank areas in the Tennessee River reservoirs, the submerged bottomlands beyond the original river channel (Isom 1969; Sections 4.1.D.2 and 10.5.A). Because mussels grow quickly in these eutrophic habitats, and because they had been largely neglected by shellers, populations were large by the 1980s, including the commercial species *Amblema plicata, Megalonaias nervosa*, and *Quadrula quadrula* (Sickel and Chandler 1982; Ahlstedt and McDonough 1993). Shellers began to exploit these stocks in the early 1980s, and Japanese buyers quickly realized that these "lake shells" produced extremely high quality nuclei (Crowell and Kinman 1993). The washboard, *M. nervosa*, was especially prized because its large size (more than 250 mm) and thick shell allowed production of large nuclei and, ultimately, large, valuable pearls (Fassler 1997). The lake shells also had a low incidence of Tolberg layers, which occur commonly in washboards from other streams (D. Hubbs, personal communication). For the second time, Japanese buyers began to focus on Tennessee River shells. Concurrently, rapid growth of the cultured pearl industry, including expansion into Australia, China, Indonesia, and Polynesia, resulted in a sharp increase in demand for nuclei (Fassler 1997). Shell prices increased from an average of $450/ton in 1978 to as high as $2,700/ton in 1986 (Crowell and Kinman 1993), and the rush was on yet again.

People scrambled to enter the fishery. The number of shelling licenses issued in Kentucky increased from 76 in 1985 to 815 in 1990, not including an estimated

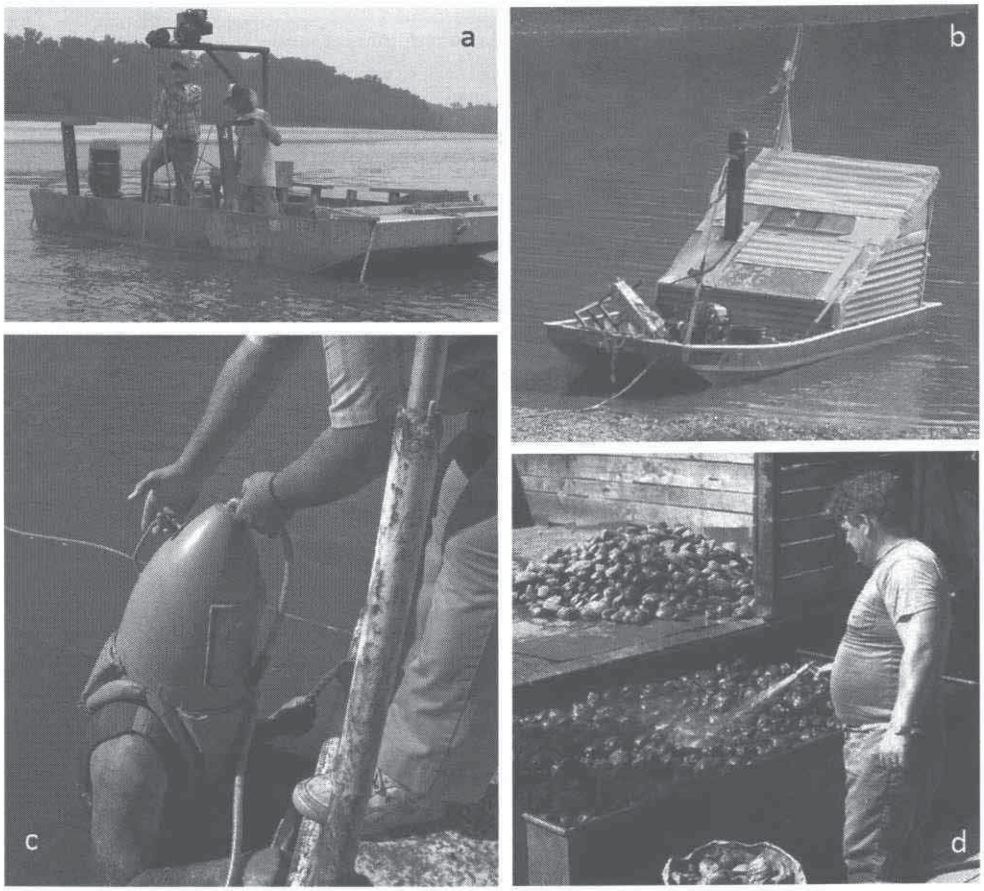


Figure 9.12. Shelling in the 1990s. (a) Brail boat on the Alabama River with gasoline powered winch to raise brail (Jeff Powell, photo). (b) Improvised dive boat on the Tennessee River. Chimney is for a homemade system that uses propane to heat river water, which is then pumped into the diver's wetsuit in winter (Don Hubbs, photo). (c) Improvised dive helmet made from bomb casing, White River, Arkansas (Keith Sutton, photo). (d) Vat for steaming mussel meats from shells (Chris Barnhart, photo).

equal number of unpermitted shellers (Crowell and Kinman 1993), and from 350 in 1989 to 2,356 in 1991 in Alabama (Ahlstedt and McDonough 1993). Tennessee had 2,355 licensed shellers by 1990 (Todd 1993), resulting in a total of at least 6,000 shellers working in the Tennessee River area. Brailing continued to be used widely, but by this time, most shellers harvested by diving using a variety of homemade equipment (Figure 9.12). Shell exports peaked in 1993 at 6,263 tons (Neves 1999), which, although large, was a fraction of peak harvests for the button industry.

Unlike the button era, harvest was now regulated to some degree, including minimum size limits, restrictions in the number of licenses issued, the type of gear permitted (e.g., several states banned diving), implementation of harvest reporting requirements, reducing the length of the harvest season, and harvest closures in some areas (Anderson et al. 1993; Crowell and Kinman 1993; Thiel and Fritz 1993; Todd 1993; Howells et al. 1996). However, harvests were often grossly underreported by shellers; in some cases, reported harvests were about one-half of the tonnage purchased by shell buyers (Anderson et al. 1993). Furthermore, many considered diving more efficient than brailing at rapidly depleting mussel stocks. Because of uncertainty about harvest levels and lack of information about mussel population dynamics, no attempts were made to quantitatively assess stocks and implement overall harvest limits accordingly. Consequently, the familiar pattern of exploitation soon repeated itself: total yields and the percentage of legal-sized mussels declined rapidly in the face of intense harvest pressure, causing a jump in prices; harvest expanded from the Tennessee River throughout the former button grounds; and quality standards were relaxed by buyers (Anthony and Downing 2001).

Compounding these problems, the invasive zebra mussel (*Dreissena* spp.) became established in the Great Lakes in 1988 and soon entered the Mississippi River system. Because zebra mussel infestation caused nearly 100 percent mortality of native mussels in the Great Lakes (Section 10.4.C), the Japanese increased their demand for shells still further in an attempt to stockpile material in the event that this catastrophe should befall mussel stocks throughout the United States. These factors touched off a buyer's war, during which prices for top-quality washboards peaked at more than $14,500/ton in 1995 (D. Hubbs, personal communication). Because a large washboard can weigh more than 2.3 kg, a single mussel could bring $40, and shellers could make several thousand dollars a day.

Things got out of hand quickly. Shellers, both independently and as agents of shell companies, scoured the country searching for marketable shells. Poaching became widespread in streams that were closed to harvest, and illegal shellers often worked at night. Despite 24-hour surveillance, law enforcement officers were unable to prevent poaching in the Duck River, Tennessee, which had large washboard populations (D. Hubbs, personal communication), and similar problems were experienced throughout the Mississippi River system (e.g., Crowell and Kinman 1993; Miller and Mosher 2008). As mussel size decreased in exploited streams, shellers often transported undersized mussels to sell in states with smaller size limits (Williams et al. 2008). Convictions for these offenses occurred, but because most violations were misdemeanors punishable by fines as low as $25 to $200 (Crowell and Kinman 1993), they were viewed as a cost of doing business easily defrayed by high shell prices. As problems escalated, they were addressed by increased penalties and coordinated law enforcement efforts. In 1998, after a 4-year investigation by the U.S. Fish and Wildlife Service, state wildlife agencies, and the U.S. Department of Justice, the Japanese-owned Tennessee Shell Company pled guilty to a felony violation of the Lacey Act, which prohibits interstate commerce in protected wildlife species (USFWS 1998). Evidence showed that the company knowingly purchased and later exported shells harvested illegally from closed waters in Michigan, Ohio, Kentucky, and West

Virginia. The company was ordered to pay $1 million in restitution to the National Fish and Wildlife Foundation to establish the Freshwater Mussel Conservation Fund for research and recovery. In this same case, 20 individuals pled guilty to an additional 136 counts of violating the Lacey Act. Other, similar convictions under the Lacey Act have occurred as recently as 2008 (USFWS 2009a).

The lower Tennessee River region assumed a distinct Wild West feel during this time. Shell buyers paid in cash and often traveled with large sums. A shell buyer from Murray, Kentucky, was arrested for the murder of her husband, as well as drug and gun charges, while on a buying trip to Alabama (Wilcox Progressive Era 2007). Another shell-buying couple in Camden, Tennessee, was murdered and robbed of $5,000 cash and about 1 ton of shells by a competitor (Wadhwani 2010; D. Hubbs, personal communication). Subsequent to the Tennessee Shell Company convictions, several witnesses, including shellers and buyers, died under mysterious circumstances, and another disappeared, her body never found (Wadhwani 2010; D. Hubbs, personal communication).

Even more quickly than it started, the boom was over. In 1996, a major die-off of pearl oysters occurred in Japan (Neves 1999). Simultaneously, the Japanese cultured pearl industry was experiencing stiff competition from Chinese producers who used nuclei from Chinese freshwater species and also had developed techniques requiring no nucleus (Fassler 1997). In addition, the Japanese had accumulated large stockpiles of shells in anticipation of zebra mussel effects, which, to date, have minimally affected most shelling grounds (Section 10.4.C). These factors, combined with a decline in the Japanese economy, resulted in dramatic decline in demand for American shell, and harvest plummeted in 1997 (Neves 1999). The Japanese pearl industry has not recovered from these blows, and demand for American shell remains low. The American shell export industry, at its peak valued at more than $50 million in Tennessee alone, is now valued at $2–4 million in that state (Wadhwani 2010). Currently prices for top-quality washboards are about $1,000/ton, 6 percent of the 1995 price, and Tennessee harvest has averaged about 1,000 ton/yr since 1997 (D. Hubbs, personal communication), similar to harvest levels during the lull of the 1970s. Meanwhile, mussel stocks in the Tennessee River are increasing after more than 10 years of low harvest (D. Hubbs, personal communication), quietly biding their time until the next pearl rush.

Chapter 10

The decline of the North American mussel fauna

Chronology and causes

> "... the destruction of our fresh-water fauna forms a chapter of the book on the destruction of our natural resources, a record which is not at all to the credit of the nation."
>
> – *Ortmann 1909b, 91*

10.1. The mussel fauna then: A view of the North American fauna prior to major impacts

Biologists today are accustomed to seeing streams with few or no mussels, and we cherish those rare places that still retain diverse and healthy faunas. Consequently, the magnitude of the loss of this natural resource in the last 200 years can be difficult to appreciate. Historically, many North American streams were literally paved with mussels, and well into the 1900s, the literature is replete with descriptions of their ubiquity and fabulous abundance. Thomas Say (1830–1838) wrote, "We have hardly a rivulet in the Union in which they [mussels] are not to be found." Simpson (1899, 288) reported, "I have seen . . . rivers where one could not step for a mile without treading on a living mussel." In the Yellow River, in northern Indiana, "The river is . . . well stocked with mussels. . . . Furthermore, these mussels are not irregularly distributed in small patches, but form a single bed which is practically continuous for the entire 20 miles" (Wilson and Clark 1912, 14). In the Green River, Kentucky, "I found a bed of live shells yesterday over 300 feet long and 50 feet wide; they were so thick that I could have filled a freight car" (Clench 1925, 71), and "the Unionidae were so thick in one place that the individuals actually touched one another" (Clench 1926, 8).

Mussel diversity and abundance reached its peak in the large rivers of the central United States. Even the largest rivers had extensive gravel and sandbars, creating shallow shoals and a variety of other habitats (Figure 10.1). In 1907, H. H. Smith (Chapter 2) described collecting at Weduska Shoals in the Coosa River, Alabama:

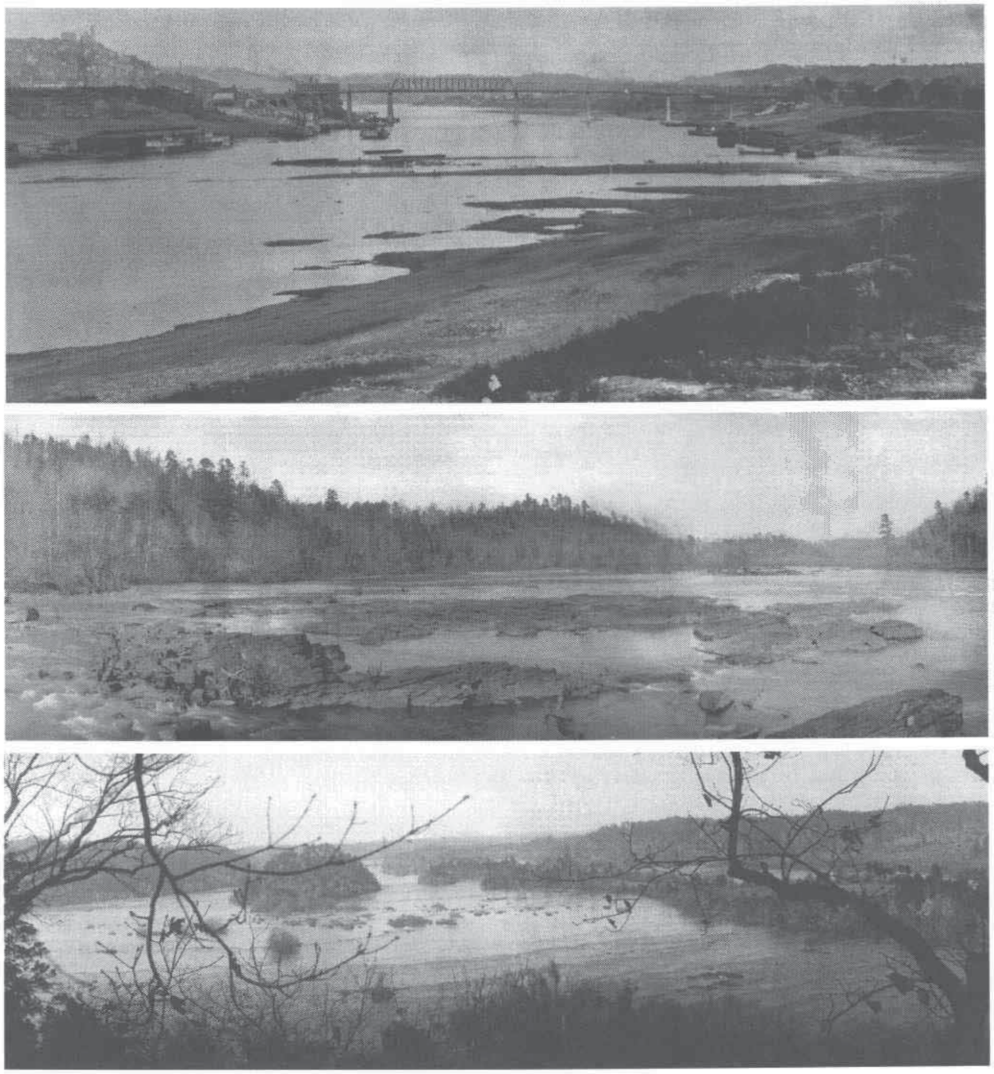


Figure 10.1. Some large rivers of the United States before impoundment. (top) The Ohio River at Cincinnati, Ohio, ca. 1888. Note people on gravel bars in the distance for scale (courtesy the Public Library of Cincinnati and Hamilton County and the Cincinnati Museum Center-Cincinnati History Library). (middle and bottom) The Coosa River, Alabama (courtesy Alabama Power Company).

"We could wade out half a mile in the rapids, which in that place are simply a succession of ledges with flat rocks or gravel between, the water swift in places, but never strong enough to be dangerous. I used to carry a large bag, and generally this and my pockets were filled in half an hour, though hardly one specimen in ten was saved" (from Goodrich 1922, 8). In the upper Mississippi River in 1867, "the unios grow so abundantly as to accumulate beds of their shells at least two or three feet thick"; during dredging for navigation in 1900 on the river in Minnesota, a mussel bed was encountered that was so thick the cutting head of the dredge had trouble penetrating it (Anfinson 2003, 49). Throughout the length of the Cumberland River in Kentucky and Tennessee, "every portion of the river bed that is at all suitable for mussels is fairly covered with them" (Wilson and Clark 1914, 7). Similar descriptions exist for rivers across the eastern United States, but perhaps nowhere was the original mussel fauna of North America better represented than at the spectacular Muscle Shoals on the Tennessee River (Box 10.1).

An overall view of the freshwater landscape prior to widespread human impacts is found in the account of an extended collecting trip by William Clench and Sheldon Remington, of the University of Michigan Museum of Zoology, in 1924 (Remington and Clench 1925, 132, 134, 137). After leaving Ann Arbor, they reported, "[In Indiana] every stream was thick with Pleurocerids, *Physa* [both snails], and often naiades [mussels].... From Nashville south to Huntsville, Ala. the collecting became very rich, every stream being loaded." Well into their trip, they encountered a polluted stream with no mussels and remarked, "It was somewhat of a new experience, for we had grown so used to finding shells in every creek.... At times it almost got monotonous." The situation today is the exact opposite. In many areas, one can visit stream after stream only to find few, if any, mussels – which gets *very* monotonous indeed, and sad – and finding a stream with a significant mussel fauna is an event to be remembered and talked about.

10.2. Early human impacts to the fauna, prehistory to 1924

10.2.A. Prehistoric impacts

Humans harvested mussels heavily for food for more than 5,000 years prior to European colonization of North America (Chapter 9). Along an 8 km reach of the Green River, Kentucky, it is estimated that humans harvested more than 200,000 mussels per year, and similar, intensive harvest occurred throughout North America (Haag 2009b). Land clearance and disturbance associated with an increasing human population resulted in substantial changes to the terrestrial landscape (Steponaitis 1986; Delcourt 1987; Mann 2005). The effects of these changes on aquatic ecosystems are poorly known, but measurable impacts may have occurred at least locally (e.g., Ekdahl et al. 2004). The spectacular abundance of mussels seen by early naturalists could have been a result of recovery from earlier human impacts following the catastrophic decline in the native human population wrought by European infectious diseases after De Soto's expedition in the 1530s. However, there is little evidence that prehistoric humans had lasting effects on the North American mussel fauna.

Continent-wide, there is no evidence of mussel species extinctions associated with prehistoric humans. Only a single North American species, the Apalachicola

Box 10.1. Muscle Shoals

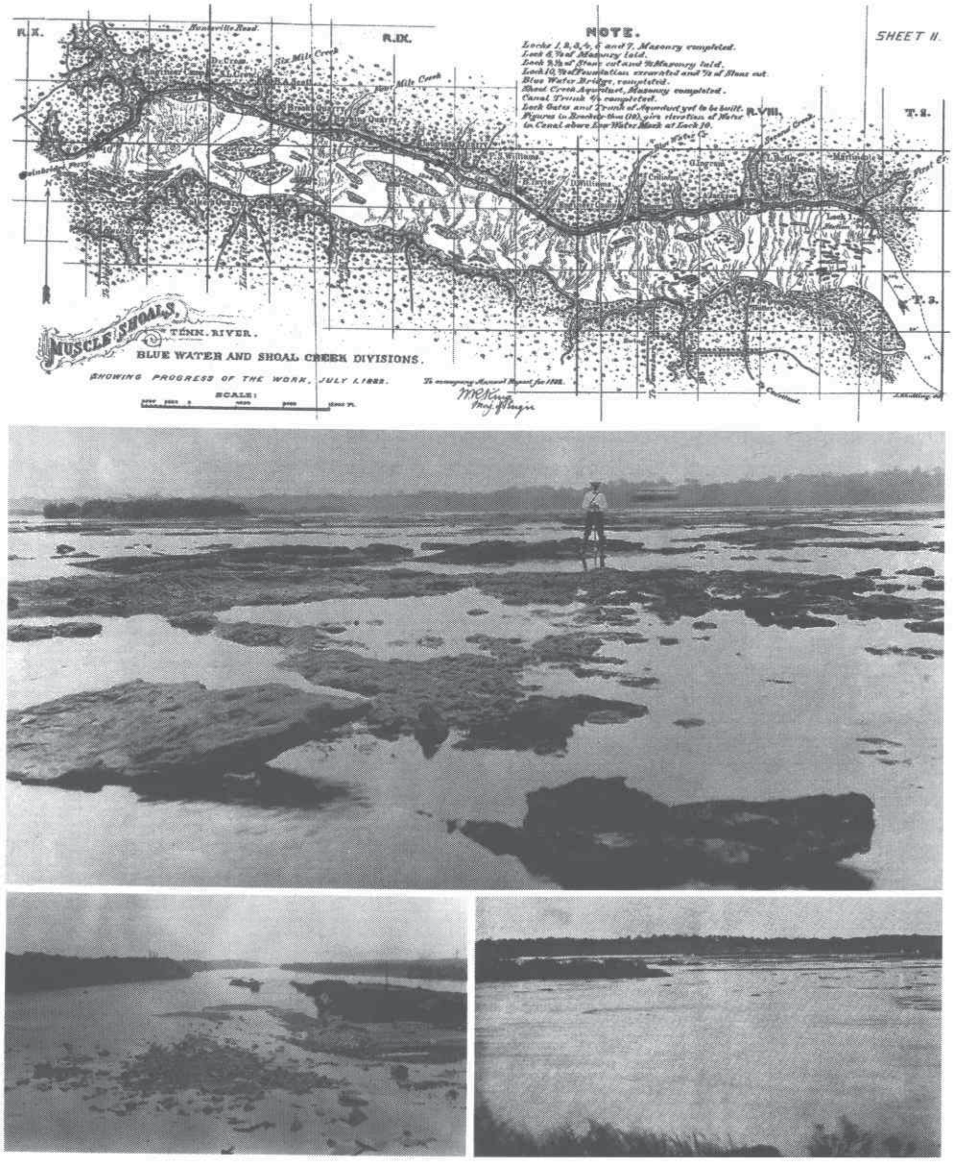
Surely the most remarkable single locality for freshwater mussels on Earth was Muscle Shoals, on the Tennessee River in northern Alabama. The abundance of mussels here was noted by the Cherokees, who referred to Muscle Shoals as *dagvnahi* or *dagunawelahi* (place of mussels; Bright 2004), and by the earliest European settlers (Davidson 1946) and is attested to by the huge prehistoric shell middens that line the riverbank (Chapter 9). Simpson (1899, 288) wrote, "The great mussel shoals on the Tennessee River . . . are literally blocked with mussel shells." In addition to the abundance of mussels, Muscle Shoals had a historical fauna of about 70 species (Stansbery 1964; Garner and McGregor 2001), making it the most diverse mussel assemblage ever reported. An exceptional feature of the fauna was the occurrence of at least 14 species of *Epioblasma*, most of which are now extinct (Garner and McGregor 2001; Williams et al. 2008).

Muscle Shoals was an 85 km complex of rocky ledges and shallow, gravelly shoals stretching from just above the mouth of the Elk River (Tennessee River kilometer (TRK) 463) downstream to about the mouth of Bear Creek (TRK 378). The shoals were formed by outcroppings of chert bedrock, which is resistant to erosion, unlike the limestone that underlies most of the Tennessee's channel (Fenneman 1938; McGregor 2002). Consequently, the river's erosive energy caused it to broaden at Muscle Shoals instead of becoming entrenched like the remainder of the river. The chert appeared at the surface in four major bands, producing four distinct groups of shoals from upstream to downstream: Elk River Shoals, Big Muscle Shoals, Little Muscle Shoals, and Colbert Shoals. Between these major shoals were short stretches of comparatively deeper, slower water. Over the length of Muscle Shoals, the river had an average gradient of about 0.8 m/km, 60 major islands, and about 60 smaller islets; it had a maximum low water depth of less than 30 cm in much of the channel; and it ranged from about 0.8 to 2.4 km wide (Davidson 1946; McGregor 2002). Prior to encountering the resistant chert layer, the river had cut through overlying layers of limestone, resulting in sheer bluffs up to 50 m high appearing alternately on the south or north shore. Overall, the shoals must have been a spectacular natural feature: "Muscle Shoals . . . is shallow, ornamented with a number of small islands, and its bed is full of the long grass which abounds in various species of Naiades [mussels]. The lover of the grand and the beautiful in natural scenery, as well as the student in science, will here find abundant sources of interest. He will be delighted with a noble river, whose beautiful and numerous islands are clothed with gigantic trees; whose high and undulating shore . . . spreads out an extensive alluvial . . . or rises abruptly from the river a mural escarpment of carboniferous limestone, which reflects its blue and somber aspect in the crystal waters at its base" (Conrad 1834, 12–13).

The diversity of mollusks at Muscle Shoals attracted naturalists from an early date, but the sheer size of the shoals prevented thorough, systematic exploration for some time. In November 1909, H. H. Smith spent a full month at Muscle Shoals, collecting mussels, aquatic snails, and land snails for a group of taxonomists, including Bryant Walker, who funded his work (Chapter 2). Smith took advantage of an extended period of Indian

(*continued*)

Box 10.1 (continued)



Muscle Shoals on the Tennessee River. (top) Navigation chart of Big Muscle Shoals, c. 1882; stippled areas indicate shallow, nonnavigable shoals (courtesy Robert Baker). (middle) Site of Wilson Dam on Little Muscle Shoals, near Florence, Alabama, prior to dam construction in 1918 (photo courtesy Tennessee Valley Authority). (bottom left) View downstream from Wilson Dam, showing unimpounded lower section of Little Muscle Shoals, September 1, 1927 (photo by E. F. Burchard, courtesy U.S. Geological Survey). (bottom right) Upper end of Big Muscle Shoals at future site of Wheeler Dam (prior to 1924) (from McKerall 1925).

summer during which the river was low and clear, and he described his collecting efforts in frequent correspondence with Walker (Bryant Walker Correspondence, University of Michigan Museum of Zoology, Ann Arbor). After his first day of collecting, Smith appreciated the grandeur of the river but seems to have been somewhat unimpressed by the fauna: "It is three miles wide [this was an overestimate], shoaly all the way across, and full of little islands. The mussels so far are a rather common lot for the most part. . . . I think we have about 30 species" (November 4, 1909). However, as he explored further, his excitement grew: "We have now about 45 species of Unionidae from the river. . . . I get lots of mussels by digging in the gravel shoals" (November 13, 1909). A few days later, he wrote, "It [a site in the Big Muscle Shoals] is an immense gravel shoal with a regular and not very strong current. Scattered over the surface are old dead mussels literally by the millions I should say. The live mussels at this season are in the gravel and must be found by digging" (November 17, 1909). By the end of his stay, Smith had come to a full appreciation of the exceptional nature of Muscle Shoals: "There is so much to do in the Unionidae that I find time for little else. How many species there are I do not know but certainly not less than 60. These shoals cannot be done as they should in a single season. . . . We have to explore a stretch 12 miles long and 2 or 3 miles wide of practically continuous shoals. . . . There are other important shoals above and below, but I am speaking only of the Mussel Shoals proper [Big Muscle Shoals] . . . . I have no doubt that there are twice as many species of mussels here as we have collected but it would take many months of hard work to get the rest" (November 25, 1909).

Although only about 70 species of mussels were reported ultimately from Muscle Shoals before it was destroyed, Smith's prediction of its potential diversity gives a tantalizing hint of what may have remained undiscovered. The shoals were visited briefly by many naturalists, but apart from Smith's work, they were never surveyed exhaustively, especially Colbert and Elk River shoals. Unfortunately, we have little or no ecological information about mussel assemblages at Muscle Shoals, including estimates of density or species relative abundance. Smith kept detailed field notes, but these have apparently been lost (J. Williams, personal communication).

The density of mussels was likely similar to other favorable locations in rivers throughout North America because density is ultimately limited by physical space. However, the exceptional diversity is explained by unique features of the habitat as well as the biogeographical location of the shoals. First, simply because of their size, the shoals evidently provided a heterogeneous mixture of habitat types, as noted by Smith: "There are marked differences in . . . different parts of the shoals. . . . A species which is very rare in one place is common in another and some kinds are confined to backwaters or to rock reefs, etc." The extensive, shallow shoals may have created habitat for small-stream species not normally found in large rivers (e.g., *Lampsilis virescens, Medionidus conradicus, Villosa iris, V. taeniata*; Ortmann 1925; van der Schalie 1939b; Hughes and Parmalee 1999; Section 4.1.D.4). Second, Muscle Shoals lies at the

(*continued*)

Box 10.1 (continued)

boundary between the uplands of the Appalachian Plateaus and the lowlands of the East Gulf Coastal Plain physiographic regions and has physical and biological characteristics of both (Section 4.1.D.3). This unusual juxtaposition of upland and lowland habitats is demonstrated by the bald cypress (*Taxodium distichum*), which reaches its upstream limit in the Tennessee River at Muscle Shoals (Shaler 1887) but occurs in this area adjacent to swift, rocky shoals, unlike its typical occurrence in swamps elsewhere in its range. Finally, Muscle Shoals represents a contact zone between the two richest mussel faunal provinces on Earth, the Tennessee–Cumberland and the Ohioan provinces (Chapter 3). Although these two faunas share many species, Muscle Shoals represented the historical downstream limit for most Tennessee–Cumberland species and the upstream limit for many Ohioan species (Ortmann 1924c, 1925; Stansbery 1964); this point represents a similar boundary for the distribution of many fish species (Boschung and Mayden 2004). The mingling of disparate habitats and two diverse faunas, combined with the sheer immensity of Muscle Shoals, resulted in the richest freshwater bivalve fauna ever seen.

Despite its beauty and spectacular fauna, Muscle Shoals was doomed from the beginning of European settlement because it formed an almost complete barrier to navigation, which, owing to its central location in the Tennessee River, effectively isolated the upper river: "[The shoals] . . . were of no earthly benefit, except to the mussels that loved these shallow waters" (Davidson 1946, 285). Efforts to overcome this obstacle began in the 1830s with the construction of a canal adjacent to but separated from the river (McGregor 2002). This canal was finally operational by the early 1900s but left the shoals themselves intact and, in fact, provided H. H. Smith with ready access by small boat to different parts of the shoals (Bryant Walker Correspondence). The canal was an impressive engineering feat, with 12 locks (including locks at Elk River and Colbert Shoals) and an aqueduct that carried river traffic *over* a major tributary entering the river from the north (Shoal Creek; Winn 1978). However, the canal proved inadequate to provide unrestricted navigation (Davidson 1946). Wilson Dam was completed in 1924 on the lower end of Little Muscle Shoals for the dual purposes of navigation and hydroelectric power generation and inundated most of Little and Big Muscle Shoals (Ortmann 1924c). Even though it is 42 m high, because of the steep gradient in this section of the river, Wilson Dam formed a pool only about 32 km long, leaving intact Elk River Shoals upstream and Colbert Shoals and a short section of Little Muscle Shoals below the dam. Arnold Ortmann collected at the remnants of Little Muscle Shoals during this short respite, and this area continued to support a diverse fauna (Ortmann 1925). Soon after creation of the Tennessee Valley Authority (inspired by the success of Wilson Dam), construction of Wheeler Dam (1936) upstream of Wilson, and Pickwick Dam (1938) downstream, inundated the remainder of Muscle Shoals.

The main portion of Muscle Shoals now lies beneath more than 6 m of silt accumulated at the bottom of Wilson Reservoir (Stansbery 1970). Nevertheless, even today, one can get a sense of what Muscle Shoals was like by visiting the Tennessee

River in the first few kilometers below Wilson Dam. The shoals are inundated by backwaters from Pickwick Dam, but the river here remains swift and relatively shallow (often less than 2 m deep), even wadeable in spots, and several islands and rock ledges can still be seen, all framed by wooded, limestone bluffs. These riverine habitats are highly altered by impoundment and operation of the hydroelectric dam (Section 10.3.C), but they continue to support a remarkably diverse and abundant mussel fauna of about 40 species (Garner and McGregor 2001; J. Garner, personal communication). However, assemblage composition is radically different from the preimpoundment fauna. Only 32 species of the original fauna remain, and with few exceptions, these are widespread species that have adapted to impoundment elsewhere in their range. Some of these species appear to have increased markedly in abundance since impoundment, and an additional eight impoundment-tolerant species have colonized the area. Most significantly, species that apparently depended on shoal habitats have disappeared, including most species endemic to the Tennessee–Cumberland province and all species of *Epioblasma*. There are still lots of mussels at Muscle Shoals, but the distinctiveness and the "glory of the mussel shoals" (Ortmann 1924c, 566) are gone.

There is a long-standing controversy over the currently accepted spelling "Muscle Shoals" versus the seemingly more appropriate "Mussel Shoals" (e.g., Ortmann 1924c; Dexter 1961). The spelling "Muscle" has been explained as either a reference to the muscle required to paddle a boat through the shoals, an archaic spelling of "mussel," or a simple clerical error (Isom 1971; Winn 1978). Regardless, "Muscle Shoals was always, surely, first of all the place of the mussels" (Davidson 1946, 23).

ebonyshell, *Reginaia apalachicola*, is present in pre-Columbian shell middens but was never encountered by early naturalists (Haag 2009b). This species persisted as late as the 1300s, but whether it went extinct in prehistoric or early historic times is unknown (Williams and Fradkin 1999). At local scales, collections of early naturalists yielded an average of 95 percent of species present in prehistoric middens at the same sites, and discrepancies between these samples are better explained by sampling error than by localized species extinctions (Haag 2009b). Furthermore, no consistent trends in species richness or evenness are seen between temporally successive prehistoric midden samples at single sites (Haag 2009b). Overall, mussel assemblages appear to have been relatively stable for thousands of years.

The only evidence of significant changes in mussel assemblages during prehistory is a steady decline in the relative abundance of *Epioblasma* spp. (Figure 10.2). The rate of decline accelerated after widespread adoption of maize agriculture about 1,000 years ago, suggesting that intensification of human disturbance exerted substantial pressures on aquatic habitats (Peacock et al. 2005), but it is unknown if this decline simply reflects long-term, natural changes in mussel assemblages. Nevertheless, all

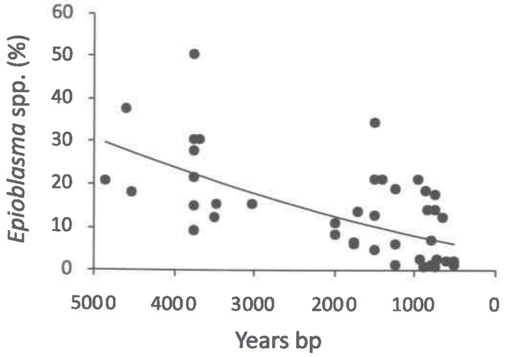


Figure 10.2. Decline in relative abundance of *Epioblasma* spp. in the eastern United States prior to European colonization; bp = before present (from Peacock et al. 2005).

species of *Epioblasma* survived to historical times, and many remained abundant until later human impacts.

Human harvest of shellfish likely occurred according to an optimal foraging model, in which harvest shifted as local stocks became depleted but well before they were extirpated completely (Raab 1992). Even if human land use had measurable effects on prehistoric mussel assemblages, these impacts also were transient in nature, allowing local populations to recover quickly via immigration from large populations elsewhere in the interconnected river landscape. By the time of European colonization, the North American mussel fauna remained intact even after thousands of years of coexistence with humans.

10.2.B. Early historical impacts

> It is generally known that the advance of civilization in a country is connected with a retreat and the disappearance of the indigenous fauna . . . yet these records chiefly concern the more highly developed forms of life (mammals or vertebrates in general), which preeminently attract attention. But there are many other forms of animal life, chiefly among the invertebrates, which suffer the same fate. Such cases generally are not noticed, but students particularly interested in such groups often have reason to deplore the disappearance of interesting creatures, which used to be abundant.
>
> – *Ortmann 1909,1*

Major changes to aquatic ecosystems commenced soon after European colonization of North America. Construction of small dams to power textile mills, gristmills, and sawmills began in New England by the mid-1600s, and by 1850, there were 500–1,000 mill dams in Ohio alone (Trautman 1981; Graf 1999). Discharge of tannery, brewery, slaughterhouse, and lumber mill wastes into streams occurred widely prior to 1850 (Trautman 1981; Anfinson 2003), and effects of nonpoint source pollution also were noted relatively early. Aggradation of the upper Mississippi riverbed was reported by 1867 and attributed to silt from recently cleared agricultural lands, bank erosion from steamboat wakes, and loss of riparian vegetation (Anfinson 2003). In the early 1800s, clearing of the highly erodible soils of the Deep South for cotton production resulted in massive erosion; during this time, the Chattahoochee River, Georgia, was reported at times to be so "stifled by mud" that it caused fish kills (Willoughby 1999). Simultaneously, reductions in spring permanency and low-flow stream discharge were attributed to forest clearing and wetland drainage (Trautman 1981).

Effects of these early impacts on mussels is poorly known. Mill dams surely destroyed mussel habitat locally and disrupted movements of host fishes, especially anadromous or migratory species (Watters 1996; Section 10.5.A). In the Erie Canal, New York, the giant floater, *Pyganodon grandis*, was reported greatly reduced in abundance "probably on account of chemical contamination from the gas works and armory at Ilion" (Lewis 1868, 245). By 1858, a decline in mussel abundance and species richness in the Scioto River, Ohio, was blamed on sedimentation and reduction in stream discharge from forest clearing (Stansbery 1970, citing Higgins 1858), and the extinction of *Reginaia apalachicola* in the Apalachicola River system was attributed potentially to sedimentation from cotton production (Williams and Fradkin 1999). When hogs were run on free range, they were considered a major threat to mussels (Kunz 1898; Smith 1899). Rafinesque (1820, 12) reported that "hogs are very fond of them [mussels], – herds of these animals are often seen searching for them in the rivers, and are devoured by them with avidity, notwithstanding the hard thick shell of many species." In Europe, mussels were historically an important food source for pigs, which were allowed to feed along riverbanks throughout the year (Tudorancea 1972).

The range and severity of human insults to streams and lakes accelerated rapidly with the Industrial Revolution after the 1860s. With little environmental regulation, industrial wastes were discharged directly into rivers, causing widespread but local elimination of mussels and other organisms (Rhoads 1899; Simpson 1899; Smith 1899; Ortmann 1918b; Remington and Clench 1925). By 1904, in the Ohio River and lower Allegheny and Monongahela rivers near Pittsburgh, "Unionidae have disappeared long ago. . . . The injurious substances discharged into the river . . . are simply amazing, and render the river entirely unfit for life; for thirty miles and more below there is not a mussel, not a crawfish, nor a fish able to live in this water" (Ortmann 1909b, 104). Drainage of acidic water formed by oxidation of sulfides in mines decimated mussel faunas in some areas (Ortmann 1909b; Wilson and Clark 1914). In the late 1800s, the Monongahela River, Pennsylvania, was so acidic at times from coal mine drainage that factories along the river had to suspend operations because the water corroded steam boilers, and railroad yards were forced to neutralize the water in large vats before using it in locomotives (Rhoads 1899).

Development of municipal sewer systems in the late 1800s resulted in point source discharge of raw sewage into streams. Small or dispersed volumes of sewage were not considered harmful to aquatic organisms, including mussels (Ortmann 1909b), but large, concentrated volumes of sewage associated with large cities resulted in severe reductions in dissolved oxygen from microbial respiration. An exceptional example was in the Illinois River, into which virtually all raw sewage and industrial waste from Chicago was diverted after 1900 via the "Chicago Sanitary and Ship Canal." In the upper river in 1912, "the water . . . was grayish, sloppy, and everywhere clouded with tufts of *Sphaerotilus* and *Carchesium* [colonial bacteria and protozoans commonly associated with sewage]. The odor was continuously foul, with a distinct privy smell. . . . Bubbles of gas were continually breaking at the surface . . . putrescent masses of soft, grayish black, mucky matter, from the diameter of a walnut to that of a milkpan, were floating on the surface" (Forbes and Richardson 1913, 507). Dissolved oxygen was as low as 0 mg/L, eliminating all mussels (38 species) from nearly 200 km of the river by 1920, and mussels remained absent in this section until at least the late 1960s (Starrett 1971).

Apparent negative impacts on mussels of sedimentation and other aspects of land clearing continued to be noted widely (e.g., Remington and Clench 1925; Ellis 1931; Goodrich 1931a; Isely 1931; van der Schalie 1938b). Sedimentation was proposed to impact mussels primarily by "smothering" but also by decomposition of organic sediments (reducing dissolved oxygen) and reducing food concentration via decreased light penetration and algal productivity (Headlee 1906; Ellis 1936). A more unusual and dramatic impact of land clearing was reported in the North Fork of the Yellow River, Indiana, where all mussels and most other aquatic organisms were killed when drained marshland adjacent to the stream was burned, "changing the water, for the time being, into a sort of lye" (Wilson and Clark 1912, 8).

10.2.C. Commercial harvest

Harvest of mussels for pearls and the button industry represented an enormous impact to mussel populations across much of North America. Large-scale pearl harvest began in the 1850s and was perhaps the first widespread historical impact to mussels (Section 9.3). Pearl hunters nearly exterminated the eastern pearlshell, *Margaritifera margaritifera*, in Pennsylvania by the early 1900s (Ortmann 1919), and in other localities, mussel beds were reported as "nearly or entirely exhausted" (Kunz 1898, 329). Local reduction in mussel abundance was evident even in larger streams. Although mussels were generally abundant in the Green River, Kentucky, in the 1920s, at one site, "most of the Unionidae have been killed here by pearl-hunters," (Ortmann 1926, 169) and in the Cumberland River, pearlers had accumulated shell piles "four and five feet high" (Clench 1925, 72). Large shell piles from pearling were common along rivers in the central United States in the early 1900s (e.g., Boepple and Coker 1912; Clark and Wilson 1912; Wilson and Clark 1912, 1914; Coker and Southall 1915). In some cases, pearling may have had indirect effects on mussel habitat. In the Clinch River, Tennessee, pearlers were reported to work "a plow drawn by a strong team" through the shoals to expose buried mussels (Boepple and Coker 1912, 10).

Although locally severe, impacts of pearling paled in comparison to harvest for the button industry (Section 9.4). Dredging and brailing may have negatively affected stream habitat, but by far the largest impact was direct mortality. During the industry's peak year of 1912, the reported harvest of 50,000 tons represented nearly 500 million mussels (Coker 1919). Assuming an average harvest of 20,000 tons/yr from 1895 to 1950 and 9,800 mussels/ton (Coker 1919), the button industry resulted in mortality of at least 11 billion mussels. Not surprisingly, mussel abundance was drastically reduced in many streams for years after cessation of harvest (Anthony and Downing 2001).

10.2.D. State of the fauna in the early 1920s

By the 1920s, the mussel fauna of North America had suffered from a staggering array of impacts, resulting in drastic reduction or complete elimination of mussels from extensive stream reaches. Remarkably, no species extinctions due to human impacts are documented prior to the 1920s. Along with *Reginaia apalachicola*, the Rio Grande monkeyface, *Quadrula couchiana*, is one of the few species that apparently disappeared prior to the 1920s. This species was endemic to the Rio Grande system in Texas and Chihuahua, Mexico, but only a few living individuals were ever found, the last in 1898. Its initial rarity and remote habitat suggests *Q. couchiana* went extinct naturally rather than from human impacts (Howells 2001). Apart from these exceptions, North American mussel diversity was largely undiminished in the early 1900s.

Harvest by the button industry and, later, the cultured pearl industry (Section 9.5) is widely and correctly cited as a major threat to mussel populations (e.g., Neves et al. 1997; Anthony and Downing 2001). However, like prehistoric harvest, shellers for the button industry moved to new localities when mussel abundance declined such that harvest was no longer cost-effective, leaving residual populations in a mostly intact habitat. This phenomenon was realized early by Simpson (1899, 288): "It is not likely that pearl-hunters or button-makers will ever completely exterminate any of the species . . . especially where they are not abundant enough to make it pay to collect." Simpson's prediction was correct. Of the approximately 50 species used to some extent in button manufacture (Anthony and Downing 2001), none are extinct and only 38 percent are currently of conservation concern, compared with 70 percent for the North American fauna as a whole (Haag 2009b). Furthermore, the most heavily targeted button species are considered currently stable even after decades of intensive harvest (e.g., *Actinonaias ligamentina, Amblema plicata, Lampsilis siliquoidea, L. teres, Megalonaias nervosa, Quadrula pustulosa, Q. quadrula, Reginaia ebena*; based on conservation assessment of Williams et al. 1993). Despite intense pressure on populations, there is no evidence that commercial harvest in the early 1900s propelled species into a sustained, downward spiral of abundance leading to imperilment or extinction.

“Conditions are fair, in some parts splendid; but there are already polluted streams, in which the fauna is gone”.

– *Ortmann 1918b, 525*

Ortmann’s description of the Tennessee River system summarized the general state of the North American mussel fauna in the early 1900s. Many streams were in deplorable condition or had sustained massive mussel harvest, but these river segments were scattered throughout a largely interconnected river landscape. Mill dams were primarily on smaller streams and did not interrupt the continuity of most river systems (Walter and Merritts 2008). The enormous reproductive potential of mussel populations remaining in high-quality stream reaches allowed recolonization of impacted areas following abatement of those impacts. As suggested by the rapid increase in mussel abundance after cessation of harvest in Lake Pepin and the Tennessee River (Sections 9.4 and 9.5), mussel populations likely recovered naturally from shifting impacts such as maize agriculture, human harvest, sedimentation, and water pollution. In the Mississippian region, the distribution of species richness remained similar to the preindustrial landscape, with greatest diversity in large rivers that provided dispersal corridors throughout watersheds. Despite the intensity of human impacts, overall, the North American mussel fauna remained intact until 1924.

10.3. Systematic habitat destruction and the first extinction wave, 1924–1984

10.3.A. Dams and stream channelization

The building of dams . . . has a deteriorating effect upon mussel life, and . . . surely will increase in the future.

– *Ortmann 1918b*

Many [streams] are being dammed for power . . . so they should be surveyed as soon as possible.

– *Remington and Clench 1925*

Biologists in the first quarter of the twentieth century foresaw the increase in construction of large dams but could have hardly imagined the extent to which the North American river landscape would be utterly transformed within a few decades. “Improvements” to large rivers for navigation had been under the oversight of the U.S. Army Corps of Engineers (USACOE) since its inception in 1802, but federal funding for large-scale, interstate river projects was controversial and often nonexistent; consequently, prior to the 1920s, large hydroelectric or storage dams, and even many navigation locks and canals, were constructed mainly by private businesses or local governments (Billington et al. 2005). For example, the Keokuk Dam on the

Mississippi River – one of the largest river development projects in the world at its completion in 1913 – was authorized by Congress and overseen by the USACOE but built with private capital (Scarpino 1985). This changed rapidly by the 1920s and 1930s in response to the transportation, power, and water needs of a rapidly industrializing society and to a series of widespread and devastating floods.

Muscle Shoals was a serious impediment to navigation on the Tennessee River since European settlement and limited industrial development of the region (Box 10.1). The culmination of efforts to overcome this obstacle came with authorization of Wilson Dam in 1918, but the impetus for this project was hydroelectric power production necessary for manufacture of munitions for World War I. However, with the end of the war, the unfinished project languished. Automobile manufacturer Henry Ford proposed to purchase the site from the federal government and invigorate the depressed region by building a 120-km-long city and industrial center; this proposal unleashed a frenzy of excitement and speculation. The Ford offer ultimately fell through, and the dam remained in federal hands and was largely completed by 1924 (Hubbard 1961). Completion of Wilson Dam simultaneously drowned the richest freshwater mussel assemblage on Earth and unleashed a frenzy of dam construction across North America.

Wilson Dam was hailed as one of the first federal, multipurpose dams, with benefits of navigation, power generation, and flood control. In the Depression-wracked 1930s, the success of Wilson Dam was largely responsible for creation of the Tennessee Valley Authority (TVA) in 1933. TVA was charged with economic development of the region by providing river improvements with an array of benefits similar to those provided by Wilson Dam (Hubbard 1961; Billington et al. 2005). Simultaneously, other federal legislation set the stage for similar river modifications nationwide. Ironically, the Rivers and Harbors Act of 1899 provided the first environmental protection for water quality by prohibiting discharge of "refuse" into rivers, but later versions of the act authorized comprehensive navigation improvements to large rivers (Anfinson 2003; Downing et al. 2003). In response to catastrophic floods in the 1920s and 1930s, the Flood Control Acts of 1936 and 1937 placed civil engineering projects on rivers entirely under the jurisdiction of the USACOE (Billington et al. 2005).

These acts initiated systematic engineering surveys of rivers, resulting in thousands of authorized dam sites and other improvement projects, and construction began almost immediately. Efforts to canalize the entire Ohio River had begun previously and were completed by 1929. The upper Mississippi River was impounded entirely by 1940, the Tennessee River by 1944 (Etnier and Starnes 1993; Anfinson 2003), and comprehensive navigation projects were completed on many other large rivers. Thousands of water storage, hydroelectric, or flood control reservoirs were built throughout North America. Reservoir construction peaked in the continental United States between the 1950s and 1970s, and more than 75,000 dams now exist (Graf 1999). In the Tennessee River system alone, there were 53 large dams (impounding more than 40 ha) by 1979, and 615 dams more than 2 m high or with more than 18,500 m^3 storage capacity (Etnier and Starnes 1993; Graf 1999).

In addition to dams, channelization of streams to drain wet, flat lands for agriculture drastically modified aquatic habitats across extensive areas, especially in the midwestern and southeastern United States. Channelization directly affects a total of about 300,000 stream km in the United States (Schoof 1980). By the 1960s, 80 to 100 percent of total stream length was channelized and straightened in some Illinois watersheds (Mattingly et al. 1993), and in western Mississippi, channelization reduced by 80 percent the number of stream segments capable of supporting a fishery of any kind (Jackson and Jackson 1989).

River modification projects culminated in 1984 with completion of the massive Tennessee–Tombigbee Waterway (TTW) in Alabama and Mississippi, the largest water development project ever undertaken in the United States. Authorized in 1946, but not begun until 1972, the TTW included construction of 10 locks and dams and channelization of 377 km of the original river channel to provide a more direct transportation route from the Tennessee River to the Gulf of Mexico (Tennessee–Tombigbee Waterway Development Authority 2007). The TTW destroyed the Tombigbee River, which was the last unpolluted, free-flowing large stream in the Mobile Basin and one of the most diverse stream systems in North America (Abell et al. 2000).

10.3.B. Other impacts

During the period of systematic habitat destruction, the mussel fauna continued to experience a wide range of severe impacts similar to those of the previous era. For example, discharge of brine wastes from oil wells in the late 1950s raised the salinity of the Green River, Kentucky, 100 times from natural levels of 0.01 to over 1 parts per thousand, which is in the range of brackish water, causing massive mussel mortality (Williams 1969). In 1967 and 1970, massive industrial chemical spills on the Clinch River, Virginia, eliminated all mollusks for more than 18 river km, reduced mussel abundance for more than 124 km, and killed all fishes for more than 100 km (USFWS 1983; Jenkins and Burkhead 1994). In Kansas, Missouri, and Oklahoma, lead and zinc mining conducted from 1850 to 1970 eliminated or drastically reduced mussel populations throughout large areas, and residual contamination of sediments, surface water, and groundwater continues to impact these streams (Angelo et al. 2007).

Concentrated discharge of raw sewage continued to be widespread. Like those in much of the United States, virtually all cities on the Chattahoochee River discharged raw sewage into the river until the mid-1960s, and most did not have secondary treatment until a decade later (Willoughby 1999). The most famous example of this period is Lake Erie, which was grossly polluted by municipal and industrial wastes by the 1960s. In 1969, only 3 of 62 public beaches were rated safe for swimming, and a tributary, the Cuyahoga River, was described as "chocolate-brown, oily, bubbling with subsurface gases, it oozes rather than flows"; the river was so oily it caught fire several times (*Time* 1969). Extremely low dissolved oxygen levels in the lake resulted in a complete shift in the benthic fauna, including a marked decline in mussel abundance (Beeton 1965; Nalepa et al. 1991), and the plight of the lake became a catalyst for the growing environmental movement.

10.3.C. The aftermath of systematic habitat destruction

By 1984, the river landscape of North America was profoundly altered. Unlike previous human impacts, habitat destruction from 1924 to 1984 was systematic and backed by the full force of the U.S. government. The most obvious result was an almost complete elimination of free-flowing large rivers in some areas. In addition to direct loss of riverine habitat by impoundment, discharge from multipurpose dams fundamentally altered seasonal flow, temperature, and oxygen regimes, eliminating or negatively impacting mussel faunas in many streams (Harman 1974; Layzer et al. 1993; Heinricher and Layzer 1999; McMurray et al. 1999). For example, a 128 km section of the Cumberland River in Kentucky remained unimpounded but lost its fauna of more than 50 mussel species due to chronically depressed water temperatures (annual maximum less than 20°C) and dramatic, nonseasonal fluctuations in flow caused by a large hydroelectric and flood-control dam upstream (Miller et al. 1984). Particularly hard hit by these impacts was the Mississippian region, which contained all of the 20 most diverse mussel assemblages on the continent (Table 3.2) and included many obligate large-river species; 15 of these river systems lost nearly all free-flowing large-river habitat. Several river systems in the Atlantic and Eastern Gulf regions are only moderately influenced by impoundment and have long, free-flowing main stem reaches (e.g., Altamaha, Delaware, Hudson, Pee Dee, Suwannee, Susquehanna; Benke 1990; Dynesius and Nilsson 1994), but these river systems have few or no obligate large-river mussel species (Chapter 4).

A less obvious but equally important outcome of systematic habitat alteration was the fragmentation of most river systems. The more than 75,000 dams in the United States severely disrupt the continuity of the river landscape and affect to some extent every major watershed in the country (Graf 1999). Density of dams by watershed area is highest in New England, with a dam every 43 km^2, but dam density is greater than one per 200 km^2 in most of the eastern and central United States (Graf 1999). East of and including the Mississippi River basin, there are only about 34 river segments longer than 200 km that remain free flowing and without major physical alterations (Benke 1990). The availability of high-quality stream habitat was reduced further by other, unrelated impacts. For example, the Cahaba River, Alabama, remains largely free flowing but lost much of its mussel fauna to municipal and industrial pollution. By 1982, only 1.9 percent of the total stream length in the contiguous United States was unaffected by flow regulation or impoundment and continued to support outstanding natural resource values, and these remaining high-quality segments were small and highly isolated (Benke 1990).

Systematic habitat destruction overlaid onto a wide variety of other impacts resulted in the first mass extinction of North American freshwater mussels. By the 1990s, at least 25 species had become extinct (Table 10.1). For most of these species, extinction is attributable to specific events. At least 12 were eliminated directly by dams, which destroyed or modified habitats throughout the entire geographic range of the species. The leafshell, *Epioblasma flexuosa*, and round combshell, *E. personata*, occurred only in the main channel of the Ohio River and the lower reaches of a few large tributaries. *Epioblasma flexuosa* was not seen after impoundment of the Ohio River (Stansbery 1970, 1971). Ortmann was apparently the last person to see *E. personata*, at the remnants of Muscle Shoals in 1924 (Ortmann 1925), but this section of the Tennessee River was highly influenced by discharge from Wilson Dam and was impounded in 1938 (Box 10.1). By the 1940s, dams had reduced the forkshell, *E. lewisii*, to one population in the Cumberland River, Kentucky, and one in the Caney Fork of the Cumberland, in Tennessee (Neel and Allen 1964; Layzer et al. 1993). Construction of Wolf Creek (1950) and Center Hill dams (1948), respectively, eliminated those populations by inundation and cold-water discharge from the dams. Similarly, by the 1950s, the entire geographic range of *E. arcaeformis*, *E. florentina florentina*, *E. propinqua*, and *E. stewardsoni* was either inundated or modified by hydroelectric dam discharge (Stansbery 1970; Johnson 1978). The flat pigtoe, *Pleurobema marshalli*, occurred only in the main channel of the Tombigbee River, and the species has not been seen since destruction of the river by the TTW (Williams et al. 2008).

Other species succumbed to a combination of systematic habitat destruction and unrelated impacts. By 1967, impoundment, stream channelization, acid mine drainage, and other impacts had reduced the narrow catspaw, *Epioblasma lenior*, and turgid blossom, *E. turgidula*, to single populations in the Stones River and Duck River, respectively, both in Tennessee (Stansbery 1970, 1976). Construction of J. Percy Priest Reservoir (Stones River) in 1967 and Normandy Reservoir (Duck River) in 1976 eliminated the last habitat for these species. By the late 1960s, dams had destroyed all habitat for the acornshell, *Epioblasma haysiana*, and the green blossom, *E. torulosa gubernaculum*, except for a single, free-flowing reach of the Clinch River in Tennessee and Virginia, where small, localized populations persisted. Massive chemical spills in this reach in 1967 and 1970 reduced the abundance of all mussel species (Section 10.3.B), but only those with larger initial population sizes or wider distributions in the river survived; *E. haysiana* was never seen again, and only two individuals of *E. torulosa gubernaculum* were found subsequently, one in 1975 and the last in 1982 (USFWS 1983).

For only a few species are the specific causes of extinction difficult to pinpoint, but small natural ranges and initial population sizes appear to have

Table 10.1. *Timeline of mussel species extinctions in North America in the twentieth century*

Species	Time of Extinction	Cause of Extinction	Life History Strategy	Last Known Occurrence
Quadrula couchiana	early 1900s	3	E	Rio Grande, TX
Epioblasma flexuosa	1920s–1930s	1	P	Ohio River, KY
Epioblasma personata	1920s–1930s	1	P	Tennessee River, AL
Epioblasma propinqua	1936	1	P	Clinch River, TN
Alasmidonta wrightiana	1930s	2,3	P	Ochlocknee River, FL
Epioblasma sampsoni	1930s–1940s	2	P	Wabash River, IL/IN
Epioblasma arcaeformis	1940s	1	P	Holston River, TN
Epioblasma f. florentina	1940s	1	P	Holston River, TN
Epioblasma stewardsoni	1940s	1	P	Holston River, TN
Epioblasma lewisii	1950	1	P	Cumberland River, KY
Alasmidonta mccordi	1964	1	P	Coosa River, AL
Epioblasma lenior	1967	1	P	Stones River, TN
Epioblasma biemarginata	1970	2	P	Elk River, TN
Epioblasma haysiana	1970	2	P	Clinch River, VA
Epioblasma turgidula	1976	1	P	Duck River, TN
Epioblasma othcaloogensis	1970s	2	P	Conasauga River, GA
Epioblasma t. torulosa	1970s	1	P	Kanawha River, WV
Lampsilis binominata	1970s	2,3	P	Flint River, GA
Quadrula mitchelli[a]	1970s	3	E	rivers in central TX
Pleurobema marshalli	1984	1	E	Tombigbee River, AL
Epioblasma metastriata	1980s	2	P	Conasauga River, GA
Epioblasma torulosa gubernaculum	1980s	2	P	Clinch River, TN
Quadrula stapes	1980s	2	E	Sipsey River, AL
Epioblasma florentina curtisii	1990s	3	P	Little Black River, MO
Pleurobema curtum	1990s	2	E	East Fork Tombigbee River, MS

Note: Time of extinction refers to probable functional extinction, defined as when all habitat was destroyed or when the species was last seen (see Haag 2009b). Taxa of uncertain taxonomic status (e.g., *Alasmidonta robusta*, *Pleurobema* spp., *Quadrula tuberosa*) are omitted from the list (see text). Causes of extinctions: 1, direct loss of all habitat by stream impoundment; 2, indirect effects of fragmentation due to habitat destruction; 3, small original range and nonimpoundment-related habitat degradation. Life history strategies are inferred from information on congeners: E, equilibrium strategist; P, periodic strategist (see Table 6.3). Adapted from Haag (2009b).

[a] *Q. mitchelli* was rediscovered in Texas in 2012 (C. Randklev, in press).

predisposed them to extinction. The lined-pocketbook, *Lampsilis binominata*, was endemic to the Apalachicola River system, occurring mostly in the main channels of the Chattahoochee and Flint rivers, but it was rare even in historical collections (Brim Box and Williams 2000). Mussels were nearly eliminated from the Chattahoochee

River by the 1920s from dams, industrial and municipal wastes, and perhaps sedimentation (Clench and Turner 1956; Sections 10.2.B and 10.3.B). The Flint River continues to support mussel populations, but these also are reduced and fragmented by dams and expansion of the Atlanta urban area (Brim Box and Williams 2000; Gillies et al. 2003). This combination of impacts likely reduced population sizes of rare species like *L. binominata* below viable levels (Section 10.6.D).

Systematic habitat destruction led directly or indirectly to extinction of about 8 percent of the North American fauna. The genus *Epioblasma* suffered disproportionately. Of the 25 recognized species and subspecies, 17 (68%) were extinct by the 1990s, and all surviving species are currently imperiled. The true number of extinctions during this era may never be known because of taxonomic uncertainty regarding some species and the potential for unrecognized cryptic diversity, but the total is likely well over 30 species. A bewildering array of shell forms of *Pleurobema* occurred only in the main channel of the Coosa River, Alabama, which is now entirely impounded or otherwise modified by dams. According to a recent concept of this group, at least three species are now extinct (*P. fibuloides*, *P. hartmanianum*, and *P. stabilis*; Williams et al. 2008). Other presumed extinct taxa are represented in historical collections by only a few individuals but have not been collected in more than 50 years (e.g., *Alasmidonta robusta*, *Obovaria haddletoni*, *Pleurobema bournianum*, *Quadrula tuberosa*). It is not known whether these were distinct species or simply aberrant individuals of extant species (e.g., Clarke 1981b; Watters et al. 2009). Finally, genetic analyses have revealed previously unrecognized cryptic diversity in several species (e.g., Serb 2006; Jones and Neves 2010; Campbell and Lydeard 2012a), raising the possibility that other cryptic species have already become extinct. For most of these taxonomic issues, specimens of questionable taxa exist only as shells in museum collections, and tissues are not available. Unless techniques are perfected for extracting usable DNA from historical shell material, the true extent of this extinction event may never be known.

10.4. Attrition, 1984 to present

By the 1980s, the rate of dam construction slowed, water quality began to improve markedly in many rivers after passage of the U.S. Clean Water Act of 1972 (Knopman and Smith 1993; Lyon and Stein 2009), and the Endangered Species Act of 1973 afforded protection for many mussel species reduced to small populations. Nevertheless, mussel populations continued to decline dramatically. Overlaid on the fragmented stream system of North America was a continuing array of severe insults to remaining high-quality streams as well as a series of mysterious mussel declines that had no clear cause. These effects began well before 1984, but combined with fragmentation and isolation, they resulted in an accelerated erosion of mussel diversity even after the most intense era of systematic habitat destruction came to a close.

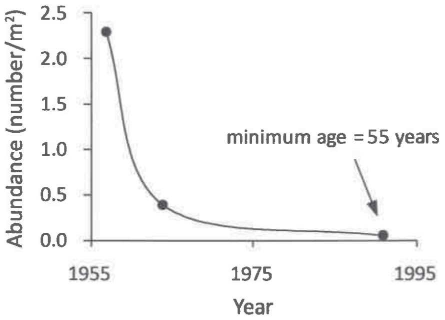


Figure 10.3. Abundance of the Ohio pigtoe, *Pleurobema cordatum*, in the Tennessee River, Alabama, following impoundment by Wheeler Reservoir in 1936 (data from Ahlstedt and McDonough 1993).

10.4.A. Delayed effects of systematic habitat destruction

Unlike deep, cold hydroelectric or storage reservoirs, rivers that were impounded primarily for navigation, such as the Alabama, lower Cumberland, upper Mississippi, Ohio, and Tennessee, retained riverine characteristics in some sections and continued to support sizeable mussel populations. These rivers lost all shallow shoal habitats, but tailwater reaches below dams retained relatively natural temperature and oxygen regimes, and flow was sufficient to keep gravel and sand substrates silt free (Voightlander and Poppe 1989). The ability to persist in these modified habitats differed greatly among species (Section 10.5.A.), but tailwater reaches often retained more than 50 percent of preimpoundment species richness (e.g., Casey 1987; Garner and McGregor 2001; Newton et al. 2011). However, recruitment of many remaining species effectively ceased because of elimination of host fishes or poor juvenile survival. These populations were composed exclusively of individuals that recruited prior to impoundment, and they declined steadily over time (Figure 10.3). In the Cumberland River, Tennessee, nonreproducing populations of *Cyprogenia stegaria, Dromus dromas, Epioblasma* spp., and *Obovaria retusa* persisted for at least 25 years after dam construction (Parmalee et al. 1980; Parmalee and Klippel 1982), and *E. torulosa torulosa* continued to be harvested by shellers in the lower Ohio River for 30 years after impoundment (Parmalee 1967). Mussel diversity in large rivers declined further as these relict individuals reached the end of their life spans (Section 10.5.A).

Channelization also resulted in delayed effects to streams beyond the channelized sections themselves. Channelization lowers the base level of a stream, which can initiate progressive upstream erosion, called *headcutting*, as the stream reestablishes a stable base level throughout the watershed. Headcutting is especially destructive and rapid in areas without bedrock or other controls on base level such as the Gulf Coastal Plain. In these regions, headcutting results in loss of stability and complete reconfiguration of the stream channel (Shields et al. 2000). Headcutting nearly eliminated mussel populations in many Coastal Plain streams (Hartfield 1993; Brown and Curole 1997). In the Buttahatchee River, Mississippi, a tributary of the Tombigbee River, a headcut initiated by dredging associated with the TTW continues to move upstream and now threatens the last population of the southern combshell, *Epioblasma penita* (Hartfield 1993).

10.4.B. Stream fragmentation and erosion of diversity from stochastic processes

Delayed effects of systematic habitat destruction also were manifested indirectly by the fragmentation of river systems. Because many remaining mussel populations were small and isolated from sources of recolonization, they were highly vulnerable to natural, chance events.

Population size fluctuates naturally because of *environmental stochasticity*, the unpredictable variation in environmental conditions. Environmental stochasticity affects all individuals in a population similarly; for example, drought can severely reduce mussel abundance in small streams (Section 4.1.D.1), and high-flow years can curtail recruitment (Section 7.3). Survival and reproduction also vary independently among individuals regardless of environmental conditions. This is called *demographic stochasticity* and refers to chance events such as variation in fertilization success among individuals or a juvenile mussel that happens to drop off a fish host in an unsuitable location. Demographic stochasticity generally cancels out and becomes inconsequential in large populations, but in small populations, a significant proportion of individuals may die or experience poor reproduction by chance (Kokko and Ebenhard 1996; Lande et al. 2003). These two random processes frequently interact in a positive feedback loop, which can lead to a downward spiral of abundance ending in population extinction (Lande 1998). For example, environmental stochasticity can reduce population size to a point where demographic stochasticity becomes important. Small populations are threatened further by loss of genetic variation, which can compromise the ability to adapt to changing environmental conditions (Franklin 1980), and in very small populations, inbreeding depression from the mating of closely related individuals can undermine most components of fitness, including metabolic efficiency, growth rate, reproductive success, and disease resistance (Gilpin and Soulé 1986).

In an interconnected landscape, local populations that have declined in abundance, become extinct, or experienced reduced genetic variability because of stochastic effects can recover by migration from other populations. This type of metapopulation structure – in which species exist as sets of local populations functioning independently but interconnected by migration – lessens the risks of species extinction due to chance events (Harrison and Taylor 1997). Systematic habitat destruction in North American streams effectively destroyed or greatly simplified mussel metapopulation structure and reduced or eliminated the potential for migration (see Strayer 2008), leaving remaining populations highly vulnerable to extinction even in the absence of additional human impacts.

The vulnerability of small populations to extinction is illustrated by many examples from the North American mussel fauna. Although stream impoundment and chemical spills were initially responsible for reducing *Epioblasma haysiana* and *E. torulosa gubernaculum* to single, small populations in the Clinch River (Section 10.3.C), environmental or demographic stochasticity were likely the final causes of extinction of these species. After completion of the TTW, the obligate large-river species, the black clubshell, *Pleurobema curtum*, and stirrupshell, *Quadrula stapes*, persisted only as single, small populations in the lower reaches of two major tributaries. These populations disappeared within 15 years of destruction of the Tombigbee River, suggesting that tributary populations were sinks sustained solely by immigration from the main river (Haag 2009b; Section 10.6.D). In the Green River, most species survived oil brine pollution in the 1950s (Section 10.3.B), but those that did not were rare even before the impact (e.g., *Hemistena lata, Leptodea leptodon, Villosa fabalis*; Ortmann 1926; Stansbery 1965), suggesting that severe reduction in abundance left these local populations vulnerable to stochastic effects.

Mussel populations in headwater streams isolated by impoundment are probably most consistently vulnerable to stochastic effects. The dynamic physical nature of these streams and their typically low mussel abundance suggest that environmental stochasticity plays a large role in limiting these populations (Chapter 8), and recovery from disturbance likely was dependent historically on recolonization from other streams. Headwater streams in Bankhead National Forest, Alabama, are isolated by a deep, hypolimnetic reservoir downstream constructed in 1961 (Haag and Warren 1998). In 2000, a severe drought reduced overall mussel abundance by an average of 75 percent and affected all species similarly (Haag and Warren 2008). All species are now at greater risk of local extinction due to stochastic events, but for those that were widespread and abundant in the forest prior to the drought, overall postdrought population sizes probably remained greater than 5,000. In contrast, species that were initially restricted to the lower reaches of larger streams were reduced to at most only a few hundred individuals, and the bleufer, *Potamilus purpuratus*, is apparently now extinct in the forest. This species can adapt to degraded habitats and remains common and widespread elsewhere in its range, suggesting that its local extinction was set into motion by isolation but finally precipitated by natural stochastic events occurring since dam construction.

Other isolated populations of common species are similarly at risk from stochastic processes. In the 1980s, the fragile papershell, *Leptodea fragilis*, disappeared from the Clinch and Powell rivers above Norris Reservoir, Tennessee (S. Ahlstedt, personal communication), and in 2009, only single individuals of the pink heelsplitter, *Potamilus alatus*, and pimpleback, *Quadrula pustulosa*, were found in the Powell River (Johnson et al. 2010a). These species were probably peripheral in the upper Clinch and Powell rivers (Ortmann 1918b), and impoundment of the lower sections of these rivers left populations small and isolated. Like *Potamilus purpuratus* in Bankhead National Forest, all three of these species are widely distributed and abundant elsewhere and often adapt to highly degraded habitats. The local extinction of otherwise common species emphasizes the pervasive threat of isolation and stochastic effects.

10.4.C. Other smoking guns

In addition to delayed effects of dams and channelization, mussel diversity in remaining high-quality tributaries continued to be lost to severe human impacts. Prior to 1990, the Little South Fork Cumberland River and Horselick Creek, Kentucky, supported two of the most important remnants of the diverse and endangered mussel fauna of the Cumberland River system. Over 15 years, chronic impacts from coal mining and oil extraction eliminated nearly all mussels from both streams, including some of the largest remaining populations of the little-wing pearlymussel, *Pegias fabula*, and Cumberland bean, *Villosa trabalis* (Haag and Warren 2004; Warren and Haag 2005). Similarly, coal mining effects continue to degrade the Clinch and Powell rivers, in Tennessee and Virginia, which harbor two of the most diverse mussel assemblages remaining on Earth (Diamond et al. 2002). Prior to 1998, a short section of the Clinch River in Virginia supported the largest remaining population of the golden riffleshell, *Epioblasma florentina aureola*. In August 1998, a tanker truck overturned, releasing 6,000 liters of chemical accelerant used in the manufacture of foam rubber into a tributary 160 m from its confluence with the Clinch River. The spill turned the river milky white and killed most invertebrates for 11 km downstream, including more than 18,000 mussels (Schmerfeld 2006). As a result, *E. florentina aureola* appears to be extirpated from the Clinch River and now persists only in a 2 km reach of a nearby tributary (Rogers et al. 2001). These streams were considered globally important conservation refugia for endangered mussels and fishes and were afforded protection accordingly under the U.S. Endangered Species Act. Extensive landownership by the U.S. Forest Service and the Nature Conservancy and designation as a Kentucky Wild River (Little South Fork) ostensibly provided additional protection (Warren and Haag 2005). Although severe impacts such as these are less common today than in previous eras, they continue despite multiple layers of environmental protection and regulation.

Invasive species are widely proposed as a factor in mussel declines, but for most, strong evidence of their widespread negative effects is lacking (Section 10.6.C). A dramatic exception is the zebra mussel, *Dreissena polymorpha*. Zebra mussels were introduced to Lake St. Clair in the mid-1980s, likely from transoceanic ships originating in freshwater or brackish European ports (Hebert et al. 1989). The ballast tanks of these ships contain millions of liters of water, and many other invasive aquatic species were introduced into the Great Lakes until replacement of freshwater ballast with saltwater at sea was required before entering North American freshwater ports (Ricciardi and MacIsaac 2000). Shortly after the appearance of *D. polymorpha*, a second species, the quagga mussel, *D. bugensis*, appeared in the Great Lakes in 1991 (Spidle et al. 1994).

Unlike other North American freshwater bivalves, *Dreissena* is epifaunal, attaching with byssal threads to the surface of hard substrates similar to marine mussels (e.g., *Mytilus*), and it has planktonic larvae. These traits allowed *Dreissena* to spread rapidly via larval drift and transport of attached adults on commercial and recreational vessels. In 1992, more than 1,000 live adult *Dreissena* were found on a barge dry-docked in Illinois. From the time of probable *Dreissena* attachment to dry-docking, the vessel traveled as much as 15,000 km throughout the Mississippi River system, during which mussels may have spawned or been dislodged several times (Keevin et al. 1992). By 1995, *Dreissena* was established throughout the Great Lakes, much of the Mississippi River system, the Hudson River, and numerous inland lakes, and it has now spread west of the Rocky Mountains to the southwestern United States (USGS 2011).

In the northern United States and Canada, *Dreissena* quickly became a dominant feature of benthic and planktonic assemblages. Benthic adults and juveniles covered literally all hard objects and reached densities of more than 100,000/m^2 (Figure 10.4). Filtering activities of these dense populations resulted in large declines in phytoplankton and small zooplankton and increases in water clarity from 20 to 100 percent, all of which had major, cascading effects on aquatic ecosystems (reviewed in Strayer 1999b).

Effects on native mussels were rapid and devastating. *Dreissena* larvae settle on any hard substrate, including native mussels and other *Dreissena*. *Dreissena* densities on native mussels are frequently 100–200 per individual (Figure 10.4) but can exceed 10,000, and the mass of attached *Dreissena* can be 3 times greater than its host (Hebert et al. 1991; Ricciardi et al. 1995; Martel et al. 2001). Heavy fouling by *Dreissena* may negatively affect native mussels by increasing costs of locomotion, interfering with valve closure, and causing toxic effects of high concentrations of waste products (Strayer 1999b). However, reduction in food availability by *Dreissena* filtering appears to be a primary mechanism because fouled native mussels have lower energy stores than nonfouled individuals (Haag et al. 1993), and mussel body condition decreases in heavily infested waters even when fouling intensity is low (Strayer 1999b). Native mussel populations were virtually eliminated in much of the Great Lakes, the St. Lawrence River system, and the Hudson River, where greater than 90 percent declines in mussel abundance occurred typically within 4 years of *Dreissena* colonization (Ricciardi et al. 1998).

The rapid spread of *Dreissena* was predicted to cause widespread native mussel extinctions or extirpations throughout North America, especially in the Mississippi River system (Ricciardi et al. 1998). However, the distribution of *Dreissena* in eastern North America stabilized somewhat by 1995, only 10 years after its initial appearance (Allen and Ramcharan 2001; USGS 2011). Although it spread quickly throughout

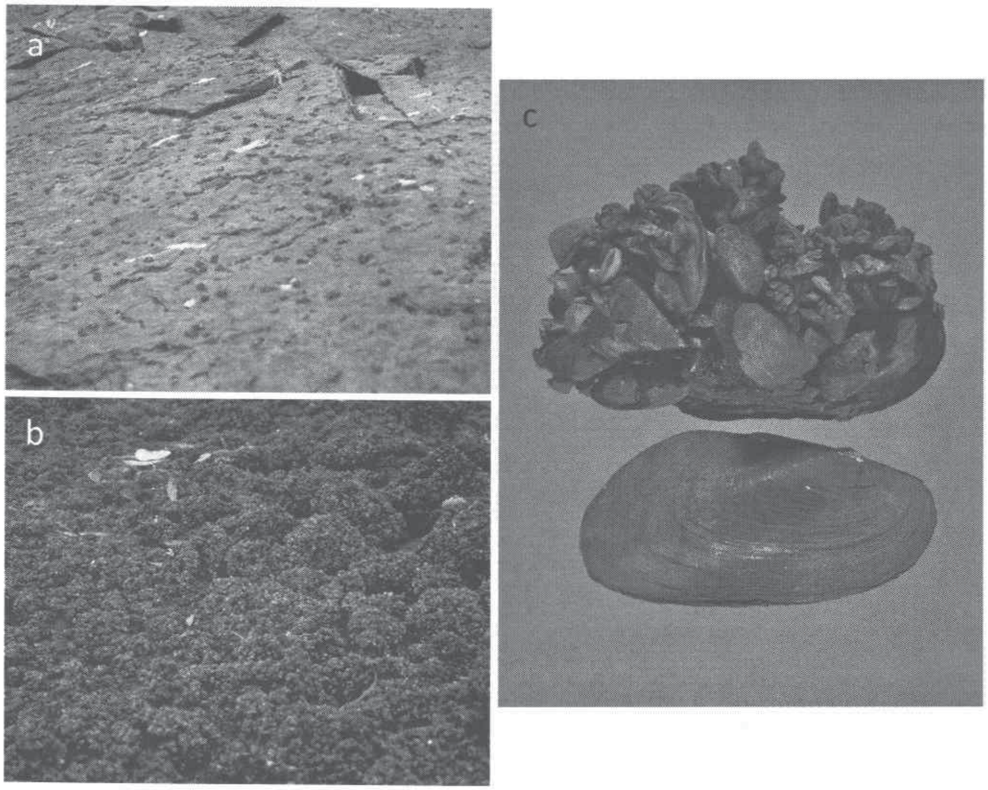


Figure 10.4. Infestation of zebra mussels (*Dreissena polymorpha*) in the Rideau River, Ontario. (a) Rocky substrates in 1994 during initial colonization showing scattered single individual *Dreissena*. (b) The same location 1 year later (1995) showing dense clusters of *Dreissena* covering all surfaces. (c) Change in *Dreissena* infestation on native eastern ellipito, *Elliptio complanata*, from 1994 to 1995 (all from Martel et al. 2001).

navigable waters of the Mississippi River basin, *Dreissena* has not reached high abundance south of about the Ohio River, even though it has been present in that region for nearly 20 years. For example, *Dreissena* has occurred at low or variable abundance in the lower Mississippi River and Tennessee River since 1994 and has not caused extensive native mussel mortality (J. Garner, personal communication), in marked contrast to the rapid, exponential population growth seen soon after colonization in northern waters. The numerous attempts to predict or model *Dreissena* distribution in North America have focused primarily on presence or absence and have not considered controls on abundance, which may strongly mediate its environmental effects (e.g., Strayer 1991; Drake and Bossenbroek 2004; Casagrandi et al. 2007; Whittier et al. 2008). Southern populations may be limited by higher summer temperatures and thus represent sink populations sustained primarily by continual reintroductions via river traffic or larval transport from northern populations (Allen et al. 1999; Elderkin and Klerks 2005). High concentrations of nutrients or suspended sediment and low concentrations of calcium and other ions also appear to limit *Dreissena* populations (Strayer 1999b; Allen and Ramcharan 2001; Whittier et al. 2008).

In addition to physiological constraints, the planktonic larval stage of *Dreissena* may limit its distribution and abundance and hence its effects on native mussels. Few freshwater riverine organisms have planktonic larvae because unidirectional flow continually depletes populations. Juveniles of another invasive bivalve, *Corbicula*, are not truly planktonic and can apparently disperse upstream by locomotion or entanglement of mucilaginous byssal threads on fishes (Section 10.6.C.2). Larval *Dreissena* lack such a structure, and the byssal threads of juveniles and adults are poorly adapted for attaching to fishes or other natural dispersal vectors. Accordingly, *Dreissena* typically does not reach high abundance in free-flowing streams without an upstream static-water source for recolonization (Allen and Ramcharan 2001). In the upper Mississippi River, *Dreissena* infestation caused native mussel mortality as high as 98 percent locally, but spatial variation in *Dreissena* abundance attributed to predation and hydrologic conditions has allowed persistence of diverse and healthy native mussel assemblages (Newton et al. 2011). Similarly, *Dreissena* abundance in the lower Ohio River is extremely variable temporally and has not caused widespread native mussel mortality (Miller and Payne 1997).

The negative effects of *Dreissena* on native mussels are unequivocal. These effects have resulted in the near-elimination of native mussels in many northern waters, particularly in lentic habitats, and have further fragmented the distribution of many species. However, the numerous controls on *Dreissena* distribution and abundance elsewhere in North American fresh waters predict that severe effects on native mussels will be localized and may have already been manifested to a large degree.

10.4.D. Enigmatic mussel declines

Even in the absence of severe point source impacts or habitat destruction, mussel populations in many streams began to decline precipitously in the 1960s. These declines are especially disturbing because they lack a conspicuous smoking gun. The distinction between these enigmatic declines and those attributable to specific events has rarely been made explicitly in the mussel conservation literature (but see Neves 1987). Because enigmatic declines often occur in otherwise apparently healthy streams, it is important to treat them separately.

The Embarras River is currently considered one of the highest-quality aquatic habitats in Illinois, but mussel abundance declined 86 percent from 1955 to 1987 (Cummings et al. 1988). Similarly, the Blue River, Oklahoma, is considered one of the state's most pristine and scenic rivers, but mussel abundance and diversity declined sharply between 1967 and 1992; at one site in 1992, the river bottom was "paved with dead shell" (Vaughn 1997b, 333). David Stansbery, at the Ohio State

University, and Herbert Athearn, a private collector, surveyed mussels extensively across the United States during the 1960s and 1970s. Their collections show that remaining unimpounded streams across North America continued to support diverse and abundant mussel faunas, but subsequently, many of these faunas declined rapidly even in the absence of additional habitat destruction or severe point source impacts. From 1966 to 1969, Stansbery collected 40 species in the Red River system, a tributary of the Cumberland River in Kentucky and Tennessee, and many species were abundant, including a collection of 375 tan riffleshells, *Epioblasma florentina walkeri* , currently one of the rarest North American species (Ohio State University Museum of Biological Diversity online bivalve database, http://www.biosci.ohio-state.edu/~molluscs/main/biv_database.html). When I participated in a survey of this watershed only 20 years later, in 1987, the physical habitat remained intact and supported a diverse fish and snail fauna. However, we found few living mussels and a total of only 17 species, but relict shells of these and many others were abundant, indicating that the mussel fauna had crashed since the late 1960s (Kentucky State Nature Preserves Commission database, Frankfort; see also Ray 1999).

Enigmatic mussel declines having no single, clear cause are reported throughout North America during this same period, especially in the central and southeastern United States (e.g., Suloway 1981; Neves 1987; Nalepa and Gauvin 1988; Distler and Bleam 1995; Howells et al. 1997; Pip 2000; Evans 2001; Poole and Downing 2004; Schanzle et al. 2004; Jones and Neves 2007; Hanlon et al. 2009). These declines appear to affect all species similarly such that survival probability is mostly a function of initial abundance rather than species-specific attributes (Section 10.5.C). An additional hallmark of enigmatic declines is that recruitment appears curtailed, and remaining populations are composed mostly of adult individuals. This suggests that juvenile mussels are particularly sensitive to the factors causing these declines, and it portends even greater declines in the near future, as remaining adults reach the end of their life spans.

Because of their wide occurrence throughout North America, these unexplained, enigmatic declines have had a more devastating effect on the remaining mussel fauna than any single factor in the postdam era. Enigmatic declines appear to have precipitated the extinction of *Epioblasma florentina curtisii, E. metastriata*, and *E. othcaloogaensis*, all of which survived systematic habitat destruction (USFWS 2000; Bruenderman et al. 2001). Populations of other species were drastically reduced, and many were left critically imperiled (Section 10.7.A).

10.5. Life history traits and patterns of species loss

Declines in mussel populations and changes in assemblage structure have been documented extensively, but patterns of decline have not been considered in an ecological context. Explanations for assemblage changes typically revolve around species' "tolerance" to impoundment or other factors, without reference to specific attributes or mechanisms that determine these responses. Understanding the ecological basis for mussel declines is essential for predicting responses to lingering effects of past impacts or future impacts and for prescribing effective conservation actions. This approach also can allow a more effective analysis of potential causes of declines in cases where they remain unclear. In this section, I consider patterns of mussel decline in the context of the host-habitat continuum presented in Chapter 8, describing how life history strategies and other ecological factors influence assemblage structure. I use this context to propose mechanisms explaining how life history traits determine the susceptibility of species to different types of insults to aquatic habitats and how these relationships have shaped the contemporary mussel fauna of North America.

10.5.A. Assemblage responses to systematic habitat destruction

Impoundment and channelization radically and fundamentally alter the physical characteristics of a stream. However, because water quality remains high in the absence of other impacts, these altered habitats can continue to support abundant and, in some cases, diverse biological communities. Radical transformation of physical habitat results in profound but generally predictable shifts in community structure according to the nature of the transformation and life history traits of organisms. Consequently, communities in highly altered habitats typically bear little resemblance to the original fauna.

The most obvious and well-documented result of habitat alteration on mussels is the shift from a lotic to a lentic fauna following impoundment. In deep storage reservoirs, consistently cold temperatures, low oxygen, and low productivity in the hypolimnion may eliminate nearly all mussel species. In shallower reservoirs with an extensive littoral zone, species typical of lentic habitats, including *Anodonta suborbiculata*, *Pyganodon grandis*, *Toxolasma* spp., and *Utterbackia imbecillis*, become dominants but do not reach the high abundances seen in riverine mussel beds (e.g., Ahlstedt and McDonough 1993; Haag and Warren 2007; Chapter 4). Nearly all lentic species are opportunistic life history strategists with rapid growth, short life span, and high population growth rate. These traits allow them to rapidly colonize and persist in unstable and stressful lentic conditions, but their abundance is limited by these conditions (Chapter 8). Radical fluctuations in water level in flood control reservoirs probably further limit populations of these species. Many of these species also have morphological adaptations for fine sediments, show greater tolerance to low dissolved oxygen than riverine species, and they are either host generalists or specialists on fishes that also can adapt to lentic conditions (e.g., sunfishes). Lentic assemblages in reservoirs contain few or no periodic or equilibrium strategists because their life history traits are incompatible with frequent disturbance and because many use obligate riverine fishes (e.g., darters, riverine minnows) that are unable to adapt to impoundment.

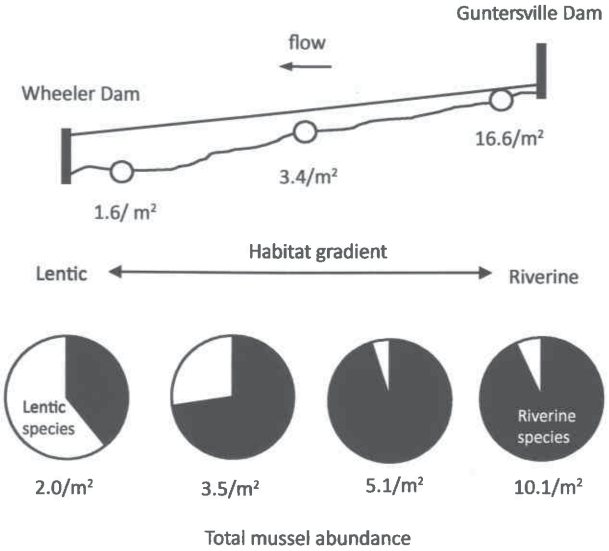


Figure 10.5. Changes in riverine mussel assemblages according to the extent of impoundment influence. (top) Mussel abundance in the original channel of the Tennessee River, Alabama, along an impoundment gradient in Wheeler Reservoir. The upstream section in the tailwaters of Guntersville Dam retains riverine characteristics, but conditions become increasingly lentic in a downstream direction as Wheeler Dam is approached (data from Ahlstedt and McDonough 1993). (bottom) Changes in the composition of mussel assemblages in the Little Tallahatchie River, Mississippi, along an impoundment gradient (data from Haag and Warren 2007).

Mussel assemblages in reservoirs having riverine characteristics retain lotic species accordant with the extent of riverine influence. In rivers impounded by navigation dams, tailwater reaches (Section 10.4.A) often support dense mussel beds with abundances comparable to free-flowing rivers, but abundance declines downstream from the dam as riverine influence is attenuated (Figure 10.5). Species composition also changes predictably along a gradient from riverine conditions below dams to lentic conditions in the lower reservoir, showing a gradual decline in riverine species (Figure 10.5).

Despite their retention of lotic species, mussel assemblages in riverine reservoirs differ markedly from preimpoundment faunas. In the Tennessee River, there is no relationship between species relative abundance before and after impoundment; many of the most abundant species prior to impoundment are now absent or rare, and several previously rare species have become common (Figure 10.6). In the Cumberland River, there is a weak, positive relationship, but species relative abundance before impoundment is a poor predictor of the postimpoundment fauna and, similar to the Tennessee River, the relative abundance of many species changed considerably. Furthermore, patterns of species loss after impoundment are highly

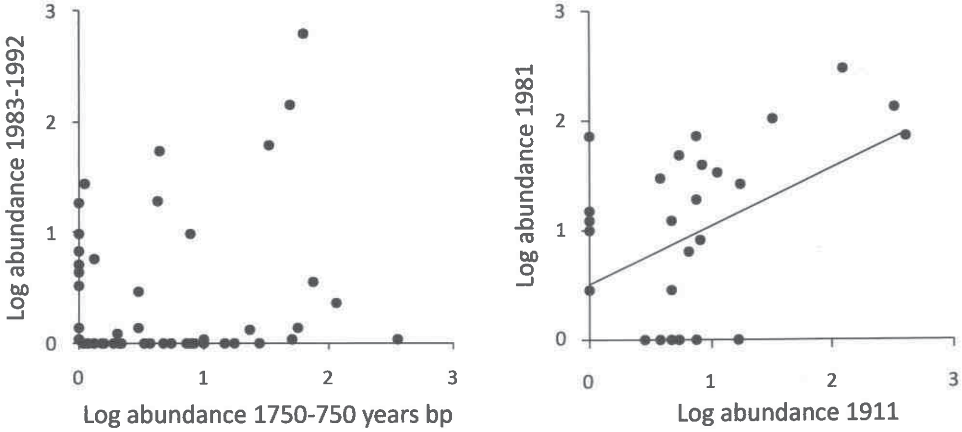


Figure 10.6. Comparison of pre- and postimpoundment mussel assemblages. In both panels, percentage relative abundance is standardized to absolute abundance based on a sample of 1,000 individuals. (left) Species abundance in prehistoric vs. contemporary assemblages in the Tennessee River, Tennessee, in the current Chickamauga Reservoir (no relationship: $r = 0.17$, $p < 0.22$; data from Ahlstedt and McDonough 1995–1996). (right) Species abundance in historical vs. contemporary assemblages in the Cumberland River, Kentucky (positive relationship: $r = 0.45$, $p < 0.05$; data from Blalock and Sickel 1996).

consistent among rivers (Table 10.2), suggesting that life history traits or other species attributes influence the ability to adapt to habitat alteration.

The ability to adapt to impoundment[1] is strikingly concordant with life history strategies. Opportunists and equilibrium strategists together make up about 75 percent of species that adapt to impoundment (Figure 10.7). Impoundment increases the extent of lentic habitat even in stream segments that retain riverine characteristics. Opportunistic species that were formerly restricted to lentic microhabitats in free-flowing rivers typically increase dramatically in response to the increase in available habitat (e.g., Bates 1962; Garner and McGregor 2001). Other opportunists that were absent prior to impoundment may colonize these recently created habitats (e.g., *Anodonta suborbiculata*; Williams et al. 2008; Watters et al. 2009). Remnant river channel habitats in impounded streams may represent unusually stable environments because dams dampen flood pulses and other seasonal variations in flow (Poff et al. 1997). Stable conditions may allow equilibrium strategists to dominate in these habitats to a greater extent than in free-flowing rivers (Chapter 8). In the impounded Little Tallahatchie River, assemblage evenness was lowest in the riverine main channel but was highest in lentic backwaters that experience frequent disturbance from water

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[1] In the remainder of this section, by *impoundment tolerant*, I am referring to species that can adapt to riverine portions of impoundments. This should not be confused with species that can adapt to lentic conditions in reservoirs, as discussed previously.

Table 10.2. *Tolerance to impoundment and life history traits of mussel species in the Cumberland, Tennessee, Ohio, Upper Mississippi, and Illinois Rivers*

Mussel species	River					% Similarity	Life history	Host
	Cumb.	Tenn.	Ohio	Miss.	Illi.			
Impoundment tolerant								
Actinonaias ligamentina	P	P	P	P	P	100	equil	generalist
Amblema plicata	P	P	P	P	P	100	equil	generalist
Arcidens confragosus	P	P	P	P	P	100	oppor	generalist
Cyclonaias tuberculata	P	P	P	P	X	80	equil	catfish
Ellipsaria lineolata	P	P	P	P	P	100	perio	drum
Fusconaia flava	P	–	P	P	P	100	equil	minnow
Lampsilis abrupta/higginsi	P	P	P	P	X	80	perio	bass
Lampsilis cardium/ovata	P	P	P	P	P	100	perio	bass
Lampsilis siliquoidea	–	–	P	P	P	100	perio	bass
Lampsilis teres	X	P	P	P	P	80	oppor	gar
Lasmigona complanata	P	P	P	P	P	100	oppor	generalist
Leptodea fragilis	P	P	P	P	P	100	oppor	drum
Ligumia recta	P	P	P	P	P	100	perio	sauger
Megalonaias nervosa	P	P	P	P	P	100	equil	generalist
Obovaria olivaria	P	P	P	P	P	100	perio	sturgeon
Potamilus alatus	P	P	P	P	P	100	oppor	drum
Ptychobranchus fasciolaris	P	P	P	–	–	100	perio	darter
Pyganodon grandis	P	P	P	P	P	100	oppor	generalist
Quadrula metanevra	P	P	P	P	X	80	equil	minnow
Quadrula nodulata	P	–	P	P	P	100	equil	catfish
Quadrula pustulosa	P	P	P	P	P	100	equil	catfish
Quadrula quadrula	P	P	P	P	P	100	equil	catfish
Quadrula verrucosa	P	P	P	P	P	100	equil	catfish
Toxolasma parva	X	P	P	P	P	80	oppor	sunfish
Truncilla (2 spp.)	P	P	P	P	P	100	oppor	drum
Utterbackia imbecillis	P	P	P	P	P	100	oppor	generalist
Marginally tolerant								
Cumberlandia monodonta	X	P	X	P	X	60	equil	?
Elliptio crassidens	P	P	P	X	X	60	equil	skipjack
Elliptio dilatata	P	X	P	X	X	60	perio	darter
Lasmigona costata	X	X	P	P	X	60	perio	generalist
Potamilus capax	P	–	P	X	X	50	oppor	drum
Pleurobema sintoxia	P	X	P	P	X	60	equil	minnow
Pleurobema cordatum	P	X	P	–	–	67	equil	minnow
Pleurobema plenum	X	P	X	–	–	67	equil	minnow
Plethobasus cicatricosus	X	P	X	–	–	67	equil	minnow
Plethobasus cooperianus	X	P	P	–	–	67	equil	minnow
Plethobasus cyphyus	X	P	P	P	X	60	equil	minnow

Mussel species	River					% Similarity	Life history	Host
	Cumb.	Tenn.	Ohio	Miss.	Illi.			
Quadrula cylindrica	X	P	P	–	–	67	perio	minnow
Reginaia ebena	P	P	P	X	X	60	equil	skipjack
Toxolasma lividus	X	P	X	–	–	67	oppor	sunfish
Impoundment intolerant								
Alasmidonta marginata	X	X	X	P	X	80	perio	generalist
Alasmidonta viridis	X	X	X	X	X	100	perio	sculpins
Cyprogenia stegaria	X	X	X	–	–	100	equil	darter
Dromus dromas	X	X	–	–	–	100	equil	darter
Epioblasma (16 spp.)	X	X	X	X[a]	X[a]	100	perio	darter
Fusconaia cor/cuneolus	–	X	–	–	–	100	equil	minnow
Fusconaia subrotunda	X	X	X	–	–	100	equil	minnow
Hemistena lata	X	X	X	–	–	100	perio	minnow
Lampsilis fasciola	X	X	X	–	–	100	perio	bass
Lemiox rimosus	–	X	–	–	–	100	perio	darter
Leptodea leptodon	X	X	X	X	–	100	oppor	drum
Medionidus conradicus	X	X	–	–	–	100	perio	darter
Obovaria subrotunda/retusa	X	X	X	–	–	100	perio	darter
Pleurobema oviforme/clava	X	X	X	–	–	100	equil	minnow
Pleurobema rubrum	X	P	X	–	X	75	equil	minnow
Pleuronaia barnesiana/dolabelloides	X[b]	X	–	–	–	100	equil	minnow
Ptychobranchus subtentum	X	X	–	–	–	100	perio	darter
Quadrula fragosa	X	X	X	P	–	75	equil	catfish
Quadrula intermedia	–	X	–	–	–	100	perio	minnow
Strophitus undulatus	X	X	X	P	X	80	perio	generalist
Villosa iris	X	X	X	–	X	100	perio	bass
V. taeniata	X	X	–	–	–	100	perio	bass
V. trabalis	X	X	–	–	–	100	perio	darter

Note: Impoundment refers here only to rivers impounded by navigation dams but retaining riverine characteristics (see text). P, species that persist as reproducing populations; X, species that were extirpated or currently persist only as small or nonreproducing populations; –, species that do not occur in a particular river. Percentage similarity is the percentage of the most frequent persistence state among the five rivers. Tolerance to impoundment was determined as species that either persisted or were extirpated in 75% or more of rivers in this example. Life history strategies are equilibrium (equil), opportunistic (oppor), and periodic (perio); see Table 6.3. Mussel occurrence data from Starrett (1971), Parmalee et al. (1980), Williams and Schuster (1989), Blalock and Sickel (1996), Hughes and Parmalee (1999), Garner and McGregor (2001), Watters and Flaute (2010), Newton et al. (2011), and USFWS (2011).

[a] *E. triquetra* only.

[b] *P. dolabelloides* only.

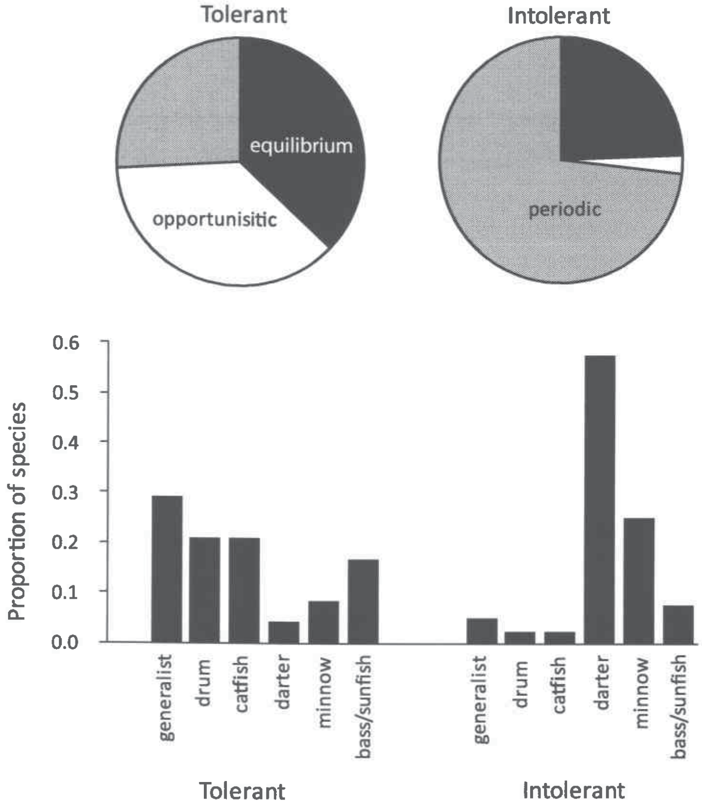

Figure 10.7. Representation of (top) mussel life history strategies and (bottom) host use in relation to impoundment tolerance. Impoundment refers here only to rivers impounded by navigation dams but retaining riverine characteristics (see text). Impoundment tolerance determined from Table 10.2; species of marginal tolerance are not included. Proportion of life history strategies and host use classes differs significantly between tolerant and intolerant species (life history: $G = 13.00$, $p < 0.005$, 2 df; host use: $G = 35.64$, $p < 0.001$, 5 df).

level fluctuation (Haag and Warren 2007). Alternatively, the long life span of equilibrium species may allow population maintenance even when suitable conditions for reproduction occur infrequently due to habitat alteration. This hypothesis is supported by the prevalence of equilibrium species among those with marginal impoundment tolerance (Table 10.2). These species appear barely able to maintain populations in impounded rivers even though adults may persist for many years.

Species intolerant of impoundment are overwhelmingly dominated by periodic strategists (Figure 10.7), and periodic strategists make up the majority of species that were driven to extinction by systematic habitat destruction (Table 10.1). Similar to equilibrium species, their response to impoundment could be explained in two ways. First, in unusually stable riverine habitats in impounded rivers, periodic strategists may be poor competitors for food or space compared with equilibrium species

(Chapter 8). This seems unlikely because total mussel abundance is often lower in impounded rivers than in free-flowing streams. A more plausible explanation is that the shorter life span of periodic strategists lowers the probability that suitable conditions for reproduction will occur in an individual's lifetime.

Host use shows even stronger concordance with impoundment tolerance (Figure 10.7). Nearly 90 percent of tolerant mussel species are either generalists or use fishes that adapt readily to impoundment (black basses, catfishes, drum, gar, sunfishes). In contrast, more than 80 percent of intolerant species are specialists on darters, sculpins, or riverine minnows, all of which were widely eliminated or greatly reduced by impoundment due to loss of shallow, shoal habitat (Voightlander and Poppe 1989; Etnier and Starnes 1993; Freeman et al. 2005). Species of marginal tolerance to impoundment include mostly specialists on riverine minnows and only a single darter specialist, the kidneyshell, *Ptychobranchus fasciolaris* (Table 10.2). However, *P. fasciolaris* is extremely rare in all the rivers in Table 10.2 (Williams and Schuster 1989; Garner and McGregor 2001).

Other deviations from these strong patterns may be explained by specific attributes of the host relationship. The few minnow specialists tolerant of impoundment either have lures associated with mantle magazines (e.g., *Quadrula cylindrica*, *Q. metanevra*; Chapter 5), which may be efficient for attracting hosts that occur at low abundance, or they use a broad range of minnow species, including impoundment-tolerant species. The impoundment-tolerant rabbitsfoot, *Q. cylindrica*, and monkeyface, *Q. metanevra*, use a wide range of minnow species, but intolerant Cumberland monkeyface, *Q. intermedia*, is a specialist on *Erimystax*, which also is intolerant of impoundment (Yeager and Neves 1986; Etnier and Starnes 1993; Yeager and Saylor 1995; Fobian 2007; Fritts et al., in press). Host use of the Wabash pigtoe, *Fusconaia flava*, is poorly known, but a closely related species, *F. cerina*, uses a wider array of minnow species than *Pleurobema decisum* (Haag and Warren 2003). Consequently, *F. cerina* may adapt to some impounded rivers, but *P. decisum* does not (Williams et al. 1992).

Mussel species that are specialists on migratory host fishes show variable responses to impoundment in accordance with the extent to which movements of these fishes are affected. The elephant-ear, *Elliptio crassidens*, and ebonyshell, *Reginaia ebena*, specialists on migratory skipjack herring, have persisted in portions of the Cumberland, Tennessee, and Ohio rivers apparently because dams on these rivers allow passage of skipjacks. In contrast, they have declined in the upper Mississippi River likely because design and operational aspects of Lock and Dam 19 impede skipjack migrations (Kelner and Sietman 2000); many other mussel species in the river that do not specialize on migratory fishes continue to show strong recruitment (Newton et al. 2011). These species also declined in free-flowing tributaries that became isolated from large rivers by impoundment. The Sipsey River, Alabama, supports a nearly intact mussel assemblage with strong recruitment and diverse year-class structure for all species except *E. crassidens* and *R. ebena* (Haag and Warren 2010). The Sipsey River is a

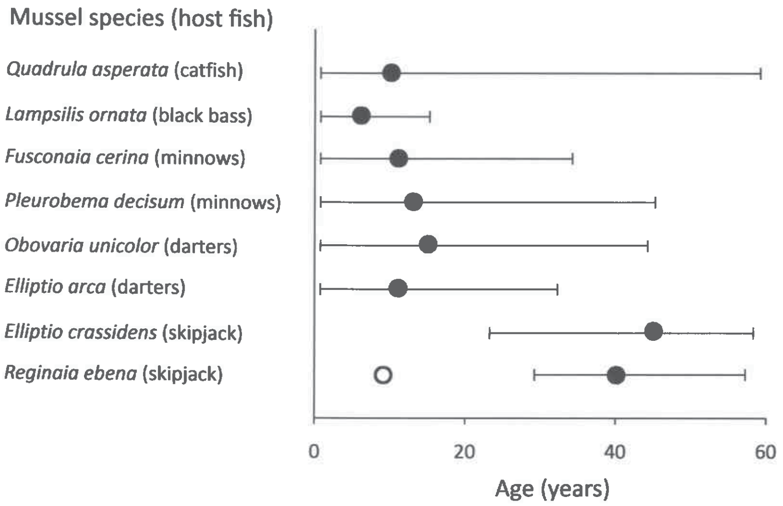

Figure 10.8. Age structure of mussel populations in the Sipsey River, Alabama, according to host use. Filled circles are average age; bars are observed age range. The open symbol for *R. ebena* represents the only individual found that was less than 25 years old (W. R. Haag, unpublished data).

tributary of the Tombigbee River, and the youngest individuals in populations of both species largely correspond to the time of completion of the TTW, which may have disrupted movements of skipjacks (Figure 10.8). Populations of *E. crassidens* in many other tributaries are now dominated by very old individuals (more than 50 years) that probably recruited prior to disruption of skipjack movements by dams (P. Freeman, C. Hauswald, J. Clayton, personal communication). The black sandshell, *Ligumia recta*, is a specialist on sauger and walleye (*Sander*) and remains common in the Ohio and Tennessee rivers because sauger have adapted well to impoundment. Populations in the Pearl River, Mississippi, and the Mobile Basin are dependent solely on walleye because sauger do not occur in these streams. Because of dams, migratory walleye are extirpated from the Pearl River and reduced to very low levels in the Mobile Basin (Ross 2001; Boschung and Mayden 2004); consequently, *L. recta* also is extirpated from the Pearl River and nearly so from the Mobile Basin, even in free-flowing stream reaches that formerly supported the species (Jones et al. 2005; Williams et al. 2008).

For a few species, disappearance in impounded rivers is not explained well by life history strategies or host use. The scaleshell, *Leptodea leptodon*, and fat pocketbook, *Potamilus capax*, are both opportunists that specialize on drum, similar to other mussel species that adapt readily to impoundment. The disappearance of *P. capax* in the impounded upper Mississippi River is especially puzzling because it is abundant in highly disturbed habitats elsewhere in its range (Miller and Payne 2006). The winged mapleleaf, *Quadrula fragosa*, and purple lilliput, *Toxolasma lividus*, have either low or marginal tolerance to impoundment, but both use reservoir-adapted host fishes and have life history traits similar to other tolerant species (Table 10.2). *Toxolasma lividus*

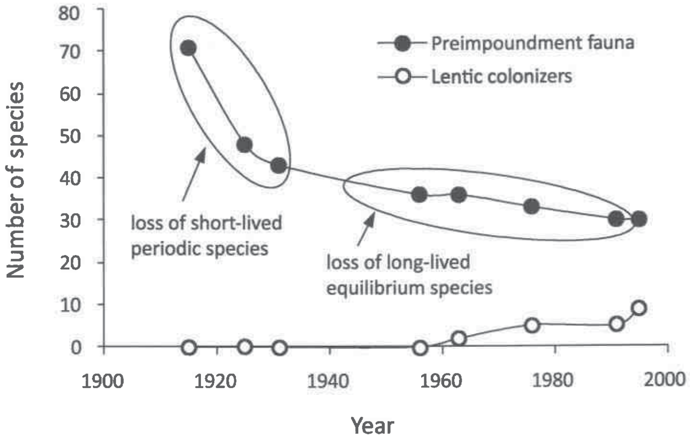

Figure 10.9. Timeline of mussel assemblage change in the Tennessee River at Muscle Shoals, Alabama, after impoundment in 1924 (data from Garner and McGregor 2001).

has become locally common in the Tennessee River in recent years, but it appears to remain absent in impounded rivers elsewhere in its range (Garner and McGregor 2001). Although life history traits and host use appear to be primary determinants of impoundment tolerance, probability of survival also may be dependent on initial abundance. All four of these species were rare in the rivers in Table 10.2 even prior to impoundment (e.g., Ortmann 1925; Neel and Allen 1964). Reduction in overall mussel abundance and fragmentation of remaining riverine habitat by dams may have reduced population sizes of these species below viable levels and rendered them vulnerable to stochastic effects.

Predictable patterns of assemblage change after impoundment according to life history strategies and host use are illustrated well in the Tennessee River at Muscle Shoals, which has an unusually comprehensive historical record (Figure 10.9). In the first 15 years after impoundment, species richness declined sharply from 71 to 43 species. Species lost during this time were almost exclusively short-lived, periodic strategists or specialists on darters or riverine minnows (e.g., *Epioblasma* spp., *Hemistena lata*, *Lasmigona costata*, *Lemiox rimosus*, *Leptodea leptodon*, *Medionidus conradicus*, *Quadrula intermedia*, *Villosa* spp.). Over the next 35 years, diversity of riverine species declined more gradually as long-lived equilibrium species intolerant of impoundment reached the end of their life spans (e.g., *Cyprogenia stegaria*, *Dromus dromas*, *Fusconaia cor*, *Pleuronaia barnesiana*, *P. dollabelloides*, *Pleurobema oviforme*, *Quadrula fragosa*). Most of these species also were specialists on darters or riverine minnows, and most disappeared by the late 1960s (Garner and McGregor 2001), at which time individuals that recruited shortly before impoundment would have been about 50 years old, the approximate maximum life span for many equilibrium species (Chapter 6). Simultaneously, the area was colonized by lentic species that had not been recorded prior to impoundment (e.g., *Anodonta suborbiculata, Lasmigona complanata, Pyganodon grandis, Utterbackia imbecillis*). In the last 20 years, lentic species continue to colonize the area, but diversity of riverine species seems to have stabilized. However, abundance of several species of low or marginal impoundment tolerance (e.g., *Cumberlandia monodonta, Elliptio dilatata, Obovaria retusa, Plethobasus* spp., *Pleurobema* spp., *Ptychobranchus fasciolaris*) has declined to extremely low levels (Garner and McGregor 2001; Figure 10.3). These species are in grave danger of extirpation due to stochastic variation in environmental conditions and recruitment (Section 10.4.B), portending further erosion of species richness. Ultimately, mussel assemblages in the Tennessee and other impounded rivers may be composed of less than 35 percent of the original riverine fauna as well as recent lentic colonizers, but the full effects of impoundment may not be seen for more than a century.

Channelization also has effects on mussel assemblages that are predictable based on life history strategies. Unlike impoundment, which may leave intact substantial portions of stable river channel, channelization and subsequent headcutting causes massive destabilization of the streambed (Section 10.4.A). Consequently, channelization results in a radical shift to assemblages composed almost entirely of opportunistic strategists (Table 10.3). Many of these species mature as early as their first year, allowing them to reproduce quickly. Populations are usually small and scattered, and they appear to fluctuate widely in response to frequent severe disturbance and reconfiguration of the streambed (W. R. Haag, observations).

10.5.B. Assemblage responses to severe point source pollution and other stressors

Unlike physical habitat destruction, severe point source impacts render conditions unsuitable to most life-forms to some extent. Consequently, these impacts typically affect all mussel species similarly, regardless of life history traits. In the most extreme examples, as in the toxic spill in the Clinch River in 1998, virtually all mussels are killed, along with fishes and aquatic insects (Section 10.4.C). In the Little South Fork Cumberland River, species persistence after coal mining impacts was not related to life history strategy or host use, and even opportunistic life history strategists and host generalists were extirpated (Figure 10.10). Instead, the probability of persistence was predicted simply by initial relative abundance such that only historically common species survived, and a similar pattern was seen after coal mining impacts in Horse Lick Creek (Warren and Haag 2005). In the Green River, the mucket, *Actinonaias ligamentina*, was "an abundant species, generally the prevailing one" in the 1920s, and continued to be the dominant species after brine waste pollution in the 1950s (Ortmann 1926, 177; Williams 1969).

A non-species-specific effect also is seen in other types of severe stress. Mussel species differ in their short-term susceptibility to *Dreissena* infestation, but these

Table 10.3. *Mussel species tolerance to channelization relative to life history traits as indicated by their occurrence (X) in small Mississippi Streams*

		Little Tallahatchie River system		Tombigbee River system	
Species	Life history	Not channelized	Channelized	Historic	Channelized
Intolerant to channelization					
Amblema plicata	equi	X		X	
Anodontoides radiatus	perio	X		X	
Epioblasma penita	perio			X	
Fusconaia cerina/flava	equi	X		X	
Lampsilis cardium/ornata	perio	X		X	
Obliquaria reflexa	perio	X			
Obovaria unicolor	perio			X	
Plectomerus dombeyanus	equi	X			
Pleurobema sp.	equi			X	
Quadrula asperata/pustulosa	equi	X		X	
Quadrula quadrula/rumphiana	equi	X		X	
Quadrula verrucosa	equi	X			
Strophitus subvexus	perio			X	
Tolerant to channelization					
Anodonta suborbiculata	oppor		X		
Lampsilis siliquoidea/straminea	perio	X	X	X	X
Lampsilis teres	oppor	X	X	X	X
Leptodea fragilis	oppor	X	X	X	
Ligumia subrostrata	oppor	X	X		X
Potamilus purpuratus	oppor	X	X		
Pyganodon grandis	oppor	X	X	X	X
Toxolasma parva/texasensis	oppor	X	X	X	X
Uniomerus tetralasmus	perio	X			X
Utterbackia imbecillis	oppor		X		X
Villosa lienosa	oppor	X		X	X

Note: Tombigbee River system data are for the Black Prairie physiographic region; historic represents assemblages prior to channelization. Life history strategies are equilibrium (equi), opportunistic (oppor), and periodic (perio); see Table 6.3. Data from McGregor and Haag (2004) and W. R. Haag and M. L. Warren (unpublished data).

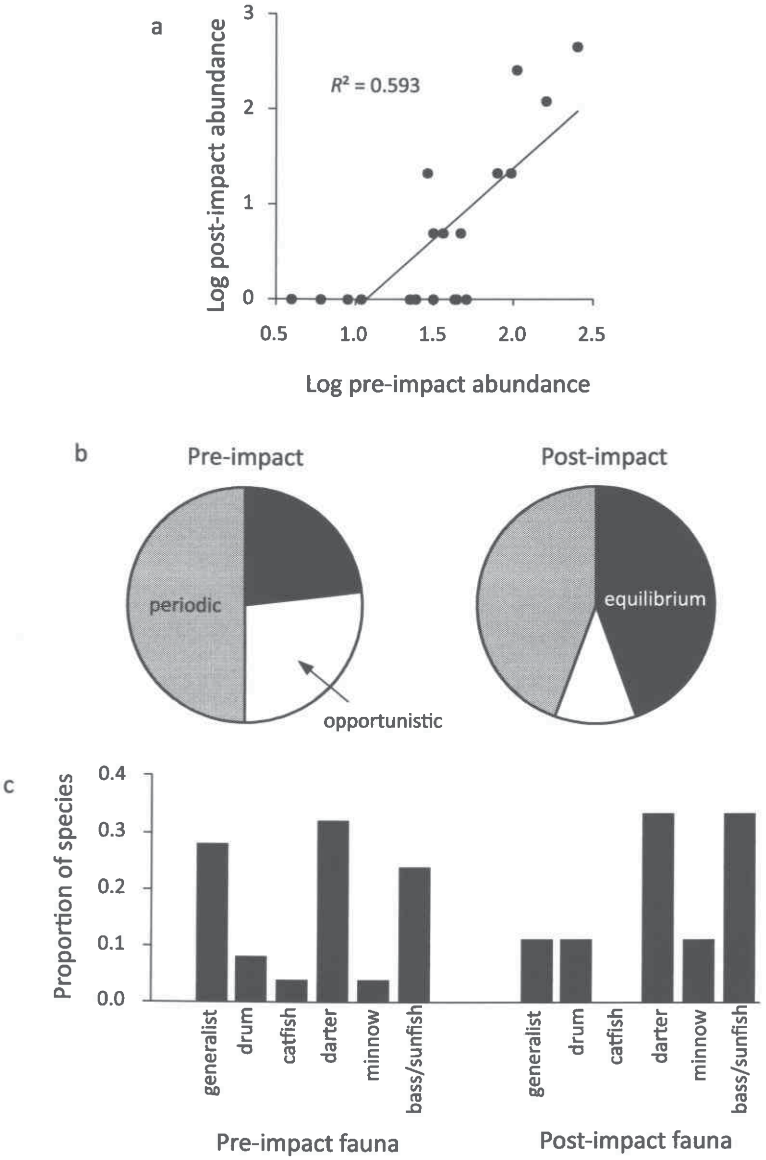

Figure 10.10. Patterns of mussel assemblage change in the Little South Fork Cumberland River, Kentucky, following severe impacts from coal and oil extraction. (a) Relationship between species abundance before and after impacts. Percentage relative abundance is standardized to absolute abundance based on a sample of 1,000 individuals. Representation of (b) life history strategies and (c) host use among the pre- and postimpact faunas. Neither the proportion of species in life history strategies nor host use classes differed significantly between the pre- and postimpact faunas (life history: $G = 1.86$, $p < 0.10$, 2 df; host use: $G = 1.93$, $p < 0.75$, 5 df) (data from Warren and Haag 2005).

differences are obscured after only a few years such that all species ultimately decline to a similar extent (Haag et al. 1993; Strayer 1999b). In small streams, mussel abundance was reduced 65 to 83 percent after a severe drought, but species abundance before and after the drought was strongly correlated, suggesting that all species suffered similar mortality rates (Haag and Warren 2008).

The characteristic persistence after severe impacts of only the previously most abundant species has led to the categorization of these species as "tolerant" to various stressors. Starrett (1971, 298) considered the threeridge, *Amblema plicata*, "one of the more pollution tolerant species" in the Illinois River because it made up 62 percent of live mussels collected in 1966. However, this species composed 50 to 60 percent of mussel assemblages in the river even prior to severe water pollution (Danglade 1914). After *A. plicata*, the washboard, *Megalonaias nervosa*, and pimpleback, *Quadrula pustulosa*, were the two most abundant species historically, and they remained among the most abundant species after severe pollution. Unlike physical habitat alteration, the characteristic responses of mussel assemblages to severe water quality impacts do not support strong differences in tolerance among species.

Responses of mussels to severe water quality degradation also demonstrate their unusually high sensitivity compared with other organisms. Despite a 65 percent decrease in mussel species richness in the Little South Fork Cumberland River from coal mining impacts, fish species richness declined during the same time by less than 10 percent, and the river continued to support diverse aquatic insect and diatom assemblages (Poly 1997; Kentucky Fish and Wildlife Information System, Kentucky Department of Fish and Wildlife Resources, Frankfort; Kentucky Division of Water, Frankfort). Similarly, during the period when Horse Lick Creek experienced a 93 percent decline in mussel abundance (Haag and Warren 2004), Index of Biotic Integrity (IBI) scores based on fish, macroinvertebrate, and diatom assemblages were rated "good–excellent" (Kentucky Division of Water, Frankfort). Industrial wastes in the lower North Fork Holston River, Virginia, eliminated nearly all mussels, but even though IBI scores were sharply lowered, the river continued to support a variety of aquatic insect taxa (Kerans and Karr 1994; Henley and Neves 1999). By the 1920s, the lower Duck River, Tennessee, lost most of its mussel fauna potentially to impacts from phosphate mines, but the snail fauna remained diverse and abundant (Ortmann 1924a). The less dramatic response of other organisms could be due to either lower sensitivity or higher mobility and recolonization potential. Regardless, mussels are clearly affected to a much greater degree than many other organisms and are among the first species to respond to water-quality degradation.

10.5.C. Assemblage responses to enigmatic declines

Similar to severe point source impacts, enigmatic mussel declines typically have non-species-specific effects (e.g., Buchanan 1987; Jenkinson and Ahlstedt 1987).

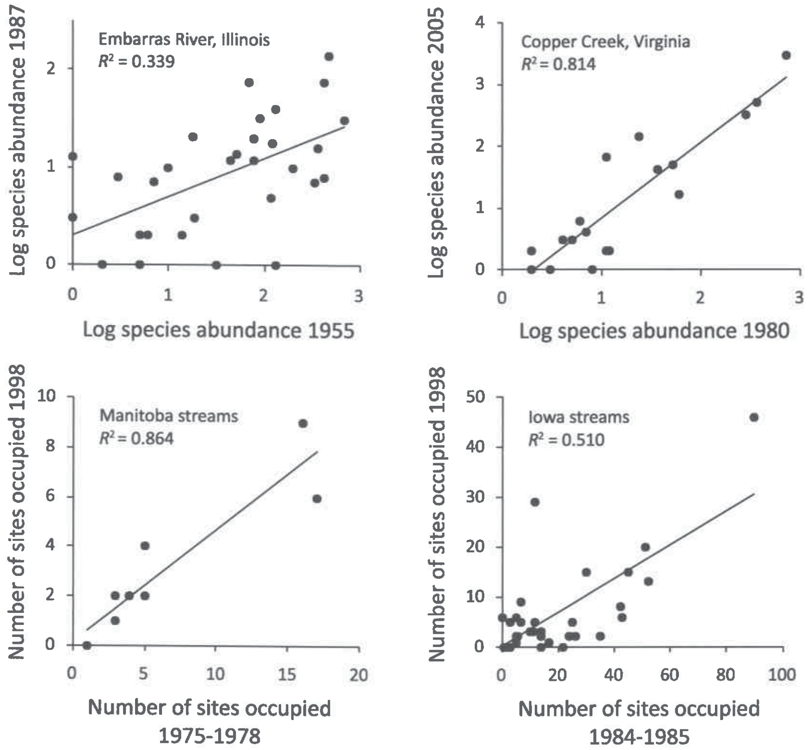

Figure 10.11. Patterns of mussel species abundance or occurrence before and after enigmatic declines in four streams. On top two panels, percentage relative abundance is standardized to absolute abundance based on a sample of 1,000 individuals. All relationships are significant at $p < 0.01$ (data from Cummings et al. 1988; Pip 2000; Poole and Downing 2004; Hanlon et al. 2009).

In streams from four disparate regions, initial species abundance or distribution is positively related to postdecline abundance or distribution and, in most cases, is a good predictor of postdecline assemblages (Figure 10.11). In the Embarras River, even the two most common species in 1987, the plain pocketbook, *Lampsilis cardium*, and pimpleback, *Quadrula pustulosa*, had declined by 71 percent and 83 percent, respectively, since 1955, similar to the 86 percent decline in overall mussel abundance (Cummings et al. 1988).

Assemblage changes after enigmatic declines also are similar to those from point source impacts in that species persistence is not related to life history strategies or host use. In the Red River, faunal composition with regard to life histories and host use was nearly identical before and after enigmatic decline (Figure 10.12). In the Embarras River, abundance declined more than 50 percent for all three life history strategies and did not differ significantly among strategies (Figure 10.13). Host use showed a similar pattern, but average decline was markedly lower for drum specialists; however, because of variation among species within host strategies, the percentage decline was

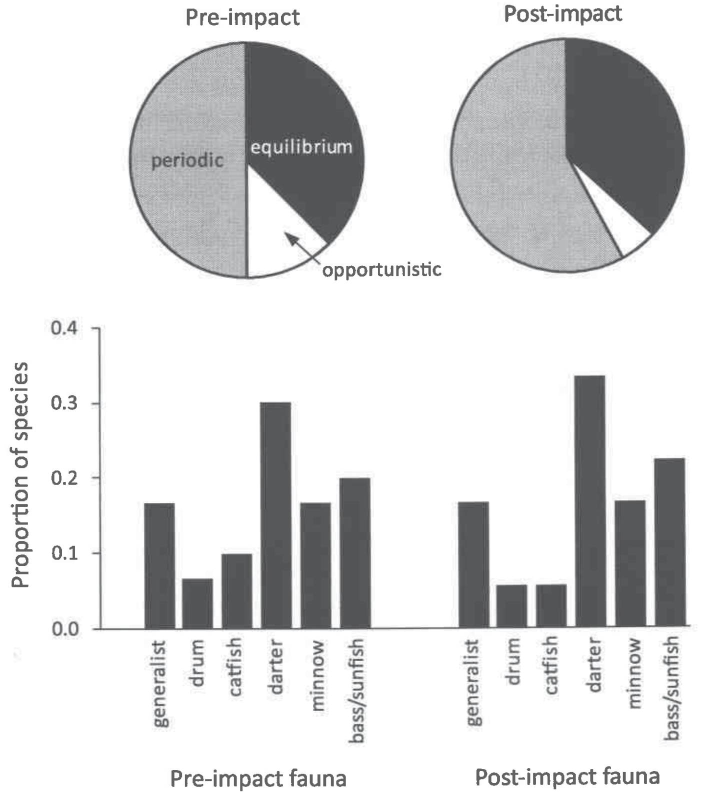

Figure 10.12. Representation of (top) mussel life history strategies and (bottom) host use in the Red River, Kentucky, before and after enigmatic decline. Neither the proportion of species in life history strategies nor host use classes differed significantly between the pre- and postimpact faunas (life history: $G = 0.84$, $p < 0.25$, 2 df; host use: $G = 0.37$, $p < 0.99$, 5 df).

significantly different only between drum and bass–sunfish specialists. These results show that enigmatic declines have pervasive effects on mussel assemblages and affect all species regardless of species attributes such as life history strategies, host use, or presumed tolerance to stressors.

Enigmatic declines may occur in concert with general degradation of aquatic habitats (e.g., Poole and Downing 2004). In many other cases, these declines are remarkable for occurring in streams that maintain otherwise healthy aquatic communities. Despite dramatic mussel declines, the Embarras River system has exceptional or only minimally impaired water quality throughout, with only 2 percent of total stream miles in the watershed considered severely impaired, and it continues to support one of the most diverse fish and crayfish faunas in Illinois (Page et al. 1997). IBI scores for fishes and aquatic insects were rated "good–excellent"; consequently, the river is used widely as a reference with which to compare more highly impacted streams (Fausch et al. 1984; Illinois Department of Natural Resources 2004). Similarly, fish

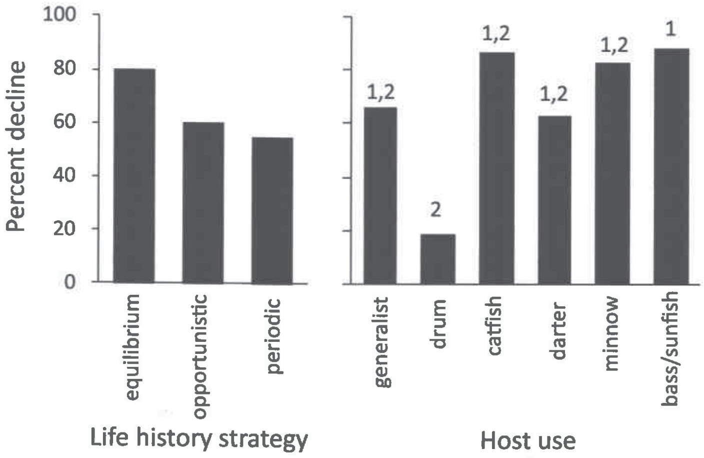

Figure 10.13. Comparison of mean percentage decline in mussel abundance among life history strategies and host use classes in the Embarras River, Illinois, from 1955 to 1987. Percentage decline does not differ among life history strategies (ANOVA, arcsine-transformed percentages, $F = 0.65$, $p < 0.53$). Percentage decline was marginally significantly different among host use classes (arcsine-transformed percentages, $F = 2.60$, $p < 0.051$); host use classes with the same number are not significantly different (Tukey post hoc test at $p < 0.05$; data from Cummings et al. 1988).

and macroinvertebrate assemblages in the Red River are rated "good–excellent," but diatom assemblages do appear to show effects of nutrient enrichment or sedimentation (Kentucky Division of Water, Frankfort). Like severe point source impacts, these patterns show that mussels are unusually sensitive to factors causing enigmatic declines.

10.6. Assessing potential causes of enigmatic declines

In contrast to the well-documented impacts of habitat destruction and severe point source pollution, the causes of enigmatic declines remain unknown. Mussel declines in general are attributed to a standard list of impacts, including habitat destruction, overharvest, invasive species, and vague factors such as "poor land use practices" (e.g., Bogan 1993; Neves et al. 1997; Watters 2000). Each of these factors has certainly played a role in some cases, but it is critical to identify specific causes of enigmatic declines rather than simply invoking the standard list. Furthermore, strong causal relationships for some of these factors have rarely been demonstrated, especially with regard to enigmatic declines. In a survey of 124 published papers dealing with mussel declines, less than half presented strong evidence of a correlation between declines and any specific factors, and few showed a direct causal mechanism (Downing et al. 2010).

Declines in amphibian populations offer a useful comparison for understanding enigmatic mussel declines because they show many striking similarities. Like most organisms, amphibians have been negatively affected for more than 100 years by many of the human impacts that affect mussels. However, severe and abrupt declines in many amphibian populations began in the 1970s or 1980s. Similar to enigmatic mussel declines, an array of species are affected, and declines often occur in otherwise high-quality habitats (Stuart et al. 2004). These declines may occur in concert with, or be exacerbated by, an array of factors, but disease, pesticides, and perhaps sensitivity to increased ultraviolet radiation appear to be proximate causes (Beebee and Griffiths 2005).

Part of the reason for our lack of progress on this topic is that enigmatic declines typically are not considered specifically but rather are conflated with other, more clear-cut impacts. Although habitat destruction and point source impacts have doubtlessly exacerbated or occurred in concert with some enigmatic declines, it is clear that these are not the proximal causes in many cases. Without knowledge of the specific causes of enigmatic declines, it is difficult to prescribe effective preventative or remedial actions. In the following sections, I review the evidence for the role of commonly invoked factors in explaining enigmatic mussel declines.

10.6.A. Sedimentation

Apart from direct habitat destruction, sedimentation is the most widely invoked explanation for mussel declines (e.g., Brim Box and Mossa 1999) and is mentioned in nearly every study on the topic. The negative impact on mussels of accelerated sedimentation from human activities has been a recurrent theme at least since the mid-1800s, and some have suggested that these effects may even have occurred prior to European settlement (Section 10.2.A). In addition to its potential effects on mussels, sediments are considered the most widespread pollutant of rivers in the United States, impairing more than 40 percent of the nation's river kilometers (Brim Box and Mossa 1999, citing USEPA 1990), and sedimentation is considered a serious threat to other aquatic invertebrates and fishes. Deposited sediments in streambeds are considered a more important factor than suspended sediment, which typically occurs at very high levels only for short periods following storm flows (Waters 1995). Deposited sediments are thought to affect aquatic organisms by filling interstitial spaces between larger substrate particles, resulting in increased embeddedness of coarse substrates. Higher embeddedness reduces available habitat for insect larvae and other organisms that live in interstitial spaces and reduces survival of fish eggs or fry. Deposited sediments also can reduce pool volume and fish cover and destabilize stream channels due to high inputs of unconsolidated materials (Waters 1995).

Despite its presumed importance, there is little or no strong evidence supporting sedimentation as a direct cause of mussel declines in free-flowing streams. Sedimentation was implicated anecdotally as early as the mid-1800s (Section 10.2.B), but the first specific evidence comprised reports of beds of dead shells buried under accumulations of fine sediments in impounded streams or other depositional environments (Ellis 1931; Scruggs 1960). Subsequent papers reported radical changes in mussel assemblages attributed to accumulation of sediments in impoundments (e.g., Bates 1962; Coon et al. 1977; Blalock and Sickel 1996; Section 10.5.A). Impoundment results in massive deposition of fine sediments and complete transformation of other ecosystem characteristics, and it differs fundamentally from the much less dramatic impacts of sedimentation in free-flowing streams. Nevertheless, studies dealing with the effects of impoundment are often cited as implicit support for the negative effect of sedimentation in unimpounded streams.

A handful of laboratory studies attempted to evaluate the effects of sediment on mussels, but none provide strong evidence for a direct, negative effect, especially with regard to the type of sedimentation typically seen in streams. The most widely cited is Ellis (1936), who reported in three paragraphs that mussels exposed to "slowly deposited silt," up to 2.5 cm deep, on the bottom of hatchery raceways had higher mortality (more than 90%) than mussels held above the bottom in wooden frames (mortality stated as "very low" but not specified). Mortality was attributed directly to silt, which interfered with feeding, and not to low oxygen or "other water conditions," but support for this assertion is not presented, nor are the physical conditions under which the experiment occurred. Imlay (1972) reported that most mussels held in battery jars in the laboratory and buried under 8–18 cm of sediment, including detritus, sand, silt, and "grit," did not reemerge from burial, and many died. However, these trials had no controls (i.e., without sediment), and such rapid and deep accumulations of sediment are unlikely in free-flowing streams.

At least two replicated, controlled studies have examined the effects of sediment on mussels. The ability of mussels to emerge from burial under sediment declined with increasing sediment depth from 5 to 25 cm, and mussels that did not emerge died, but emergence ability varied among species (Marking and Bills 1980). This study shows conclusively the negative effects of deposited sediments, but it was designed to evaluate the effects of sudden deposition of a large volume of sediment as in discharge of dredge spoil onto mussel beds. Like the Imlay (1972) study, these acute effects do not reflect the more subtle and gradual accumulations of sediment and reduction in substrate embeddedness typically seen in free-flowing streams. In another study, mussels exposed to high concentrations of suspended sediment had reduced food clearance rates and shifted to catabolism of stored energy reserves (Aldridge et al. 1987). However, the effect of suspended sediment was confounded with high turbulence (to simulate commercial barge traffic), and turbidity was simulated using diatomaceous earth, which is abrasive and inorganic, unlike natural sediments, which may carry large quantities of adsorbed nutrients (Waters 1995). Consequently, these results may not be broadly applicable to natural situations.

Field studies provide even less information about the impacts of sedimentation on mussels. Houp (1993) reported that stream sedimentation over 11 years caused a change in a mussel assemblage, favoring "silt-tolerant" species. The conclusion of assemblage change was based on raw numbers of each species collected on two dates, but sample effort, standardized species abundance, or sampling error were not reported. The occurrence of sedimentation was based on casual and incidental observations with no measurement of substrate or landscape characteristics. It is therefore impossible to conclude from this study that sedimentation affected mussels or even that significant sedimentation or assemblage change occurred. In another study, large mussels from a site with mud substrate appeared to grow slightly more slowly than individuals in sand or gravel (Kat 1982b). However, mussels were equally abundant in all substrate types, variation in growth among individuals was not reported, and there was no effect of substrate on growth of smaller individuals. Similarly, in Lake Erie, mussels in silt grew more slowly than those in gravel or sand (Stansbery 1970), but substrate effects were confounded with depth because silty sites were in the "deep lake" (depth not given), while gravel and sand sites were in shallow water, and no statistical testing of results was conducted. Despite their limitations, these studies are cited widely as support for the negative effects of sedimentation on mussels.

In a major review of the effects of sedimentation on mussels, Brim Box and Mossa (1999, 103) report that "only a few studies (e.g., Cooper 1987, Stewart and Swinford 1995) . . . have specifically attributed changes in mussel populations to agriculturally derived sediments." In reality, neither study makes this link conclusively if at all. Cooper (1987) does not specifically discuss the effects of sedimentation on mussels, but rather mollusks in general (including snails), and abundance was measured only for fingernail clams (Sphaeriidae), which decreased only after periods of high bed load movement. Stewart and Swinford (1995, 60) provide a baseline description of water and habitat quality in a stream for use in future monitoring but did not measure mussel abundance and concluded that "no data are available on the probable levels of suspended silt that may cause deleterious effects on the [mussel] fauna."

In addition to the lack of empirical evidence, a number of observations are inconsistent with the proposed pervasive, negative effects of sedimentation on mussels. Although many mussel species are characteristic of relatively silt-free gravel substrates, these habitat associations are variable, and many species occur frequently or primarily in fine sediments or other fully embedded substrates (Coker et al. 1921; Downing et al. 2000; Brown and Banks 2001; Brim Box et al. 2002; Mueller et al. 2011; Chapter 4). Categorizations of species' tolerance to sedimentation are based on anecdotal or weak evidence, often differ among studies (see Brim Box and Mossa 1999), and, in some cases, do not correspond with observed habitat affinities or responses to sedimentation. For example, the yellow sandshell, *Lampsilis teres*, and washboard, *Megalonaias nervosa*, are considered intolerant to sedimentation (Brim Box and Mossa 1999), but both can be dominant species in depositional habitats (Ahlstedt and McDonough 1993; Haag and Warren 2007; Williams et al. 2008).

Conversely, the fluted-shell, *Lasmigona costata*, was considered tolerant of sedimentation by Houp (1993), but it has disappeared from even riverine sections of reservoirs (Section 10.5.A). Habitat associations are likely determined by life history traits, host use, feeding requirements, predation, and competition (Chapter 8), and responses to sedimentation should vary predictably among species similar to assemblage changes seen after impoundment (Section 10.5.A). In contrast, enigmatic mussel declines attributed to sedimentation affect all species similarly, regardless of ecological differences among species.

Other studies showed conclusive associations between landscape variables and mussel assemblages or declines (Morris and Corkum 1996; Arbuckle and Downing 2002; Gillies et al. 2003; Poole and Downing 2004). These studies propose plausible hypotheses about the relationships between landscape factors and sediment transport to streams and resulting effects on mussel populations but could not specifically identify sediment itself as a causal factor. Attempts to relate mussel abundance to direct measurements of sedimentation or substrate embeddedness similarly provide little support for a primary role of sedimentation. In some cases, mussel abundance was negatively correlated with embeddedness but also with other intercorrelated habitat factors (Baldigo et al. 2003–2004; Nicklin and Balas 2007). These studies did not address mussel declines specifically, and the observed patterns may simply reflect natural habitat affinities of species in those streams. In the Big River, Missouri, mussel species richness and abundance were lowest at sites with high average embeddedness and sediment deposition (Roberts et al. 2009), but these sites also had high sediment concentrations of zinc, cadmium, and lead from mine tailings, which was considered the primary cause of mussel declines. In the Clinch River, mussel species richness was negatively associated with urban and agricultural land use, but these factors explained little of the variation in richness, and substrate embeddedness was not a significant factor. Rather, the distribution of species richness was attributed primarily to impacts from coal mining and past toxic spills (Diamond et al. 2002).

Despite demonstrated associations between mussel declines and land use in several areas, these factors do not show unequivocal negative relationships with mussel assemblages. The highest mussel species richness in New York is found in two streams heavily affected by agriculture, having high turbidity and nutrient concentrations (Strayer and Jirka 1997). Species richness and distribution changed little in the upper Susquehanna River from 1955 to 1997, despite high nutrient and sediment loading (Strayer and Fetterman 1999). Admittedly, these studies occurred in areas with less intensive agriculture than the Great Plains or Gulf Coastal Plain. However, the lower St. Francis River in Arkansas is one of the siltiest rivers I have ever seen and flows through one of the most intensely farmed regions in the United States, yet this stream supports large and healthy populations of at least 36 species, including several rare or endangered species (Jenkinson and Ahlstedt 1993–1994). Although mussels declined throughout the Embarras River, Illinois, from 1955 to 1987, the decline was least severe in the upper river, which was considered "adversely affected by siltation" from agriculture (Cummings et al. 1988, 3).

A commonly proposed mechanism by which sedimentation adversely affects mussels is "smothering," and juveniles are considered especially vulnerable (Ellis 1931; Brim Box and Mossa 1999). Juvenile survival under a range of conditions has been studied carefully because of the interest in rearing juveniles in captivity for use in conservation (Chapter 11). Juveniles reared with fine sediments (deposited and suspended) had higher or similar growth and survival compared with juveniles reared without fine sediment (Hudson and Isom 1984; Gatenby et al. 1996). Juvenile mussels reared in 15 cm of sediment (70% sand, 30% silt) had high survival, maintained position within the top 1 cm, and were observed pedal feeding on sediment particles (Yeager et al. 1994; Section 1.4.A). Moreover, juveniles in streams are frequently found in depositional areas behind boulders (Neves and Widlak 1987). These results do not support low tolerance of juveniles to sedimentation but rather suggest that they depend to some extent on fine sediments for optimal growth. Consequently, higher sensitivity of juveniles to sedimentation cannot reasonably be used to explain the lack of recruitment in streams experiencing enigmatic declines.

Sedimentation also has been proposed to affect mussels indirectly by disrupting aspects of the glochidia–host relationship. Brim Box and Mossa (1999) proposed three mechanisms for this: (1) reduction of fish populations by sedimentation, (2) reduced visibility of mantle lures to fishes due to increased turbidity, and (3) reduced ability of conglutinates of *Ptychobranchus* to adhere to rocks (Chapter 5) due to a coating of sediment. None of these mechanisms are likely explanations for widespread non-species-specific mussel declines. There is little evidence for reduction of fish populations as a factor in enigmatic mussel declines (Section 10.6.B). The potential for disruption of specific host infection strategies by sedimentation is untested, but this mechanism would affect species differentially according to host strategies. High concentrations of suspended clay (1,250–5,000 mg/L) were associated with reduced glochidia attachment and metamorphosis success on host fishes in the laboratory (Beussink 2007). However, even in heavily agricultural watersheds or naturally turbid streams, such high suspended sediment levels are typically seen only for very short periods during storm flows (Borah et al. 2003; Schwartz et al. 2011). Consequently, interference of glochidial metamorphosis by suspended sediment is an unlikely explanation for mussel declines across a range of stream types and landscapes.

A final but crucial inconsistency regarding sedimentation as a cause of enigmatic mussel declines has to do with historical patterns of sediment input into streams. Although sediment is currently considered a major pollutant, there is debate about its relative importance today compared with previous eras. Soil conservation methods such as no-till farming have dramatically reduced soil loss since the 1960s (Blevins and Frye 1993). Sedimentation rates in a small Wisconsin stream increased 4–6 times above presettlement rates following clear-cut logging from 1890 to 1920 and remained

5 times higher than presettlement during peak agricultural activity in the 1920s to 1930s, but rates have decreased in the last several decades (Fitzpatrick et al. 1999). In an Oklahoma reservoir, sediment deposition decreased 83 percent from 1934 to 1987 largely because of conversion from row-crop agriculture to pasture, and recent inputs from roadway erosion, stream bank erosion, and stored stream channel sediment were not significant contributors to contemporary deposition (McIntyre 1993). In Ohio reservoirs, sedimentation rates from agricultural watersheds declined dramatically after the 1940s–1950s, coincident with adoption of soil conservation measures, even though the amount of agricultural land remained constant; however, sedimentation rates were relatively constant over the last 60+ years in urbanized watersheds (Renwick et al. 2005). The widespread perception of high contemporary soil erosion is based primarily on a model, the universal soil loss equation (USLE), not on empirical data, and it predicts loss of sediment from agricultural fields or other exposed ground but not input into streams; consequently, current sedimentation in streams may be overestimated (Trimble and Crosson 2000). For example, sediment input to streams from a 3 km^2 watershed in the 1970s was 8 percent of the amount estimated by the USLE; in contrast, during widespread soil erosion during the Dust Bowl of the 1930s, sediment input to the same watershed was 123 percent of USLE predictions.

These observations suggest that sedimentation rates in recent decades must pale in comparison with those of the late 1800s and early 1900s. For example, nearly all forests in the entire southeastern United States were clear-cut from about 1890 to 1920 (Clark 1984). It is possible that these historical impacts continue to impact stream communities despite recent reduction in sediment input. Sediments deposited years ago may continue to flow through stream systems, and reduction in sediment inputs may cause channel instability as streams downcut into previously deposited sediments (Costa 1975; Walter and Merritts 2008). Nevertheless, mussel populations in free-flowing streams across the continent survived intense soil erosion and sedimentation for more than 60 years. Despite Goodrich's (1931a) unquantified perception that mussel populations declined in the Conasauga River, Georgia, from 1917 to 1930 due to sedimentation from agriculture, road construction, and stream bank clearing (the same activities invoked today), this river continued to support a diverse and abundant fauna into the early 1970s (Hurd 1974). From the 1970s to the 1990s, mussel populations in the river crashed abruptly, a result attributed once again to "poor land use practices" (Evans 2001). If land use practices are poor today, they must have been exceedingly poor in the early 1900s. How did mussels survive?

Because of these inconsistencies and an almost complete lack of direct evidence, it is difficult to consider sedimentation a proximate, pervasive cause of enigmatic mussel declines in free-flowing streams. Excessive sedimentation and its associated effects are certainly not good for mussels or streams in general, and it is prudent to continue to encourage reduction of this potential source of stress. It is plausible, and even likely, that localized, severe sedimentation caused elimination of mussel populations or assemblage changes similar to those seen in impoundments or channelized streams (Section 10.5.A). But sedimentation generally results in long-term, gradual degradation of stream habitats (Waters 1995). Why did mussel populations in so many streams crash abruptly in the last few decades despite a long prior history of sedimentation? And why do healthy mussel assemblages persist in very silty streams? If some species are indeed "tolerant" of, or even dependent on, silt – which seems the case based on observed habitat affinities – these species should be relatively unaffected by sedimentation. Why do enigmatic declines seem to affect all species similarly? These questions suggest that other widespread and insidious factors have played more important roles in mussel declines.

10.6.B. Host fishes

The requirement of having a fish host for reproduction is frequently considered a conservation liability for mussels (e.g., Neves 1993). Indeed, loss of host fishes appears to be a major factor driving mussel assemblage changes in impounded streams (Section 10.5.A). However, for several reasons, disruption of the host relationship cannot explain enigmatic mussel declines. First, although fish populations have declined widely across the continent, in general, fishes appear more resilient than mussels to many types of impacts (Section 10.5.B), and many streams that have experienced enigmatic mussel declines maintain diverse fish faunas (Section 10.5.C). In the Red River, abundance of mussel species remaining after the decline is unrelated to abundance of their host fishes during the same time period (Figure 10.14). Furthermore, the proportion of host generalists extirpated from the stream was similar to specialists (Figure 10.12), showing that broad host range did not increase the probability of persistence. Similar declines across a spectrum of host use have been reported in other streams (Poole and Downing 2004). Second, many imperiled mussels use relatively common host species, including fishes tolerant of degraded habitats (e.g., Bauer 1988; Haag and Warren 2003). Finally, stream habitat degradation often results in predictable changes in fish assemblages, including shifts in trophic and taxonomic structure (Schlosser 1982b; Fausch et al. 1984; Karr et al. 1985). These species-specific patterns would decrease abundance of some host species, but not others, and cannot explain enigmatic mussel declines across host guilds.

10.6.C. Invasive species

Hundreds of nonindigenous animal and plant species are now established in fresh waters of North America, including mammals, reptiles, fishes, crayfishes, bivalves, snails, and planktonic organisms as well as pathogenic microorganisms (Strayer 2010).

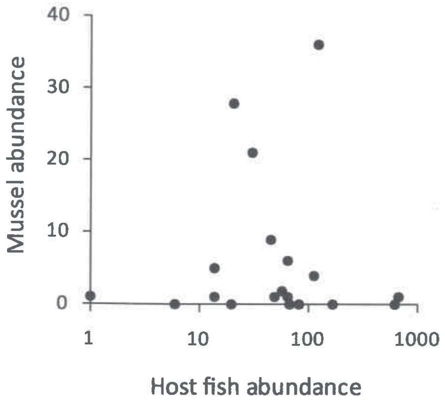

Figure 10.14. Lack of relationship between mussel species abundance and host fish abundance in the Red River, Kentucky, after enigmatic mussel decline. Host generalists are not included. Mussel abundance is the number of live individuals for each species found during surveys in 1987 (Kentucky State Nature Preserves Commission database, Frankfort). Host abundance is the summed abundance of all known host species for each mussel species (host use data from Cummings and Watters 2010). Fish data are composite capture frequencies from seine and electrofishing collections conducted from 1983 to 2000 (Kentucky Division of Water, Frankfort). Note log scale for fish abundance.

About 15 percent of nonindigenous species become invasive after colonization of a new environment (Simberloff 1996). Invasive species may alter native aquatic communities by predation or competition, by modifying physical aspects of the environment, or as parasites or vectors of disease (Strayer 1999b). Aquatic ecosystems in south Florida have been radically transformed by invasive plants and animals, which constitute more than 25 percent of resident species (Ferriter et al. 2005). Zebra mussels (*Dreissena*) have caused major ecosystem changes in parts of North America, including near-elimination of native mussel species (Section 10.4.C). To date, these effects have been relatively localized, and enigmatic mussel declines occurred either before appearance of *Dreissena* in North America or in streams not colonized by this species. Only two invasive aquatic species are established widely throughout eastern North America and have occurred commonly with native mussels for a sufficient period of time such that they may be considered potential causes of enigmatic mussel declines.

10.6.C.1. Common carp

The common carp (*Cyprinus carpio*) was introduced intentionally into North America as a food fish as early as the 1830s but was stocked widely from the 1870s to the 1890s by the U.S. Fish Commission and other groups (Fritz 1987). By 1900, carp were prominent components of fish assemblages across the continent and soon were blamed for negative effects on aquatic habitats and native game fishes. Carp are primarily benthic omnivores that feed by rooting in soft substrates, and large carp can penetrate more than 100 mm into the bottom (Ross 2001). Feeding activities of adult carp can cause increased turbidity and water column phosphorous concentrations due to suspension of fine sediments; increases in phytoplankton due to increased nutrient availability; decreases in benthic macroinvertebrates from direct predation or habitat alteration; and decreases in aquatic plant cover by uprooting, decrease in light penetration, or direct herbivory (Roberts et al. 1995; Zambrano and Hinojosa 1999; Parkos et al. 2003). In a reservoir where carp were removed, sediment export decreased and benthic macroinvertebrate assemblages shifted from burrowing chironomid midge larvae and tubificid worms to species characteristic of coarser sediments, but dominance shifted again to tubificids after carp recolonized the reservoir (Barton et al. 2000). In addition, predation by juvenile carp can suppress zooplankton abundance (Meijer et al. 1990). Direct and indirect effects of carp are suspected to be important in structuring aquatic communities in lentic and wetland habitats (Parkos et al. 2003).

The effects of carp in streams are virtually unstudied, as are their effects on mussels. Carp feeding activities may not result in elevated turbidity, depending on substrate characteristics (Crivelli 1983), and therefore may have less pronounced effects in streams with coarse substrates and little aquatic vegetation (Etnier and Starnes 1993; Parkos et al. 2003). Carp have molariform pharyngeal teeth adapted for crushing and sometimes feed heavily on mollusks. In the Mississippi River, 73 percent of carp fed on zebra mussels (Bartsch et al. 2005). In a lake in Montenegro, carp fed heavily on mollusks but selected thin-shelled snails (*Valvata*) over more abundant zebra mussels, fingernail clams, and heavy-shelled snail species and avoided larger snails (more than 10 mm) altogether (Stein and Kitchell 1975). There are no reports of carp feeding on native North American mussels, but they surely must do so on occasion. However, predation is likely limited to very small individuals of thin-shelled mussel species. In addition to predation, carp feeding activities may have negative indirect effects on mussels, especially in lakes and lentic microhabitats in streams, but overall, they seem unlikely to be a cause of enigmatic mussel declines. The best argument against the widespread negative effects of carp is simply that they have coexisted at high abundance with mussels for more than 100 years and continue to do so in many areas.

10.6.C.2. Asian clams

The Asian clam, *Corbicula fluminea*, is a more plausible culprit in mussel declines. *Corbicula* was first discovered in North America either in Nanaimo, British Columbia, in 1924 or in the Columbia River, Washington, in 1938; the 1924 record is doubtful because *Corbicula* has not been recorded there since (Counts 1981). *Corbicula* is native to southeastern Asia, where it is used widely by humans as food, and it was likely brought to North America by immigrants in the 1920s (Britton and Morton 1979). Over the next 30 years, it spread as far as the Colorado River system in Arizona but appeared suddenly 3,100 km to the east in the lower Ohio River in 1957 and shortly after in the Escambia River, Florida, in 1960, both apparently by unknown human vectors (McMahon 1982; Counts 1986). By the 1970s, *Corbicula* had spread across most of the United States and is now reported from all contiguous states, except Montana, Maine, North Dakota, New Hampshire, and Vermont (Counts 1986). *Corbicula* is still expanding its range in New England (Nedeau 2008), but its northern distribution is limited by intolerance to temperatures less than about 2°C, and it may experience winter kill even in southern parts of its range (Graney et al. 1980).

Corbicula has high fecundity, fast growth, and early maturity (3–6 months), and it is hermaphroditic and able to self-fertilize (McMahon and Bogan 2001). Because of these traits, *Corbicula* is highly invasive and is able to thrive even in disturbed habitats. Abundance may exceed 10,000/m^2, but it fluctuates dramatically seasonally (Gardner et al. 1976; Eng 1979). *Corbicula* does not require a fish host and releases large numbers of juveniles, which are easily suspended in river currents and can be transported downstream great distances. Small adults also may disperse downstream by "ballooning" achieved by producing long mucous threads (Prezant and Charlermwat 1984). The rapid spread of *Corbicula* shows that upstream and interdrainage dispersal also is efficient, but these mechanisms are poorly known. Human transport has undoubtedly played a large role in interdrainage transfers. In Massachusetts ponds, where *Corbicula* winter kills frequently, it is found mostly near public boat launches, suggesting that boaters reintroduce the species regularly (Nedeau 2008). Natural upstream dispersal also occurs rapidly. In a South Carolina stream, *Corbicula* moved upstream about 1.2 km/yr (Voelz et al. 1998). This movement was attributed to crawling by juveniles or adults, but entanglement of juvenile byssal threads on waterfowl or, more likely, fishes may allow more rapid upstream dispersal (McMahon 1982; Barnhart et al. 2008). Nevertheless, even in regions where it has been present for more than 40 years, it remains absent in some headwater streams, where it may be limited by periodic drought (Strayer 1999b; Haag and Warren 2008).

The appearance of *Corbicula* in the eastern United States coincides closely with the timing of enigmatic mussel declines. *Corbicula* first appeared in Illinois in 1962, roughly corresponding with mussel declines in the Embarras and other rivers between the late 1950s and the 1980s (Cummings et al. 1988). In the Altamaha River, Georgia, populations of fingernail clams (Sphaeriidae) crashed and ultimately disappeared over a 1 year period during which newly arrived *Corbicula* reached abundances greater than 700/m^2, and anecdotal observations suggested that unionid abundance also declined dramatically (Gardner et al. 1976). Similarly, colonization of *Corbicula* in the Little Tennessee River, North Carolina, in 2004 coincided with a sharp decline in native mussel species (R. Butler, personal communication).

Despite this compelling temporal concordance, most evidence that *Corbicula* has strong and pervasive negative effects on mussels is equivocal. Proposed mechanisms by which *Corbicula* may negatively affect mussels include competition for food and space; ingestion of mussel sperm, glochidia, and juveniles; and lethal effects of ammonia and low dissolved oxygen produced by periodic *Corbicula* die-offs (reviewed in Strayer 1999b). Dense *Corbicula* populations can remove a substantial percentage of suspended material from the water (Cohen et al. 1984; Lauritsen 1986; Leff et al. 1990), in some cases resulting in major ecosystem changes (Phelps 1994), and filtration rates of individual *Corbicula* are approximately 4 times higher than *Elliptio complanata*, despite the native mussel's much larger size and tissue mass (Leff et al. 1990). In field experiments, growth of *Elliptio* sp. appeared to decrease with increasing *Corbicula* density (Belanger et al. 1990). However, the magnitude of difference in average growth was small (about 1.8 mm/5 months with no *Corbicula* compared to 1.1 mm with *Corbicula*), there was no correlation between *Corbicula* density and mussel growth (see Strayer 1999b), and *Elliptio* apparently survived (and grew) even at *Corbicula* densities of 3000/m^2. The only conclusive evidence of negative feeding interactions is from a laboratory study in which survival and growth of juvenile mussels in 0.4 liter containers decreased with increasing numbers of *Corbicula*; juvenile mortality was 30 percent in controls but 100 percent in the presence of eight or more *Corbicula* (representing a density of about 1,300/m^2) (Yeager et al. 2000). Glochidia and juvenile mussels also were ingested by *Corbicula* through the siphons or captured by the foot during pedal feeding, where they became entangled in pseudofeces. In another experiment, recently metamorphosed juveniles (2–4 days old) were displaced from the substrate and washed downstream more frequently in the presence of *Corbicula*, but older juveniles (14–21 days old) were not displaced (Yeager et al. 2000).

Corbicula populations frequently experience massive die-offs in response to low dissolved oxygen in summer or to cold temperatures. Elevated ammonia and reduced dissolved oxygen (DO) concentrations due to decay of *Corbicula* tissues after die-offs have been proposed as lethal to mussels. Die-off of *Corbicula* occurring at 10,000/m^2 in an artificial stream resulted in DO below a level that caused mortality of juvenile mussels in another study (1–2 mg/L; Sparks and Strayer 1998), and ammonia peaked at levels 10 times higher than lethal concentrations for adult mussels and 40 times higher for juveniles and glochidia (Cherry et al. 2005). Similarly, decomposing *Corbicula* tissues in 1 liter flow-through test chambers (1 hour turnover time) resulted in substrate pore water ammonia concentrations that exceeded lethal limits for mussels, and pore water ammonia was always higher than in the water column (Cooper et al. 2005). These results show that *Corbicula* die-offs could cause mussel mortality in some situations. However, they are difficult to apply to real-world situations, primarily because of the low flow and small volume in the test chambers and the high abundance of *Corbicula* used. Effects of *Corbicula* die-offs on water quality are probably much less dramatic in flowing streams and at *Corbicula* densities more commonly seen in the wild.

Despite its potential to reach extraordinarily high abundance, typical average density of *Corbicula* is more modest, ranging from less than 1 to 300/m^2 (Smathers 1990; Miller et al. 1992a, 1992b; Haag and Warren 2008). Even when present

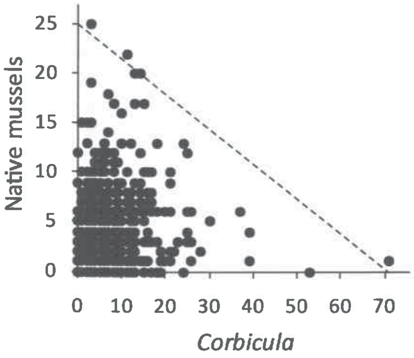

Figure 10.15. Abundance (number/m^2) of native mussels and Asian clams (*Corbicula fluminea*) in quadrat samples from the Sipsey River, Alabama, 1999–2008 (W. R. Haag and M. L. Warren, unpublished data).

at high densities, *Corbicula* often coexists with diverse, dense, and reproducing mussel assemblages. In the Ohio River, *Corbicula* occurred at 1,475/m^2 along with a mussel assemblage of 26 species and overall density of 150/m^2 (Miller et al. 1986). Furthermore, within a stream site, *Corbicula* and mussels often occupy different microhabitats such that the highest abundance of *Corbicula* occurs where mussel abundance is low, and vice versa (Vaughn and Spooner 2006b; Figure 10.15). This nonoverlapping distribution has been explained by competition that makes mussels unable to persist in habitats with high *Corbicula* abundance (e.g., Belanger et al. 1990). However, the opposite explanation is equally plausible, if not more likely. The high filtration rate of *Corbicula* is offset by its fast growth and high metabolic rate such that its equilibrium resource requirements may be comparable to or even higher than slower-growing mussels; this means that *Corbicula* may in fact be a poorer competitor (Strayer 1999b; Vaughn and Spooner 2006b). Within the context of mussel life history strategies, *Corbicula* can be considered an extreme example of an opportunistic species that thrives only in unstable habitats where competition from other species is low (Chapter 8). Consequently, in streams with large mussel populations, *Corbicula* may reach high abundance only in habitats unsuitable for native species but can occupy a wider range of habitats in streams that have lost their mussel fauna. Such a relationship could explain the frequent observation that *Corbicula* populations explode when mussel populations decline due to other, unrelated factors (McMahon and Bogan 2001).

Abundance of *Corbicula* therefore may be a symptom of mussel declines rather than a sole or initial cause. However, negative effects of *Corbicula* on mussels cannot be discounted altogether. As mussel populations begin to decline from other impacts, a concomitant increase in abundance of *Corbicula* may hasten the decline by having a negative effect on survival of juvenile mussels. Negative effects on water quality may have occurred during the initial phases of *Corbicula* colonization if it reached very high abundance typical of recently arrived invasive species. Massive die-offs occurring during equilibration to stable levels may have caused extensive mortality of native mussels. In several streams that have experienced enigmatic mussel declines, I have seen that much of the substrate is composed of old, weathered *Corbicula* shells, but few live individuals are present, suggesting a boom and bust cycle after initial colonization. But again, if *Corbicula* are poor competitors for food, an initial decline in mussel abundance may have been necessary to facilitate explosion of the *Corbicula* population. Like common carp, another difficulty with invoking *Corbicula* as an explanation of enigmatic mussel declines is that mussels can coexist with high densities of *Corbicula*, and enigmatic declines have occurred even in streams that have been inhabited by *Corbicula* for more than 25 years (e.g., Hanlon et al. 2009). Although *Corbicula* have been prominent constituents of bivalve faunas in the eastern United States for nearly 50 years, we are still a long way from understanding their interactions with native mussels.

10.6.D. The role of stochastic processes

Because of the fragmentation of stream systems after systematic habitat destruction, enigmatic mussel declines may simply have been an inevitable result of natural stochastic processes in isolated populations (Section 10.4.B). Despite the many examples of population extinction from these effects, they are unlikely to be generally responsible for enigmatic mussel declines. The risk of extinction due to demographic and environmental stochasticity is inversely proportional to population size. Consequently, we would expect rare species to decline more rapidly from these effects, while more abundant species are relatively unaffected or decline more gradually over a longer period. Furthermore, life history traits such as age at maturity and reproductive investment are predicted to influence vulnerability to stochastic processes (Kokko and Ebenhard 1996), and species that use more mobile host fishes are expected to be less vulnerable than species whose hosts have low dispersal distances (Strayer 2008). These expectations are at odds with the typical pattern in which all species in assemblage experience proportionally similar declines regardless of initial abundance or life history attributes (Section 10.5.C).

The critical population size below which stochastic effects become important is unknown for mussels. Across a range of other organisms, demographic stochasticity is considered an improbable cause of extinction in populations larger than 50–100 individuals (Shaffer 1981; Kokko and Ebenhard 1996). Similarly, a population size of 50 reproducing adults is considered sufficient to avoid inbreeding depression, and 500 is considered sufficient to maintain potential for adaptive change (Franklin 1980). Maximizing long-term chances of persistence may require much larger population sizes, and differences in life histories and mating systems can increase minimum viable population sizes still further (Kokko and Ebenhard 1996; Traill et al. 2010).

Nevertheless, severe reductions in population size appear necessary for rapid manifestation of stochastic effects.

Enigmatic declines are notable for their occurrence throughout even large stream reaches or river systems, but initial population sizes in these streams are unknown. In healthy streams, total mussel population size at individual sites ranges from 11,000–50,000, corresponding to average densities of 2–38 mussels/m^2 (Smith et al. 2001; Haag and Warren 2010). Throughout the length of French Creek, Pennsylvania, total mussel population size is estimated at 22 million animals with an average density of about 10/m^2, and even the rarest species in the stream has a population of about 22,000 individuals (Smith and Crabtree 2010). French Creek is similar in size (3,200 km^2 watershed) to streams, such as the Embarras (6,306 km^2) and Red Rivers (3,838 km^2), that have experienced enigmatic mussel declines (Section 10.4.D). Even if these rivers had substantially lower initial densities, they doubtlessly supported very large mussel populations. It seems inconceivable that these large populations – especially those of dominant species – would be subject to rapid declines from stochastic processes even after isolation from other populations.

Another piece of evidence against stochastic processes comes from biogeographical patterns. The observation that species richness increases in successively larger areas, the species–area relationship, is one of the most pervasive patterns in ecology. The slope (z) of the log–log relationship between area and species richness varies according to whether assemblages in a particular region (say, a river system) function as isolates (or "islands"; i.e., they function more or less independently), or as subsets of a regional, or "mainland," fauna (i.e., they are dependent on colonization from a larger species pool). On the basis of studies of a large number of organisms, z is about 0.27 for isolates and 0.15 for regional subsets (Rosenzweig 1995). The species–area relationship therefore allows us to make predictions about expected species richness in a particular river system using the equation

$$S_t = \left(\frac{A_t}{A_r}\right)^z S_r,$$

where S_t is the predicted number of species in a tributary; S_r is the observed number of species in the regional pool (in this case, in the entire river system); A_t and A_r are the watershed area of the tributary and the entire river system, respectively; and z is the slope of the species–area relationship (Sheldon 1987). We can then evaluate whether a tributary functions as an isolate or as a subset of a regional fauna by comparing whether observed species richness in the tributary conforms more closely to predicted values generated using the z value for isolates (0.27) or regional subsets (0.15).

This approach was applied to the fish fauna of a tributary in a large river system (Sheldon 1987). The tributary was predicted to behave as a subset of the regional fauna and to have an excess of fish species, many of which are maintained by immigration from larger rivers. Consequently, severing the connectivity between the tributary and

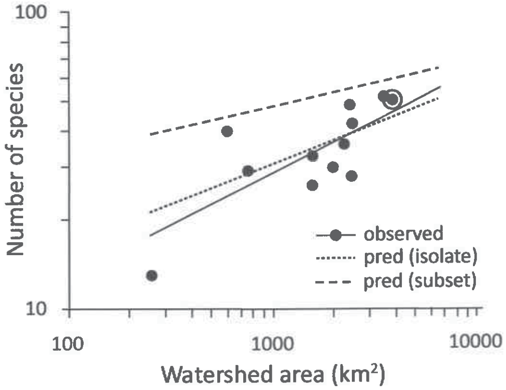

Figure 10.16. Species–area relationships for major tributaries of the Cumberland River, Kentucky and Tennessee. Predicted lines (pred) were generated using slopes (*z*) for streams functioning as isolates (0.27) and subsets of a regional fauna (0.15) (see text). The circled point is the Red River system (from M. L. Warren and W. R. Haag, unpublished data).

the remainder of its river system would produce a large extinction debt, resulting in a sharp decrease in diversity over time.

I applied the same approach to a data set for mussels in the Cumberland River system, to evaluate whether, in the absence of other impacts, the Red River and other tributaries could have functioned as isolates after destruction of the regional species pool in the main stem Cumberland River or if these were regional subsets having an excess of species sustained by immigration. The species–area relationship using the *z* value for isolates predicts observed mussel richness in tributaries remarkably well, but the relationship for subsets consistently overestimates richness by a wide margin (Figure 10.16). This strongly suggests that tributaries, including the Red River, functioned largely independently of the main stem Cumberland River. There was certainly dispersal and exchange of individuals among streams over time, particularly in the lower reaches of tributaries, and a few species may have indeed been sustained primarily by immigration from the main stem (Section 10.4.B). However, isolation from the regional species pool followed by loss of species from stochastic processes cannot be invoked as an explanation for enigmatic mussel declines; rather, these tributary systems were large enough to support nearly their entire historical faunas, and other factors must be responsible for the drastic loss of species.

10.6.E. Other insidious factors

The abrupt and pervasive nature of enigmatic mussel declines suggests that one or only a few serious but insidious factors have affected streams similarly over a large area in a relatively short time. This is a reason sedimentation has received so much attention despite a lack of supporting evidence: sedimentation is ubiquitous and can be implicated nearly anywhere. However, for the reasons given in Section 10.6.A, it seems clear that we should focus on other factors. Plausible factors need to be not only ubiquitous but, because enigmatic declines often seem to affect mussels to a much greater extent than other organisms, they also must be something to which mussels are inordinately sensitive or something specific to mussels. The following factors could satisfy these requirements: (1) synthetic pesticides; (2) ammonia and associated compounds; (3) other endocrine disrupters; and (4) disease. These factors have been considered for many years (e.g., Fuller 1974) and have received increased attention recently. Nevertheless, I believe the potential importance of these factors has been overshadowed by continued focus on sedimentation or vague factors such as "poor land use practices."

10.6.E.1. Pesticides

Widespread use of synthetic pesticides began in the United States in the 1940s. Pesticide use increased exponentially and became commonplace in the mid-1960s, peaked about 1982, and has been relatively stable since (Nowell et al. 1999). Herbicide use increased most dramatically in part because of adoption of no-till agricultural methods (see subsequent discussion). Agriculture consumes about 77 percent of total pesticide use, but although residential homes and gardens make up only about 1.2 percent of U.S. land area, they represent 12 percent of annual pesticide consumption (Aspelin 2003). Pesticides also are used widely in controlling forest pests in silviculture and in controlling vegetation on highway right of ways. Where I live, the trucks that apply herbicides along highways often do not turn off the sprayer as they approach a small stream but simply continue spraying across the stream valley. Over 20,000 pesticides are currently registered for use in the United States, and more than 1 billion tons is applied annually on as much as 17 percent of the total area of the country (Aspelin 2003). Pesticide residues are a pervasive presence in the air, surface water, and groundwater and in tissues of animals, including humans (Nowell et al. 1999).

The negative effects of pesticides on wild animals, plants, and humans have been noted widely and, along with severe water pollution, were a catalyst in the rise of the environmental movement in the 1960s (e.g., Carson 1962). Early synthetic insecticides used from the 1940s to the 1970s were acutely toxic to many life-forms in addition to targeted pests. Most infamous is the organochlorine pesticide DDT, but many equally toxic compounds were used widely. As early as 1950, extensive fish kills attributed to pesticide application occurred in 14 tributaries of the Tennessee River system alone, and throughout the 1960s, pesticide-related fish kills were common across the United States (Johnson 1968). DDT was reported to essentially eliminate aquatic insect populations, but recolonization by aerial adults occurred rapidly (Johnson 1968). Many of these compounds also are powerful endocrine disrupters, causing an array of sublethal effects, including abnormal thyroid function, feminization or masculinization, decreased fertility, and alteration of immune function

(Colburn et al. 1993). Furthermore, most are highly persistent in the environment. The half-life of DDT is about 15 years in soil, 350 days in surface waters, and 31 years in groundwater (Howard 1991). Many of these compounds vaporize readily and are dispersed globally in the atmosphere; DDT was detected in Antarctic penguins as early as the 1960s (George and Frear 1966). Because they are insoluble in water, they can accumulate in sediments and animal body fat at concentrations 10^5–10^7 times ambient concentrations in water (Lu and Metcalfe 1975). Consequently, organisms experience chronic exposure over long periods, even minute ambient quantities can cause widespread ecological effects, and these pesticides or their residues remain common contaminants in aquatic ecosystems today.

Pesticides in current use are generally less persistent than earlier compounds, and their safety is widely touted. These compounds target biochemical pathways specific to plant or insect pests, and many are not acutely toxic to other organisms, except at very high concentrations not typically seen in the environment. However, these compounds are far from benign and are a ubiquitous presence in many rural watersheds that have few other human impacts. For example, from 1999–2000 all water samples from the Flint River system, Alabama, had detectable levels of at least two current-use pesticides, and 64 percent of samples had mixtures of at least five pesticides (Hoos et al. 2002). Atrazine, first registered in 1958, remains one of the most important and widely used herbicides in the world and is applied to most of the corn crop in the United States (USEPA 2011). Atrazine is persistent under some conditions and is prone to leaching into surface and ground waters. In 2007, atrazine was detected in 75 percent of stream water and 40 percent of groundwater samples in agricultural regions in the United States and is frequently present in drinking water and precipitation (Graymore et al. 2001; Wu et al. 2010). Even in nontarget organisms, atrazine acts as an endocrine disrupter and can accumulate in tissues (Allran and Karasov 2000). It is implicated in global amphibian declines because concentrations commonly seen in surface waters can alter development of sex characteristics and cause edema (possibly due to renal dysfunction) in frogs, and chronic exposure can be lethal (Howe et al. 1998; Allran and Karasov 2000; Hayes et al. 2002); similar effects are seen in fish (Graymore et al. 2001). There also is evidence of reproductive effects in humans, and atrazine was banned in the European Union in 2004 (Wu et al. 2010). I have singled out atrazine as an example, but many other current-use pesticides are of similar concern (Colburn et al. 1993; Wang et al. 1994; Donald et al. 1999), and the full range of environmental effects of modern pesticides is poorly known.

Current-use pesticides can have a broad range of indirect environmental effects. Pesticide registration in the United States requires testing only of the active ingredient and not the formulation applied to the field. Most pesticide formulations contain a wide variety of other ingredients, including surfactants, which allow penetration of the waxy cuticle of plants. The active ingredient in the common herbicide Roundup (glyphosate) is not toxic to frogs, but the surfactant (MON 1040) causes high mortality

(Howe et al. 2004; Relyea 2005). Pesticides degrade into a variety of metabolites after application, and some of these compounds can be more toxic or toxic to a broader array of organisms than the pesticide itself (Graymore et al. 2001). The effect of most of these metabolites is unknown, and their behavior may differ from the parent compound. High concentrations of the herbicide metolachlor occurred in the Embarras River, Illinois, only during planting season, but a metabolite was persistent and ubiquitous year-round (David et al. 2002). Pesticides can have cascading environmental effects. At common environmental concentrations, atrazine and likely other herbicides can kill aquatic macrophytes, periphyton, algae, and possibly bacteria; in turn, these effects result in decreased dissolved oxygen and primary production, followed by increases in nitrites, nitrates, and ammonia, and finally, reduced growth or higher mortality of zooplankton, invertebrates, amphibians, and fish (Graymore et al. 2001).

Rapid increases in pesticide use from the 1960s to the 1980s can be linked circumstantially to enigmatic mussel declines because the timing and spatial extent of these events coincide closely. While conducting mussel surveys, I have talked with farmers at several different places, including the Red River, Kentucky, who stated to the effect "this river used to be full of mussels until we went to no-till." Another farmer reported that he frequently used mussels as bait until they disappeared abruptly, and he directly implicated adoption of no-till as a cause (M. L. Warren, personal communication). The rapid decline of mussels in the Conasauga River, Georgia, was coincident with adoption of no-till practices and widespread installation of drain tiles in agricultural fields that delivered runoff directly to the river (P. Johnson, personal communication). No-till farming methods dramatically reduce soil loss from fields and presumably inputs to streams (Section 10.6.A) and also appear to reduce greenhouse gas emissions (Omonode et al. 2010). However, no-till typically depends on increased herbicide treatment instead of tillage to control weed pressure (Blevins and Frye 1993). Although soil loss is reduced, water runoff from fields is not reduced as effectively, and water penetration may be increased. Consequently, pesticides and fertilizers may continue to be transported to streams and groundwater. Even in conventional farming methods, mechanical weed control was largely abandoned in favor of herbicide use during the 1960s and 1970s. Because they are applied mainly during the growing season, particularly during preparation for planting, pesticides are typically present in streams at highest concentration from about April–July (Graymore et al. 2001; Hoos et al. 2002), coinciding with the period of mussel reproduction and juvenile recruitment for most species. Finally, the occurrence of enigmatic declines appears concentrated in the central United States, especially within areas of intensive agriculture. For example, the Embarras and Red river watersheds both support intensive corn and soybean production.

Pesticides have long been implicated in mussel declines, and it was assumed that early life stages are more sensitive to exposure than adults (e.g., Fuller 1974; Neves 1993). However, given their pervasive presence in the environment, research on the effects of pesticides on mussels is curiously limited. Most mussel toxicity research has focused on heavy metals and other contaminants such as ammonia (reviewed in Keller et al. 2007). Heavy metals are doubtless important in some cases but are associated primarily with point source industrial or mining discharges, and the prevalence of elevated ammonia in natural waters remains unclear (but see Section 10.6.E.2). Pesticides may have received less attention because, although some studies show high sensitivity of mussels to pesticides (Conners and Black 2004), others show that acute toxicity to expected environmental concentrations is low, including for early life stages, and mussels may be less sensitive than some other aquatic organisms (reviewed in Keller et al. 2007; see also Milam et al. 2005; Bringolf et al. 2007a, 2007b). I am aware of only one field study that specifically attributed a mussel die-off to acute pesticide poisoning (Fleming et al. 1995).

As for amphibians, acute toxicity of active ingredients may not reflect the potential role of pesticides in mussel declines. Although the active ingredient in the herbicide Roundup, glyphosate, was not acutely toxic to glochidia or juvenile mussels, the acute threshold for the surfactant was the lowest reported for any organism, and high mortality occurred at levels exceeding expected environmental concentrations (Bringolf et al. 2007c). Chronic or sublethal effects also may be important. Juvenile mussel growth was reduced at sublethal concentrations of atrazine and permethrin (Bringolf et al. 2007b, 2007c). Similarly, three different insecticides were not acutely lethal to mussels, but they reduced shell closure responsiveness and caused a 40–96 percent decrease in acetylcholinesterase (ChE) activity relative to controls, suggesting that chronic exposure could lead to high mortality; furthermore, higher concentrations of insecticide were required to depress ChE activity in *Corbicula*, suggesting a higher sensitivity of native mussels (Moulton et al. 1996; Doran et al. 2001). Environmental concentrations of atrazine altered mussel movement and aggregation behavior (Flynn and Spellman 2009), suggesting that endocrine disruption may occur similarly to that seen in frogs. High concentrations of estrogenic compounds from an agricultural watershed (likely originating from pesticides) produced physiological responses in mussels indicative of interference with sexual differentiation and development (Gagné et al. 2001). These studies show that pesticides can negatively affect mussels in many ways, but the full range of long-term effects remains unknown.

Several other important pieces of the pesticide story are missing. First, all toxicity tests on pesticides to date were conducted without sediment. Some types of pesticides or associated compounds such as surfactants can adsorb to sediments where they accumulate at higher concentrations and persist longer than in the water column (see Yeager et al. 1994, Bringolf et al. 2007c). Because juvenile mussels appear to feed predominantly within the sediment, they may be exposed to higher and chronic concentrations of these contaminants, potentially explaining the lack of recruitment in many streams experiencing enigmatic declines (Yeager et al. 1994). Second, pesticides may interact antagonistically or additively with other compounds, and their effects may change according to environmental conditions (Cairns et al. 1975). Toxicity to frogs of atrazine and alachlor in combination was about 2 times greater than exposures to single chemicals (Howe et al. 1998), and similar additive effects of pesticides are demonstrated for mussels (Conners and Black 2004). Interactions of pesticides with other contaminants or with environmental conditions have not been well studied in mussels. Third, indirect biotic effects of pesticides may be important. Reductions of algae and bacteria populations by herbicides may critically decrease mussel food resources, particularly for rapidly growing juveniles. Tadpoles exposed to environmental concentrations of atrazine had higher incidence of trematode infestation than controls, suggesting that exposure reduced parasite resistance (Koprivnikar et al. 2007). Finally, almost nothing is known about the effects of earlier, persistent pesticides on mussels. Like many other organisms, mussels accumulate these compounds at high rates. *Amblema plicata* exposed to the organochlorine insecticide dieldrin at 20 parts per trillion concentrated the compound 2,500 times above this level (Fikes and Tubb 1971). Pesticides such as DDT had catastrophic effects on fishes and other aquatic organisms, and it is likely that they had similar acute or chronic effects on mussels. These compounds often accumulated at high concentrations in lake or stream sediments, where they may have had catastrophic effects on juvenile mussels and may have limited recruitment for many years.

Considering the pervasive presence of pesticides in streams and lakes and the widespread effects of these compounds on aquatic ecosystems, it is puzzling that they have not received more intense scrutiny as a potential factor in enigmatic mussel declines. Many case studies of mussel declines – even in intensely agricultural watersheds – do not mention pesticides as a possible cause but focus instead on sedimentation (e.g., Cummings et al. 1988; Arbuckle and Downing 2002; Poole and Downing 2004; but see Fuller 1980). Similarly, most general reviews of mussel declines mention pesticides only in passing (e.g., Bogan 1993; Neves et al. 1997; Downing et al. 2010). Commonly invoked causes of mussel declines may be only indirect mechanisms that interact with pesticide contamination. For example, because many pesticides or surfactants can adsorb to sediment particles, sedimentation may be simply a vector for pesticide transport to streams rather than a primary cause of declines. Similarly, the observation that mussel declines in an agricultural landscape were less severe in watersheds with deep alluvial deposits (Arbuckle and Downing 2002) could be explained by a greater capacity for pesticide degradation during movement through these deposits, in contrast to steeper watersheds, where contaminants are delivered to streams more rapidly. Such a mechanism could explain the persistence of mussels in rivers that flow through extensive alluvial plains (e.g., the St. Francis River, Arkansas) despite intensive row-crop agriculture in these watersheds. The more severe declines seen for mussels compared to other aquatic organisms could be a function of higher sensitivity to direct or indirect effects of pesticides or may be simply an artifact of the higher recolonization potential of fishes and aquatic insects. Enigmatic mussel declines could be a legacy of past use of persistent pesticides, but the potential for continuing effects of current-use compounds also is high.

10.6.E.2. Ammonia and other nitrogenous compounds

In addition to pesticides, ammonia is one of the few pollutants of pervasive occurrence sufficient to warrant its examination as a cause of enigmatic mussel declines. Ammonia occurs naturally as a metabolic waste product of aquatic organisms, particularly heterotrophic bacteria that feed on organic matter. It exists in two forms, ammonium (NH_4^+) and unionized ammonia (NH_3), the latter of which is highly toxic to aquatic organisms. The potential for ammonia toxicity in natural systems is reduced by nitrifying bacteria that rapidly convert ammonia to nitrates, which are far less toxic. However, this balance can be disrupted by high inputs of nitrogenous compounds, such as fertilizers, and even nitrates may have a range of negative effects on aquatic organisms, including acting as endocrine disrupters (Pelley 2003; Camargo and Alonso 2006). Furthermore, bacterial nitrification declines with decreasing dissolved oxygen concentration and can therefore result in further increases in ammonia in eutrophic situations. Mussels, especially in early life stages, are more sensitive to unionized ammonia than other organisms, and high sensitivity is seen across a range of species and life histories including species that are adaptable to other human impacts such as impoundment (Augspurger et al. 2003; Wang et al. 2007). The inordinate and broad sensitivity of mussels to ammonia, along with the timing of human–induced changes in nitrogen cycling, makes ammonia toxicity a potentially important factor in enigmatic mussel declines.

The most obvious and acute anthropogenic sources of ammonia or other nitrogenous compounds are point source inputs of organic matter from industrial waste, municipal wastewater treatment plants, and agricultural feed lots. Like heavy metal contamination, these sources doubtless have negative effects on mussel populations locally but are relatively limited in occurrence. Atmospheric deposition of nitrogenous compounds from combustion of fossil fuels represents a widespread non-point source and can cause acidification of surface waters, but this effect is most prevalent in highly industrialized regions and in poorly-buffered waters, which support few mussel species (Camargo and Alonso 1996; Section 4.1.C). Agricultural fertilizers represent another widespread non-point source of nitrogen but have a much greater potential for affecting mussels in a variety of habitats. Similar to pesticide contamination, enrichment of streams and lakes by synthetic fertilizers is nearly ubiquitous and has increased exponentially since the 1960s (Vitousek et al. 1997) and is therefore coincident with enigmatic mussel declines both in scope and timing.

Enrichment by fertilizers can result in eutrophication of aquatic ecosystems through increased primary production of organic matter which, in turn, results in increased decomposition rates and reduced dissolved oxygen and potentially, increases in ammonia (Strayer 2008). Because running waters are usually well-oxygenated, eutrophication is generally considered less severe in streams than in lakes (Vitousek et al. 1997). However, eutrophication – as well as acidification – may negatively affect some mussel species that are dependent on low-productivity and poorly-buffered habitats (e.g., *Alasmidonta* spp., *Margaritifera margaritifera*; Strayer 1993). A much broader threat is that high inputs of nitrogen from fertilizers could cause increases in ammonia, leading to direct toxicity for a wide range of mussel species.

Nitrogenous compounds in rivers have more than doubled since the 1960s (Vitousek et al. 1997), but the extent to which these increases pose a threat to mussels remains unclear. In agricultural watersheds in Michigan, the presence of row-crop agriculture was strongly associated with elevated nitrate concentrations in streams but not with ammonia, suggesting that nitrifying bacteria eliminate much of the ammonia that is either delivered as runoff or produced in situ (Johnson et al. 1997). Similarly, in the Conasauga River, Georgia – a stream that has experienced a severe, enigmatic mussel decline (Section 10.6.A) – levels of total nitrogen in water samples and the concentration of δN^{15} (an indicator of anthropogenic nitrogen enrichment) in snail tissues were positively correlated with the percentage of agricultural land upstream of study sites (Sharpe and Nichols 2007). Ammonia also was positively correlated with agricultural land use but concentrations never exceeded current US Environmental Protection Agency (USEPA) acute criteria for the protection of aquatic life (5.6 mg N/L), and exceeded chronic criteria (1.2 mg N/L) only once, immediately after dairy cow manure was applied to a field adjacent to the river. However, current USEPA criteria were developed prior to availability of mussel ammonia toxicity data and are not protective of mussels due to their inordinate sensitivity. On the basis of proposed revisions to these criteria (USEPA 2009; see also Wang et al. 2008), total nitrogen in the Conasauga River exceeded chronic criteria for the protection of mussels (0.26 mg N/L) at all agricultural sites for much of the 6-month duration of the study (Sharpe and Nichols 2007).

An additional concern is that enrichment and eutrophication could interact with sedimentation to further disrupt nitrogen cycling. Increases in substrate embeddedness from sedimentation could reduce interstitial oxygen concentrations, which reduces the ability of nitrifying bacteria to detoxify ammonia delivered to streams by agricultural runoff or produced in situ by decomposition of organic matter; this effect could be most severe in areas with alkaline waters, such as the midwestern United States, because the balance between nontoxic ammonium and toxic unionized ammonia is shifted toward unionized ammonia at higher pH (Strayer 2008). Ammonia concentrations in the upper Mississippi River were higher in sediments than in the overlying water, a result attributed to sedimentation and reduced oxygen concentration in the substrate (Frazier et al. 1996). Maximum ammonia concentrations (10 mg N/L) were more than 3 times higher than acute lethal levels for mussels but were found only in sediments more than 8 cm deep and not at shallower depths typically inhabited by juveniles. However, adult mussels that burrow more deeply also are sensitive to ammonia but lethal levels are not well known (T. Augspurger, personal communication). Moreover, the higher and potentially highly toxic levels of ammonia in sediments suggest that routine water testing may underestimate the threat to mussel populations even when more appropriate criteria are used. Indeed, adsorption of ammonia onto sediment particles was considered a potential explanation for the low ammonia concentrations seen in water samples from agricultural streams in Michigan (Johnson et al. 1997; see previous discussion).

The ubiquity and timing of increased enrichment of streams by nitrogenous fertilizers, the inordinate and broad sensitivity of mussels to ammonia, and the potential interaction with sedimentation – another ubiquitous factor in streams – provides a compelling, alternate or additional explanation for enigmatic mussel declines. Like pesticides, the effects of ammonia and other nitrogenous compounds are complex and vary widely according to environmental conditions and other factors. Despite its challenges, this topic is the focus of increased recent research, which may clarify its role in mussel declines.

10.6.E.3. Other endocrine disrupters

A more recent contaminant threat involves endocrine disrupters from human and agricultural pharmaceuticals. Pharmaceuticals, including birth control drugs, antidepressants, hormones used in cancer therapy, and livestock growth hormones, are increasingly common in rivers and lakes worldwide and originate mainly from municipal sewage effluents or livestock confinement facilities (Gagné et al. 2001; Fent et al. 2006). These compounds can have sublethal effects in wild animals similar to pesticides, mimicking natural hormones such as estrogen and altering normal physiological processes, particularly those related to metabolism and reproduction. Endocrine disrupters in municipal effluents affect mussels in a number of complex ways, including by increasing serotonin and dopamine levels and inducing spawning in gonadal tissue in vitro (Gagné and Blaise 2003; Gagné et al. 2004). Chronic exposure to estrogenic compounds in effluents caused feminization of male mussels, but these individuals did not produce eggs, suggesting major disruption of reproductive function (Gagné et al. 2011). A similar mechanism caused the collapse of a minnow population in a lake experimentally spiked with environmental concentrations of an estrogenic contaminant (Kidd et al. 2007). The long-term effects of these compounds on mussels and aquatic organisms in general are unknown. At present, these effects are probably limited to areas near municipal sewage discharges (e.g., Gagné et al. 2004), and their relatively recent occurrence makes them unlikely culprits in most enigmatic mussel declines. However, as these compounds become more prevalent in the environment, the scope of their potential effects on mussels will increase.

10.6.E.4. Disease

Marine bivalves are affected by many diseases caused by viral, bacterial, fungal, trematode, and protozoan parasites. These diseases are most prevalent in cultured bivalves but also occur in wild populations, and they can cause rapid and extensive mortality. Most identified bivalve diseases are highly species specific, and even closely related species may be resistant (Lane and Birkbeck 2000; Allam et al. 2006), or prevalence and virulence differ among species (Lassalle et al. 2007; Beaz-Hildalgo et al. 2010). However, exposure to environmental contaminants can weaken bivalve immune responses, making them more susceptible to infectious disease and broadening pathogen host specificity (Pipe and Coles 1995; Morley 2010).

The potential role of disease in freshwater mussel declines has received the least attention of any proposed mechanism. Mussels commonly harbor a variety of metazoan parasites, especially mites and trematodes. Trematodes can castrate mussels by consuming gonadal tissue, but the incidence of trematode infection is normally low and often differs among species (Section 6.2.C). Trematode infection has not been linked to mussel declines (e.g., Scholla et al. 1987), and there is evidence that trematodes may be more sensitive to environmental contaminants than mussels themselves (Grizzle and Brunner 2009). Similarly, mites are common, often ubiquitous, parasites or commensals of mussels, but strong, adverse effects have not been shown (Grizzle and Brunner 2009). As filter feeders, healthy mussels accumulate a large and diverse bacterial flora, and bacteria may represent an important food source (Section 1.4.A). Bacterial species present in mussels may be highly transient based on seasonal changes in the ambient bacterial flora (Nichols et al. 2001). Potentially pathogenic bacteria have been found in healthy mussels, but these have not been linked to disease (Starliper et al. 2008). The bacterium *Vibrio* is an important pathogen of marine bivalves (Allam et al. 2006) but was among the dominant bacteria in European *Anodonta cygnea*, in which it is apparently nonpathogenic or even commensal (Antunes et al. 2010). Viruses have rarely been reported from freshwater mussels, but this is likely due to methodological limitations for their detection (Grizzle and Brunner 2009).

The only pathogen specifically linked to mass mussel mortality is the *Hyriopsis cummingii* plague virus, which seriously affected the freshwater cultured pearl industry in China (reviewed in Grizzle and Brunner 2009). This disease causes lesions of the alimentary tract and digestive gland and, ultimately, death. Two different viruses have been isolated from diseased *Hyriopsis*, and injection of purified bacterial-free homogenate from infected mussels caused disease symptoms in healthy individuals, suggesting a viral agent. These viruses are found primarily in cultured *H. cummingii* and did not produce disease in other freshwater species. The only report of disease in North American freshwater mussels is the “spongy disease” of western pearlshells, *Margaritifera falcata* (Pauley 1968). This condition was characterized by watery lesions that destroyed up to 90 percent of foot tissue. Affected individuals were lying on the surface of the substrate, and many died, but apparent healing of damaged tissue was observed in some individuals. The cause of this condition is not known, and it apparently has not been reported since or in other areas.

The specific chronology of most enigmatic declines is poorly known: mussels simply disappeared between two consecutive samples separated by 10–20 years. In some cases, however, direct observations of mass die-offs in a short period are suggestive of an infectious agent. In January 1986, at least 36 percent of mussels died during a few weeks in a 15 km reach of the Tennessee River (Jenkinson and Ahlstedt 1987). Similar rapid die-offs occurred in 1982 and 1985 throughout 720 km of the upper Mississippi River (Thiel 1987). Along with dead mussels, live but moribund individuals with gaping shells are often present during these events. Although all mussel species were affected similarly, die-offs were not accompanied by fish kills or mortality of other aquatic organisms (including *Corbicula*). Furthermore, there was no evidence of contaminants or low dissolved oxygen, and in some cases, glycogen deposits were present in dead individuals, suggesting that they had not starved (Jenkinson and Ahlstedt 1987).

Because of the rapid pace of these die-offs, disease was considered a likely cause. Yellow colonies of a gram-negative bacterium were found in both moribund and apparently healthy individuals in the Tennessee River, but moribund mussels had 10 times higher numbers of total and yellow bacteria (Scholla et al. 1987). However, yellow bacteria composed less than 5 percent of all bacteria cultured from these individuals, and the proliferation of bacteria in moribund individuals could have represented opportunistic or secondary colonization of mussels initially stressed by another factor (Jenkinson and Ahlstedt 1987). In mussels associated with a die-off in the Mississippi River, 37 bacteria taxa were isolated, but the dominant species was the same in both healthy and moribund individuals. Furthermore, although several species were isolated only from either healthy or moribund individuals, none of the bacteria found only in moribund individuals were present in more than two individuals (see Grizzle and Brunner 2009).

These results do not support a bacterial cause of these die-offs. In bacterial diseases, infected individuals typically show pure or nearly pure cultures of pathogenic species, in contrast to the diverse flora of healthy individuals (Starliper et al. 2008). However, use of a culture medium unsuitable for a particular species can greatly affect results (Grizzle and Brunner 2009). Indeed, the yellow bacterium present in Tennessee River mussels did not grow well on media used by Scholla et al. (1987). The potential for a viral agent in these declines was not assessed. The apparent non-species-selective nature of these die-offs and of enigmatic mussel declines in general also is inconsistent with the high specificity of most other bivalve diseases, whether bacterial or viral. Nevertheless, the potential for disease as a factor in mussel declines cannot be ruled out. For example, even if *Corbicula* is not directly responsible for these enigmatic declines, it could have been a vector for alien diseases; the relatively early appearance of spongy disease in Washington (near the point of initial *Corbicula* colonization) gives circumstantial support for this idea. Diseases of wild organisms are difficult to study because of their transient nature. Most of the mussel die-offs discussed previously were first reported by commercial shellers on large rivers. Such frequent monitoring of small streams is uncommon, and most potential disease events would go unnoticed.

10.7. The mussel fauna now: Fragmentation, isolation, and the extinction debt

The mussel fauna of North America today is a mere shadow of the fauna that existed 100 years ago. It would be difficult to assess the extent to which the fauna as a whole has declined, but vast reaches of rivers that were once paved with mussels are now nearly or completely barren, and only a handful of rivers continue to support mussel assemblages resembling historical conditions. Indeed, most people today are unaware that freshwater mussels even exist, in contrast to their ubiquitous cultural presence in the past (see Table 1.1). Populations of many wild creatures have declined drastically since European settlement of North America. However, the extinction rate for freshwater mussels eclipses that of any other group of organisms on the continent, except possibly for freshwater snails, and rivals even the high extinction rates seen in tropical rainforest communities (Ricciardi and Rasmussen 1999). Why did mussels suffer to such a greater extent than other organisms?

The decline of the North American mussel fauna is attributed to the sum of multiple impacts over the past 100 years (e.g., Bogan 1993; Neves et al. 1997). This is an accurate assessment but can be applied to nearly any group of organisms. Consideration of specific impacts and their chronology – as attempted in this chapter – allows a better understanding of why mussels have declined so dramatically. The systematic and rapid destruction of riverine habitat by dams is the single most important factor in the decline of the North American mussel fauna. Many other habitats have been greatly reduced by humans, including a more than 98 percent loss of numerous forest, grassland, and wetland types (Noss et al. 1995), but large rivers were destroyed almost completely within the region of highest mussel diversity. Few other organisms have experienced such complete loss of habitat, and indeed, most mussel species lost in the first extinction wave were large-river species whose entire distributional range was either inundated or drastically altered. Because dam construction has subsided (in part because nearly all large rivers are impounded), the direct effects of systematic habitat destruction have largely been manifested. However, systematic habitat destruction has underpinned and magnified all other previous and subsequent impacts to streams, and its indirect effects have only begun to be felt.

In most of North America, remaining mussel populations are highly fragmented and restricted to isolated tributaries. Mussels have much lower dispersal capability than other aquatic organisms, including fishes, crayfishes, and especially insects. Even though mussel larvae can hitchhike on fishes, the typically short duration of the reproductive period and parasitic stage makes long-distance dispersal a slow process, and natural dispersal appears especially low among small streams (Kelly and Rhymer 2005; Berg et al. 2007). Consequently, even small decreases in dispersal can increase the likelihood of extinction of isolated populations (Strayer 2008). Many aquatic animals are isolated by habitat destruction to a greater extent than terrestrial organisms. For example, destruction of old-growth forests leaves a two-dimensional mosaic of remnant old-growth and successional habitats that can exchange immigrants in many directions over a long period of time. In contrast, fragmentation of dendritic river systems can completely separate remaining populations (Fagan 2002). In the Cumberland River system, the distribution of mussel diversity shifted dramatically after systematic habitat destruction (Figure 10.17). Historically, the highest diversity was found in the main stem, which provided a dispersal corridor throughout the entire system, and there was high overlap in species composition between the main stem and large tributaries (see Table 4.4). Today, highest diversity is found in isolated tributaries, and much of the main stem supports few species. Remnant main stem assemblages are composed almost entirely of impoundment-tolerant species and recent lentic colonizers (Section 10.5.A). Consequently, most populations in tributaries are completely isolated and have no potential for recolonization or immigration from other populations.

In the fragmented landscape of the postdam era, enigmatic declines were a critical factor in propelling the remaining fauna to imperiled status. These declines resulted in the loss of many diverse assemblages that were potentially self-sustaining even after fragmentation, and they eliminated or reduced populations in extensive stream reaches that could have served as sources for recolonization after more localized impacts in those watersheds. Because enigmatic declines left behind only the most historically widespread and abundant species, populations of species that had limited distributions or were rare historically were reduced to critically low levels (Section 10.7.A). Furthermore, dense mussel assemblages provide multiple ecosystem services that may facilitate optimal mussel growth and maintenance of high mussel diversity (Section 1.5). Loss of these services after drastic reduction of overall mussel abundance may have cast remaining populations into a downward spiral from which they have been unable to recover.

10.7.A. The second extinction wave

Fragmentation and isolation followed by enigmatic declines created a situation in which impacts that were previously of only local importance grew to have global

Figure 10.17. Distribution of mussel diversity in the Cumberland River system, Kentucky and Tennessee, (upper) before and (lower) after systematic habitat destruction. Numbers in squares are species richness in main stem reaches; numbers in circles are tributary systems. Rectangles in the lower panel are major dams (from M. L. Warren and W. R. Haag, unpublished data).

ramifications for species survival. For example, the toxic spill in the upper Clinch River in 1998 affected only 11 km of stream but more than halved the remaining population of *Epioblasma florentina aureola* (Section 10.4.C). Commercial mussel harvest in the interconnected river landscape of the early 1900s had few or no lasting effects on diversity, but today, increased mortality from harvest in small, remnant populations could push them over the edge to extinction. Even natural factors, such as drought, now pose an immediate threat to many species. The largest remaining population of the triangle kidneyshell, *Ptychobranchus greeni*, was reduced about 80 percent during the severe drought of 2000 but has no source of immigrants to aid its recovery (Haag and Warren 2008). Although I argued that stochastic effects were not important in causing enigmatic mussel declines (Section 10.6.D), they certainly pose a dire threat to the survival of small, isolated populations remaining after those and other impacts.

Currently 120 North American mussel species are considered threatened or endangered, and an additional 72 species are of special concern, representing about 70 percent of the remaining mussel fauna (Williams et al. 1993). At least 40 of these species have been reduced to only one or two populations, and many of these are exceedingly small (Table 10.4). The speckled pocketbook, *Lampsilis streckeri*, currently inhabits only about 10 km of stream in Arkansas (USFWS 1991), and only three living individuals of the Ochlocknee moccasinshell, *Medionidus simpsonianus*, have been seen in the past 40 years, including two in 1974 and one in 1993 (J. Williams, personal communication). These species are in imminent danger of extinction from isolated events or natural, stochastic fluctuations in recruitment or survival. This number of critically imperiled species is conservative because others persist only in a handful of extremely small and potentially nonviable populations (e.g., Texas fatmucket, *Lampsilis bracteata*; Carolina heelsplitter, *Lasmigona decorata*). Many other species exist in multiple populations, but only one or two are large and robust, creating an illusion of security. The Alabama spike, *Elliptio arca*, remains widespread in the Mobile Basin, but only one large population exists, in the Sipsey River, Alabama (Haag 2004). Loss of this population would immediately place the species in much greater jeopardy. This type of rapid degradation of a species' conservation status happens frequently. In the 1980s, the little-wing pearlymussel, *Pegias fabula*, existed in three large populations and about five small populations. By 2000, coal mining and oil drilling eliminated two of the large populations, and most of the smaller populations appear to have declined or disappeared due to stochastic effects, leaving only a single viable population (Warren and Haag 2005).

Even though about 90 percent of North American species remain extant, the legacy of systematic habitat destruction overlaid with enigmatic declines and multiple, localized impacts created a large extinction debt in which the full effects of these events have yet to be manifested. In the face of stochastic effects alone, many critically imperiled species have a low probability of long-term survival, and some are probably already functionally extinct. Continued attrition from stochastic effects and inevitable human impacts will hasten these extinctions and compound the debt by pushing more species to critical status. Payment on this debt has already begun, as evidenced by the loss in the 1970s–1990s of several species whose distributions were reduced by systematic habitat destruction (Table 10.1). The large number of critically imperiled species today suggests that this initial payment on the debt is only the beginning of a second extinction wave that will surpass the first. During the first extinction wave, extinctions averaged about 1 percent of the fauna per decade, but this rate is predicted to increase to as much as 6 percent in coming decades

Table 10.4. *Critically imperiled mussel species in North America, defined as species that are reduced to one or two populations*

Species	Primary hosts	Life history strategy	Faunal province
Alasmidonta triangulata	generalist	P	Apalachicolan
Amblema neislerii	generalist	E	Apalachicolan
Arkansia wheeleri	generalist	P	Mississippi Embayment
Dromus dromas	darters	E	Tennessee–Cumberland
Elliptio chipolaensis	generalist	P	Apalachicolan
E. nigella	generalist	P	Apalachicolan
E. spinosa	generalist	P	Southern Atlantic
E. steinstansana	minnows	P	Southern Atlantic
Epioblasma o. obliquata	darters	P	Ohioan
E. o. perobliqua	darters	P	St. Lawrence–Great Lakes
E. penita	darters	P	Mobile Basin
E. florentina aureola	darters	P	Tennessee–Cumberland
E. florentina walkeri	darters	P	Tennessee–Cumberland
Fusconaia burkei	minnows	E	Escambia–Choctawhatchee
F. lananensis	minnows	E	Sabine–Trinity
Hemistena lata	minnows	P	Ohioan
Lampsilis streckeri	black basses	P	Interior Highlands
L. virescens	black basses	P	Tennessee–Cumberland
Margaritifera marrianae	unknown	E	Escambia–Choctawhatchee/ Mobile Basin
Medionidus parvulus	darters	P	Mobile Basin
M. simpsonianus	darters	P	Apalachicolan
M. walkeri	darters	P	Apalachicolan
Obovaria retusa	darters	P	Ohioan
Plethobasus cicatricosus	minnows	E	Ohioan
P. cooperianus	minnows	E	Ohioan
Pleurobema rubellum	minnows	E	Mobile Basin
P. hanleyanum	minnows	E	Mobile Basin
P. taitianum	minnows	E	Mobile Basin
Pleuronaia gibberum	minnows	E	Tennessee–Cumberland
Popenaias popei	generalist	E	Western Gulf
Potamilus metnecknayi	freshwater drum	O	Western Gulf
Ptychobranchus jonesi	darters	P	Escambia–Choctawhatchee
Quadrula cylindrica strigillata	minnows	P	Tennessee–Cumberland
Q. intermedia	minnows	E	Tennessee–Cumberland
Q. petrina	catfishes	E	Western Gulf
Q. sparsa	minnows	E	Tennessee–Cumberland
Reginaia rotulata	unknown	E	Escambia–Choctawhatchee
Toxolasma cylindrellus	sunfishes	O	Tennessee–Cumberland
Truncilla cognatus	freshwater drum	O	Western Gulf
Truncilla macrodon	freshwater drum	O	Western Gulf

Note: A population is defined here as a collection of occurrences within a contiguous stream system that can conceivably exchange immigrants. For most species, populations extend less than about 80 stream km. Species occurring only in one population but covering much more than 80 km of contiguous habitat (e.g., several species in Altamaha River, Georgia) are not included. Host use was determined from information in Cummings and Watters (2010); when unknown, host use was inferred from information for congeners. Life history strategies are P, periodic; E, equilibrium; and O, opportunistic (see Table 6.3). Faunal provinces are from Haag (2010). Table adapted from Haag (2009b).

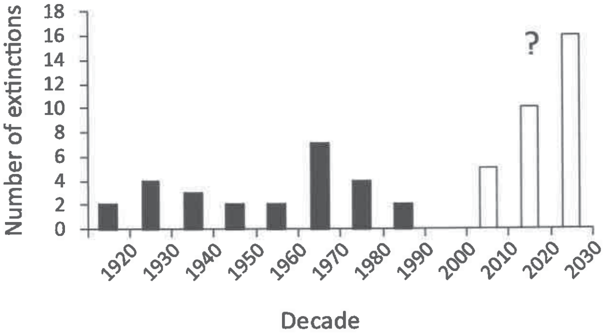

Figure 10.18. Mussel species extinctions in North America per decade; open bars are hypothetical.

and could result in loss of nearly half of the North American fauna (Ricciardi and Rasmussen 1999; Figure 10.18).

10.7.B. Life history traits and the second extinction wave

The first extinction wave was composed of a nonrepresentative sample of North American species. These species were primarily large-river specialists of the Mississippian region that lost nearly their entire habitat, but other regions without an obligate large-river fauna experienced few or no extinctions (Table 10.1). Furthermore, they are overwhelmingly composed of periodic life history strategists (Figure 10.19), and many were specialists on darters or riverine minnows. Impoundment pushed these species to extinction because of their dependence on host species that could not adapt to altered habitats and a life history strategy that did not allow them to weather long periods of conditions unsuitable for reproduction. Notably, no opportunistic life history strategists were lost during the first extinction wave.

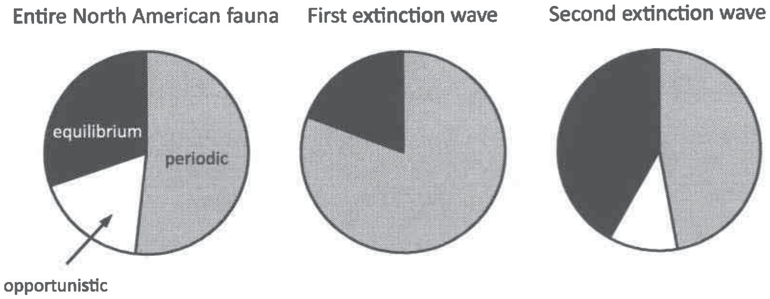

Figure 10.19. Representation of species among life history strategies for the North American mussel fauna as a whole, the first extinction wave, and the second extinction wave. The proportion of species in life history strategies does not differ significantly between the entire fauna and the second extinction wave ($G = 2.31, p < 0.25$, 2 df).

Based on attributes of critically imperiled species, the second extinction wave will affect the fauna much more broadly (Table 10.4; Figure 10.19). Unlike the first extinction wave, critically imperiled species occur across all biogeographical regions, except the Pacific. The representation of life history strategies among these species is nearly identical to that of the North American fauna as a whole and includes several opportunistic species. Critically imperiled species have a broad range of host use, including generalists, and several use fishes tolerant to environmental degradation (e.g., black basses, catfishes, freshwater drum). A few are large-river specialists that are marginally tolerant of impounded riverine habitats (e.g., *Obovaria retusa, Plethobasus*), but most are narrowly endemic species with restricted initial distributions. Critically imperiled species are present in nearly all faunal provinces with endemic species, but few yet occur in provinces without an endemic fauna (e.g., Upper Mississippi, Great Plains, Northern Atlantic). This shows that although systematic habitat destruction continues to affect the fauna, attrition in isolated stream reaches will be the main proximal cause of the second extinction wave. Life history traits of a few species, particularly opportunists, preadapt them to persistence and even expansion in highly altered habitats. Overall, attrition affects most species similarly, and the probability of persistence will be based primarily on initial abundance and distribution rather than on species-specific characteristics.

The sum of multiple impacts to the aquatic landscape would likely have caused some extinctions even with a lesser degree of direct habitat destruction and fragmentation. For example, nearly the entire historical range of *Pegias fabula* remains unimpounded, but its restricted distribution primarily within coal-bearing regions was a particular liability. However, the combination of systematic habitat destruction and enigmatic declines greatly increased the vulnerability of all species such that localized impacts became events of global importance to species survival. The magnificent freshwater mussel fauna of North America is at a critical point. The outcome of conservation efforts in the next 30 years will determine whether the potential for loss of half or more of the fauna is realized.

Chapter 11

Mussel conservation

The challenge of protecting a fragmented resource

11.1. Taking stock of the situation

The current plight of freshwater mussels is often described with dire phrases such as "the most endangered fauna on Earth." These statements are accurate, and the urgency of the mussel conservation crisis cannot be overemphasized. Nevertheless, it's necessary to put this crisis in context. There are still lots of mussels in North America, and many species are thriving. The estimated mussel population in the upper Mississippi River alone currently exceeds the human population of the United States, even after tremendous commercial harvest, construction of multiple dams, a long history of severe water pollution, and the invasion of zebra mussels (Newton et al. 2011). Some areas seem to be in better shape than others. Arkansas is noteworthy for having many rivers that still support spectacular mussel faunas. Mussels are incredibly abundant in many rivers and lakes in New England and southeastern Canada, even though probably more than 90 percent of the mussels there are the eastern elliptio, *Elliptio complanata*. The ubiquity and abundance of the giant floater, *Pyganodon grandis*, and paper pondshell, *Utterbackia imbecillis*, in farm ponds tells us that freshwater mussels will be around for a long time.

Nevertheless, we now stand to lose as much as half of the North American species in the next 100 years (Ricciardi and Rasmussen 1999). This prediction is based essentially on the assumption that all species of conservation concern today will decline at the same rate and will not survive the next century. The validity of this assumption is hard to evaluate. The conservation status of many species remains poorly known, and in many cases, conservation concern is assigned to a species not because of current imperilment but because of the potential for it to become imperiled in the future (e.g., Williams et al. 1993). The federally endangered pink mucket, *Lampsilis abrupta*, has always been rare (Section 11.4.C), and it seems to be holding its own or increasing, even in some impounded rivers (R. Butler and D. Hubbs, personal communication). Additional populations of rare species continue to be discovered (USFWS 2009b; Simmons 2011), and mussel populations in some streams appear to be rebounding, potentially because of restriction of commercial harvest or improvements in water quality associated with the Clean Water Act (Miller and Lynott 2006; Newton et al. 2011). Unfortunately, these encouraging stories are in the minority, and much of the news about mussel conservation is grim. The extent of the second mussel extinction wave is as yet unknown, but without immediate conservation action, it is clear that a significant proportion of the fauna will be lost within a human generation.

Mussel conservation began in the early 1900s in response to declines of commercially valuable species caused by overharvest and water pollution. Initial efforts included large-scale captive propagation and stocking of commercially valuable species (Section 11.4), enaction of minimum size limits, and periodic closure of shelling grounds in a few areas (Section 9.4). In 1921, then U.S. commerce secretary and future president Hebert Hoover convened a national conference on fish and mussel depletion at the Fairport Biological Station on the Mississippi River (Anfinson 2003; Section 2.2.B). The conference resulted in additional, modest restrictions on mussel harvest and it broadened awareness about river conservation. However, regulations on mussel harvest were not enacted widely, and these and other efforts were largely negated by continued overfishing and systematic habitat destruction.

Conservation of mussels for their own sake began in earnest after passage of the U.S. Endangered Species Act in 1973. In 1976, 23 mussel species were designated as endangered, but 75 species are now protected under the act. During this time, mussel conservation efforts have expanded accordingly. Mussel conservation is now a high priority for federal, state, provincial, and tribal agencies as well as conservation organizations such as the Nature Conservancy and the World Wildlife Fund. These efforts have received considerable media attention and raised public awareness about the mussel conservation crisis. The broad and growing interest in mussel conservation is encouraging, but protecting this highly fragmented resource is an enormous challenge that must be tackled on several fronts.

11.2. More on the extinction debt: Can we protect what's left?

Modern mussel conservation efforts initially focused on protecting remnant populations of endangered species. For example, in 1983, the Nature Conservancy purchased 14 ha at Pendleton Island, on the Clinch River, Virginia, to protect one of the most diverse remaining mussel assemblages in the world at the time. However, because of coal mining and other impacts upstream, mussel abundance there declined more than 90 percent by 2009, and several species have disappeared (J. Jones, personal communication). Similarly, coal mining impacts nearly eliminated mussels from Horse Lick Creek, Kentucky, despite the majority of the watershed being in U.S. Forest Service or Nature Conservancy ownership (Haag and Warren 2004). Even in the absence of severe human impacts, natural catastrophes can reduce the size of isolated populations to below viable levels, negating the most stringent protection efforts.

11.2.A. The lonely hearts club: Minimum viable population size

The greatest challenge of protecting isolated populations is maintaining at least a minimum number of individuals necessary to ensure long-term persistence. Determination of this minimum viable population size is a central focus of conservation biology and is concerned with the number of individuals needed to safeguard populations against genetic effects such as inbreeding depression and the effects of natural fluctuations in environmental conditions and survival (Section 10.4.B).

Reduction of population size can result in decreased individual fitness, referred to as an *Allee effect* (Stephens et al. 1999). A common Allee effect is decreased fertilization success due to sperm shortage or difficulty finding mates. Complete fertilization failure of *Elliptio complanata* was reported at densities less than 10/m^2, suggesting that sperm limitation can occur even at moderate densities (Downing et al. 1993). However, such a high minimum threshold for fertilization is clearly unrealistic for most if not all species. Few mussel species regularly occur at densities greater than 10/m^2 (Section 8.1), and many species were rare even prior to human impacts (Section 11.4.C). Females of many species are consistently fertilized at very low population densities, a phenomenon attributable to efficient sperm transfer rather than facultative hermaphroditism (Sections 1.4.C.2 and 6.2.A). Sperm limitation may occur to some extent in the sparsest of populations. The Appalachian monkeyface, aptly named *Quadrula sparsa*, persists in the Powell River, Tennessee and Virginia, at densities less than 0.03/m^2 (the name actually refers to the sparseness of tubercles on the shell rather than its rarity). In recent years, biologists have had trouble finding gravid females, suggesting sperm limitation; however, recent recruitment has occurred at some sites, showing that fertilization can occur at least occasionally even at extremely low densities (Johnson et al. 2010a, 2010b). Efficient fertilization appears to be one of the few things mussels have going for them, but other negative effects of small population size pose serious threats to species survival.

Allee effects also could be manifested if facilitative feeding interactions break down as overall mussel density declines. In this case, individual fitness would decrease because a decline of keystone species reduces energy transfer from the water column to the sediment (Spooner and Vaughn 2009; Section 8.5). The importance of loss of facilitative feeding interactions and other ecosystem services is unknown and is an important research topic for mussel conservation.

Small populations also can decline from purely stochastic effects. Consider a mussel population in an isolated headwater stream. Because abundance is limited by frequent natural disturbance, facilitative feeding interactions are likely of little importance in these habitats (Section 8.6). If efficient sperm transfer allows fertilization, individual fitness – as measured by survival or reproductive rates – should not be affected directly by population size. However, random variation in environmental conditions or survival and reproduction could result in a series of years with low or negative population growth, casting the population into a downward spiral of abundance (Section 10.4.B). At this point, Allee effects such as sperm limitation or inbreeding depression may compound the problem, but small populations are often driven to extinction solely by environmental or demographic stochasticity (Lande 1998).

Minimum viable population size has not been determined for any mussel species. Accurate estimates of these thresholds may be difficult to obtain and will vary considerably according to differences in life history strategies, habitat characteristics, and many other factors (Shaffer 1981; Gilpin and Soulé 1986). For example, long life span likely increases the probability of persistence in the short term, and populations in highly variable habitats such as small streams may be more prone to extinction from natural events than those in larger streams (Section 11.2.B). If loss of facilitative feeding interactions is important in mussel declines, determination of minimum viable population size for a particular species is especially complex because it is tied to the abundance of other species. Furthermore, minimum population thresholds cannot account for the unpredictable occurrence of severe human impacts, which can nullify overnight the most carefully derived estimates. Estimates of minimum viable population size for mussels are needed to provide general conservation guidelines, but many populations clearly have already reached a critical level.

11.2.B. Long-term viability of isolated populations

Some mussel species have an amazing ability to persist at extremely low population densities. The southern clubshell, *Pleurobema decisum*, was abundant in the Cahaba River, Alabama, in the early 1900s but was extremely rare by 1972. The species was not found during the 1980s and 1990s and was considered extirpated from the river. By 2005, water quality improvements resulted in an increase in overall mussel abundance, and one live *P. decisum* was found. In 2011, 25 live individuals, including recent recruits, were found at a single site where the species was not detected previously despite intensive effort. This species apparently persisted at undetectable levels for more than 30 years, until conditions improved (P. Johnson and J. Williams, personal communication). The ring pink, *Obovaria retusa*, persists in the Green River, Kentucky, and the Tennessee River, but only single individuals have been found about every 10 years since the 1960s (Garner and McGregor 2001; R. Butler personal communication). In an extensive survey of the Ouachita River, Arkansas, single individuals of the Ouachita rock-pocketbook, *Arkansia wheeleri*, and spectaclecase, *Cumberlandia monodonta*, were found among more than 23,000 mussels examined (Posey 1997). During 10 years of sampling in the Sipsey River, Alabama, only five individuals of *Strophitus subvexus* were found among more than 10,000 mussels;

more than one individual was never found in a single year, but most individuals were young, indicating recent recruitment (W. R. Haag and M. L. Warren, unpublished data). The ability to persist at low density is another of mussels' few conservation assets, but the question remains whether these represent viable populations in the long run.

Persistence probably varies according to life history strategies and attributes of the habitat occupied by the population. Equilibrium strategists appear particularly able to persist at low density for long periods. Long life span and low annual mortality allow these species to weather long periods of adverse conditions, and populations can be maintained by low annual recruitment (Chapter 7). These traits have doubtless kept the number of species extinctions from being higher than it is now. Nearly all species that persist at low density in impounded streams are equilibrium strategists (Section 10.5.A). Persistence also is facilitated by occurrence throughout long stretches of stable, large-river habitat such that overall population size may be modest despite low density. Nevertheless, if average population growth rate (λ) over time is less than 1, long life span may only prolong the inevitability of extinction. Without recent improvements in water quality in the Cahaba River, it is doubtful that *P. decisum* would have persisted there indefinitely. Indeed, many long-lived species have or are expected to disappear from impounded large rivers despite occasional reproduction (Section 10.5.A).

Periodic strategists appear less able to persist as small populations for extended periods. Similar to equilibrium species in large rivers, *Arkansia wheeleri* and *Strophitus subvexus* persist at low densities in the Ouachita and Sipsey rivers, respectively, likely because their occurrence throughout long stream reaches results in modest overall population sizes and allows exchange between local populations. The Duck River dartersnapper, *Epioblasma ahlstedti*, persisted at undetectable levels in the Duck River, Tennessee, for nearly 20 years but rebounded dramatically after improvements in flow regime and water quality (Section 11.3.A). However, few other examples exist of periodic species persisting during extended periods of unfavorable conditions (Section 10.5.A). Isolated populations of periodic strategists in small streams should be especially vulnerable to extinction because of frequent disturbance. Most periodic species are relatively short-lived, and population growth is dependent on higher average annual recruitment compared with equilibrium strategists (Chapter 7). Consequently, a series of poor reproductive years could quickly cast these species into a downward spiral of abundance. Furthermore, in contrast to large rivers, both population density and population size may be low in small streams because of the limited extent of available habitat.

Opportunists can persist in highly disturbed habitats, but small, isolated populations also are vulnerable to extinction from stochastic events. These species are capable of rapid population growth in favorable conditions, but their short life spans do not allow them to weather extended periods of adverse conditions. Accordingly, several local populations of otherwise widespread opportunistic species have become extinct, apparently from stochastic effects (Section 10.4.B). Frequent local population extinctions were probably a natural occurrence for opportunistic and periodic species, but isolation and fragmentation now limit opportunities for recolonization after these events.

The chances for long-term survival of many small, isolated populations should be considered tenuous at best, regardless of life history traits or other species attributes. Even so, protection and enhancement of existing critical habitats is obviously vital to protect remaining mussel assemblages and prevent further extinctions in the short term. Accordingly, habitat protection through broad, watershed-scale initiatives is a primary focus of many mussel conservation efforts (e.g., Alderman and Adams 1993; Saunders et al. 2002; Palmer and Pallant 2009). These initiatives seek to minimize threats to habitat integrity by, for example, establishing riparian buffer strips to reduce sedimentation. Although the direct role of sedimentation in mussel declines is unclear (Section 10.6.A), it is prudent to minimize this potential threat, and these conservation actions have many other positive impacts, including increasing bank and channel stability, lowering water temperatures, and reducing inputs of nutrients and agricultural chemicals. However, because of the large extinction debt, conservation of mussel diversity in the long run rests on our ability to increase and extend remaining populations such that they have the ability to weather natural events and even localized human impacts.

11.3. Habitat restoration

The necessity of increasing the number of populations of imperiled species is not a new idea and is a central goal of all species recovery plans under the Endangered Species Act. However, for many species, past destruction of most available habitat limits the options for reestablishment of additional populations. Habitat restoration is therefore essential for mussel conservation, and several exciting opportunities for restoration exist in North America.

11.3.A. Tailwater restoration

Perhaps the greatest potential for habitat restoration in the short term is in tailwater reaches downstream of large dams. In vast stretches of rivers across North America, physical habitat remains intact but upstream dams result in chronically low water temperature and oxygen concentration and highly altered seasonal flow regimes (Dynesius and Nilsson 1994; Poff et al. 2007; Figure 11.1). These impacts are most severe with hydroelectric dams because water is typically released from the cold, oxygen-poor reservoir hypolimnion, and high flows coincide with periods of peak power demand, but flow may cease entirely at other times, resulting in radical daily water level fluctuations (Gore et al. 1989). Flood control dams also fundamentally alter flow

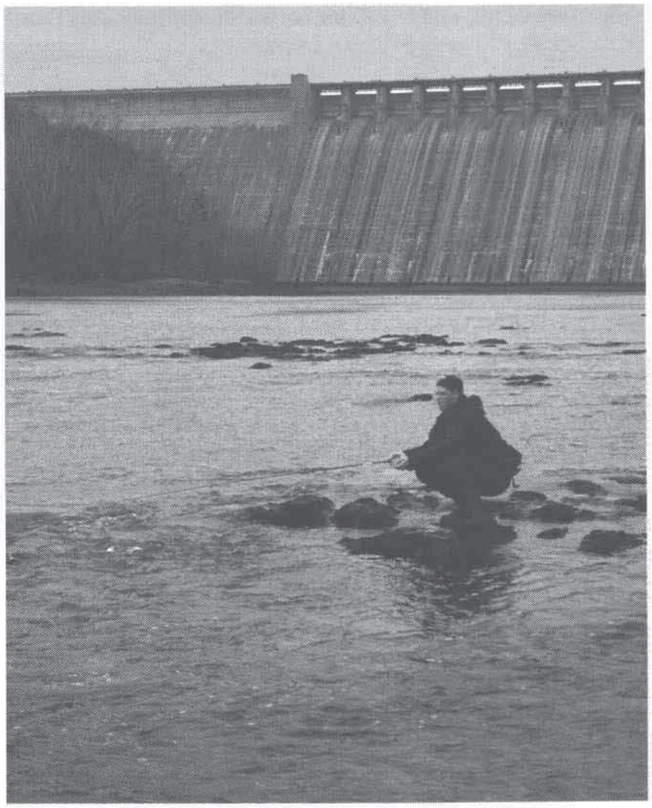

Figure 11.1. Regulated tailwater reach of the White River, Arkansas, below Bull Shoals Dam showing intact, large river shoal habitat (Keith Sutton, photo). Because water temperature rarely exceeds 23°C, this section of the river supports a major sport fishery for non-native trout, but native mussels and warmwater fishes have been nearly eliminated for more than 100 km (Robison and Buchanan 1988).

regimes because reservoir levels are drawn down in autumn to maximize storage capacity for winter rains, and water is retained in spring to raise reservoir levels for summer recreation, resulting in a loss of spring flood pulses and late summer low flows. Flow alteration results in profound changes in aquatic assemblages and, in many cases, loss of the entire mussel fauna (Section 10.3.C).

Attempts to rehabilitate tailwaters began in the late 1980s and include broad initiatives by agencies such as the Tennessee Valley Authority (TVA) and the U.S. Army Corps of Engineers (USACOE) as well as conservation organizations such as the U.S. Fish and Wildlife Service and the Nature Conservancy (Bednarek and Hart 2005; Konrad et al., in press). Restoration of more natural flows resulted in marked improvements in fish and aquatic insect assemblages in numerous streams (Bednarek and Hart 2005; Layzer and Scott 2006; Olden and Naiman 2010). The effects on mussel assemblages are unknown in many rivers because dam releases previously eliminated or greatly reduced populations. In streams less severely affected by dam release, existing mussel assemblages have responded positively, in some cases dramatically, to flow improvements. Mussel recruitment appears to have increased in the Green River, Kentucky, downstream of Green River Dam, after restoration of more natural flows, and effects are evident even 80 km downstream (Konrad et al., in press; J. Layzer personal communication). In the Duck River, Tennessee, improvements in flow and oxygen concentration begun in 1991 downstream of Normandy Dam have been accompanied by a more than 2-fold increase in mussel abundance and range expansion of several endangered species (Ahlstedt et al. 2004; Hubbs et al. 2011).

Opportunities for tailwater restoration are especially exciting and vital in the Cumberland and Tennessee river systems, where hundreds of kilometers of large-river habitat are intact physically but unsuitable for mussels and other organisms because of altered temperature and flow. These rivers formerly supported more than 50 mussel species, and restoration would allow reestablishment of diverse assemblages, including numerous endangered or endemic species for which recovery efforts are now limited by a lack of suitable reintroduction sites. These habitats represent essentially the only chance to recover these species and could provide dispersal corridors linking remnant mussel assemblages in isolated tributaries. Similar opportunities exist in other river systems, notably the Mobile Basin, which also has an endangered large-river fauna.

Restoration of some of these tailwaters has begun through the TVA's Reservoir Releases Improvement Program and similar efforts on the Coosa River, Alabama (Bednarek and Hart 2005; Alabama Power 2010). Despite improvements, these efforts have been limited because hydroelectric power generation continues to negatively impact flow regimes (Bednarek and Hart 2005; Layzer and Scott 2006).

Conflicts with other natural resource agendas also pose impediments to restoration of regulated rivers. In the southeastern United States, many cold tailwaters support recreational fisheries for trout species native to Europe or the western United States that could not survive in the region at normal stream temperatures. Sport fishery groups and many state fisheries agencies strongly oppose restoration of natural temperature regimes in these rivers. The 128 km reach of the Cumberland River below Wolf Creek Dam in Kentucky represents prime, recoverable large-river mussel habitat, but this reach was eliminated from consideration for restoration by the USACOE largely because of a popular trout fishery requiring temperatures less than 20°C (Tippit et al. 1997). Consequently, tailwater restoration often focuses on improving flow regime and oxygen concentration but does not address temperature (Olden and Naiman 2010). Low water temperature is a primary cause of mussel declines in tailwaters because gametogenesis is suspended (Heinricher and Layzer 1999). Repairs to Wolf Creek Dam after 2006 necessitated greatly reduced dam discharge for an extended period, resulting in elevated water temperatures even far downstream. Simultaneously, gametogenesis and glochidial release were observed for the first time in remnant, formerly nonreproducing mussel populations downstream in Tennessee (Hubbs 2010).

Resource managers ultimately will be faced with the choice between survival of imperiled native mussel species and perpetuation of feral populations of nonnative trout.

Tailwater restoration for the benefit of native stream biota poses other, more practical problems. Potential reductions in hydropower production are perhaps the most serious issue. In some cases, restoration of natural flows could result in low oxygen concentration in eutrophic, downstream reservoirs because of increased retention time and water temperature (Tippit et al. 1997). Many dams lack structural features allowing flexibility in water release (e.g., surface vs. hypolimnetic), and retrofitting to include these features is expensive. However, a variety of new technologies and approaches to address these issues is becoming available as the importance of restoring ecological function is increasingly acknowledged worldwide (Olden and Naiman 2010). Predictions of negative impacts from flow restoration based solely on model predictions (e.g., Tippit et al. 1997) are hard to evaluate, and trial-and-error adaptive management may be necessary in these complex systems (Poff et al. 2003; Richter et al. 2003).

In the long run, ecological services provided by restored rivers may outweigh the costs of restoration and could help ameliorate potential negative side effects. For example, the filtering capacity of restored mussel assemblages could play a large role in maintaining high water quality. Rehabilitation of dam tailwaters represents perhaps the single most effective way to reduce extinction risk for a large number of mussel species through habitat restoration, and it deserves innovative and bold consideration of how this goal can be reconciled with other societal needs.

11.3.B. Dam removal

A more direct and far-reaching approach to restoring mussel habitat and river connectivity is to remove the dams themselves (Figure 11.2). As early as the 1830s, Henry David Thoreau advocated removal of a dam on the Concord River, Massachusetts, for the benefit of anadromous fishes (see Graf 2001). For many dams that continue to provide multiple benefits of hydroelectric power, flood control, water storage, and navigation, removal is clearly unrealistic at this time. However, removal of nonfunctional dams has accelerated in recent years, especially in the northeastern United States, with its abundance of antiquated mill dams. Most dams removed so far in the United States have been small, privately owned dams for which liability and maintenance costs were the main impetus for removal (Doyle et al. 2003). There is a small but growing trend for removal of even large, functional dams solely for the benefit of aquatic resources (Shuman 1995; Hart et al. 2002). In 1999, Edwards Dam on the Kennebec River, Maine, a functioning hydropower dam, was the first to be removed by mandate because its license was not renewed by the Federal Energy Regulatory Commission; this decision was based primarily on the dam's negative

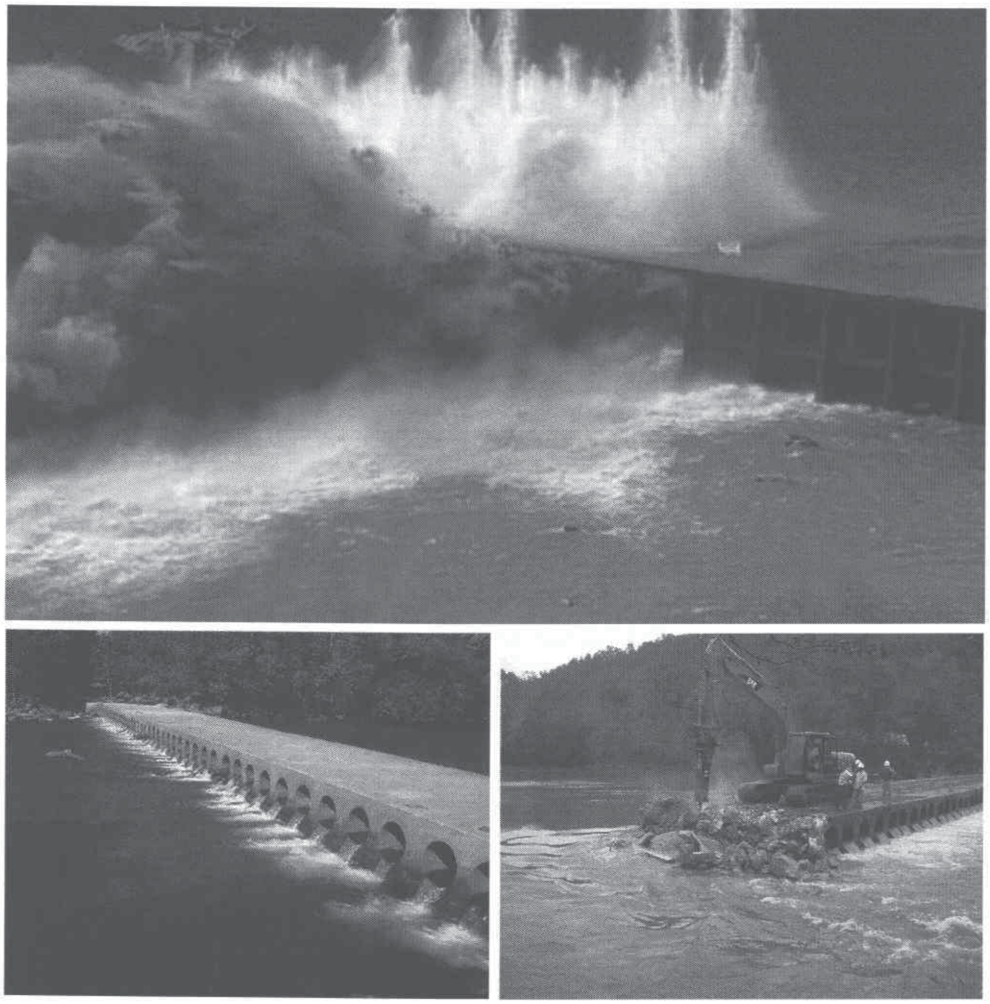

Figure 11.2. Dam removal. (top) Demolition of Embrey Dam on the Rappahannock River, Virginia, 2004 (U.S. Department of Defense, photo, courtesy Integration and Application Network image library, http://ian.umces.edu/imagelibrary/). (bottom) Removal of a large concrete ford on the Cahaba River, Alabama, 2004 (Paul Freeman, photos).

effect on anadromous fishes (Shuman 1995; Doyle et al. 2003). Another high-profile, recent example is the proposal to remove four large, functioning dams on the Snake River, Idaho, solely for the benefit of salmon (Kareiva 2000). Debate over this proposal has brought dam removal to prominence as a conservation strategy.

In most cases, benefits to mussels have been tangential to the primary goals of dam removal. For example, removal of Edwards Dam also is expected to benefit mussel species, such as the alewife floater, *Anodonta implicata*, that depend on anadromous host fishes (Smith 1985; Nedeau et al. 2000). Dam removal specifically for restoration of mussel populations has only just begun. Cuddebackville Dam, on the Neversink

River, New York, was removed in 2004 primarily to increase habitat for the endangered dwarf wedge mussel, *Alasmidonta heterodon* (Baldigo et al. 2003–2004). Similarly, Dillsboro Dam on the Tuckasegee River, North Carolina, was removed in 2010 to create additional habitat for and link isolated populations of the endangered Appalachian elktoe, *Alasmidonta raveneliana* (J. Fridell, personal communication). Across North America, hundreds of opportunities exist for removal of nonfunctional dams to benefit mussels and other aquatic ecosystem values. For example, removal of a series of three antiquated and nonfunctional navigation dams on the Green River, Kentucky (Dams 3, 5, and 6; Dam 4 failed in 1965) would restore more than 150 km of critical large-river habitat and connect isolated mussel assemblages in the watershed. Because of the widely recognized negative effects of impoundment and habitat fragmentation on mussels, dam removal will become an increasingly important conservation strategy.

In addition to its cost and contentious nature, dam removal poses potentially serious threats to existing mussel populations. In the short term, dam removal can cause high mussel mortality from stranding in the drained reservoir (Sethi et al. 2004). In most of North America, this will mainly affect widely distributed, lentic species of low conservation concern. However, in some areas, particularly the Northern Atlantic province, several imperiled species adapt readily to reservoirs, and dam removal or rapid reservoir drawdown has caused high mortality (Nedeau et al. 2000). Reservoirs accumulate deep sediment deposits that may be contaminated with toxic substances. When a dam is breached, sediments are mobilized, often resulting in channel incision above the dam and aggradation below and downstream transport of toxins (Hart et al. 2002; Doyle et al. 2003). These processes can impact streams for years after dam removal as the stream reestablishes a new base level. After dam removal in a Wisconsin stream, mussel abundance immediately downstream declined 30 percent after 3 years (Sethi et al. 2004).

Ironically, small dams may have allowed survival of mussel populations in watersheds impacted by other factors. Prior to flow improvements, remnant mussel populations in the Duck River were confined mainly to reaches below old mill dams (Ahlstedt et al. 2004), and this phenomenon is seen in many other rivers (Singer 2010; W. R. Haag, observation). These small reservoirs likely acted as sinks for sediment, nutrients, and toxins; increased food availability from plankton production; buffered depressed water temperature from larger dams upstream; and increased oxygenation through water flow over the dam (Singer 2010). Loss of these benefits after dam removal may endanger mussel populations in watersheds that continue to be affected by other impacts.

At this time, we have little experience with dam removal, and this strategy should be used with caution until we learn how to minimize potential negative impacts. Nevertheless, long-term benefits to mussel populations will likely outweigh short-term negative impacts in many cases. Dam removal and tailwater restoration is necessary to increase habitat availability and connectivity within our river systems and ultimately improve chances for long-term persistence of isolated mussel populations.

Dams frequently end up costing considerably more than initial projections, and including long-term costs of maintenance and environmental impacts, total cost to society is orders of magnitude higher (Babbitt 2002). Environmental costs are difficult to quantify because they include intrinsic, nonmarket values, but economists can readily estimate short-term costs of lost power revenue, flood control, water supply, and recreation (Smith 2006). Natural resource benefits will remain contentious, but continued loss of ecosystem function and integrity will heighten their value. In addition, more concrete issues (pardon the pun) will come increasingly to the fore. By 2020, 85 percent of U.S. dams will reach the end of their planned operational life spans (Doyle et al. 2003). These aging dams pose major safety issues and economic costs. Wolf Creek Dam on the Cumberland River was built on extensive karst formations; consequently, it nearly failed in the 1960s and is now undergoing a third round of extensive and costly repairs since its construction in 1951 (USACOE 2011). This dam may never be completely sound, and its failure threatens Nashville, Tennessee, and other sizable communities. Currently 32 percent of dams in the United States pose serious safety risks (Graf 2001). From a purely economic perspective, dam projects that greatly exceeded cost estimates but have fallen far short of projected benefits, especially those with vast, negative environmental impacts (e.g., Tennessee–Tombigbee Waterway; Stine 1993), will be particular candidates for reevaluation. Proposals that seem radical today, such as removal of Glen Canyon Dam on the Colorado River (Glen Canyon Institute 2011), may become plausible solutions to increasingly complex problems in the future. In the short term, tailwater restoration and removal of nonfunctional dams is a viable and essential conservation strategy. In the not-so-distant future, removal of large dams will become increasingly viable and necessary, and strategic prioritization of dams whose removal will have the greatest positive impact on ecosystem integrity should begin now.

11.3.C. Channelized streams

Rehabilitation of channelized streams also will greatly increase available mussel habitat and restore connectivity to river systems (Section 10.3.A). In the Mississippian Embayment province, mussel assemblages are limited by widespread channelization and an absence of stable stream habitat (Haag and Warren 2007). To some extent, channelized streams can rehabilitate themselves when left alone, and much of the lowland mussel fauna of this region appears resilient and adaptable. Development of stable point bars, pools, and other heterogeneous channel features can occur within a few decades of channelization (Jackson and Jackson 1989). Drainage canals constructed in lowland watersheds of Arkansas from the 1940s to the 1960s have been colonized by at least 23 mussel species, including the endangered fat pocketbook, *Potamilus capax* (Ahlstedt and Jenkinson 1991). Natural recovery is threatened by continued channel maintenance and removal of large woody debris, which is an important source of streambed stabilization in watersheds without erosional controls such as bedrock (Jackson and Jackson 1989; Shields et al. 2007).

The extent of recovery from channelization often is limited even in the absence of additional disturbance. In natural, lowland streams, extensive meanders absorb much of the erosive energy of high flows. Straightening these streams can cause perpetual destabilization characterized by repeated cycles of headcutting and channel erosion (Simon 1989; Shields et al. 2000). Increasing stability of these streams requires structural or engineering solutions such as restoration of meanders, installation of erosion control structures, addition of large woody debris, and riparian plantings (Gore and Shields 1995; Shields et al. 2007). However, because channelized streams often become deeply incised, they may remain permanently isolated from their floodplains (Kroes and Hupp 2010).

One of the most difficult issues associated with channelization is migration of headcuts into unchannelized reaches, which threatens many remnant mussel assemblages (Section 10.4.A). The only effective way to protect these stream reaches involves construction of a grade control structure – essentially a small dam – that halts upstream progression of channel erosion (Simon and Darby 2002). While this can protect upstream habitats, it also creates a permanent barrier that can effectively isolate aquatic assemblages.

In addition to catastrophic effects on aquatic organisms and wetlands, channelization has many direct, negative economic impacts, including loss of private property from bank erosion; undermining of bridge foundations, roads, pipelines, and other instream structures; and decreased water quality and quantity (USEPA 2005). As early as 1972, U.S. assistant secretary of the interior Nathanial Reed said, "Stream channel alteration . . . is undoubtedly one of the most destructive water management practices," and "I think we are kidding ourselves if we do not admit that the vast majority of stream channelization [projects] have had a devastating effect on our nation's waterways" (Gillette 1972, 890). There is now broad consensus about the high environmental and economic costs of channelization, and restoration projects are becoming increasingly common (Bravard et al. 1999). Small-scale restoration can be relatively inexpensive, costing less than 10 percent of initial channelization costs, but larger projects that restore a more complete array of environmental functions are expensive (Nunnally and Keller 1979; Whalen et al. 2002; Figure 11.3). As with dams, full consideration of the long-term environmental and societal costs of channelization will likely make restoration a wise investment.

11.3.D. Addressing enigmatic mussel declines

A critical conservation need is identification of specific factors responsible for enigmatic mussel declines (Section 10.6). This is vital to preventing future declines and to rehabilitating affected stream reaches, which include hundreds, if not thousands, of

Figure 11.3. A restored section of the Kissimmee River, Florida. The previous dredged channel (now backfilled) is the straight feature running diagonally across the right of the photo (U.S. Army Corps of Engineers, Jacksonville District, photo).

kilometers of otherwise suitable habitat. Without knowing the causal factors, no specific preventative or remedial actions are indicated. For example, improving "land use practices" is such a broad charge that it is unlikely to have tangible effects in the short term. Similarly, reducing sediment inputs alone may be ineffective if sedimentation is not directly responsible for these declines.

No studies have systematically evaluated potential causal factors of enigmatic mussel declines. A systematic approach that can integrate disparate sources of information is desperately needed particularly to evaluate the potential role of pesticides and ammonia (see Downing et al. 2010; Norris et al. 2012). A first step should be to evaluate the concordance of large-scale temporal and spatial patterns of declines with historical and current trends in pesticide and fertilizer use. Pesticide use data are available from many sources and often extend into the early 1960s or before (e.g., Nowell et al. 1999). Establishing the temporal chronology of mussel declines is often difficult because of infrequent sampling, but full use of museum collections, published literature, and survey reports can allow reconstruction of temporal trends for many streams.

A second step should involve extensive surveys of sediment and water contamination. Associations between contaminant concentrations and severity of mussel declines could reveal gradients of cause and effect, strengthening evidence for the role of a specific factor. This will be complicated by the large number of compounds to be measured and the unknown mode of action or tolerance criteria for most (e.g., pesticide surfactants or metabolites vs. active ingredients). However, unlike pesticides, measurement of ammonia is more straight-forward and specific toxicity thresholds are available for mussels. Measurement of ammonia concentrations in water and sediment can allow direct assessment of the potential of this factor to limit mussel populations in otherwise suitable habitats. Similar measurements also could provide important information about whether past-use, persistent pesticides continue to affect mussel populations and the potential threat posed by current-use pesticides. Many data on sediment and water contamination already exist, but additional measurements will be needed in undersampled areas and to assess the occurrence of other, previously unmeasured compounds.

Finally, experimental study of the effects of compounds occurring commonly in the environment should be continued and expanded to substantiate or eliminate causal mechanisms suggested by correlative studies. Experimental exposure studies across life history stages should focus especially on chronic or sublethal mechanisms such as effects on growth and reproduction. In addition to laboratory studies, field enclosure or transplant experiments will allow evaluation of these effects in more natural contexts (e.g., Gagne et al. 2004). Unlike many organisms, sedentary mussels lend themselves well to in situ field exposures, and this approach – coupled with the availability of cultured juvenile mussels – can be a powerful tool for assessing the ability of a particular habitat to support mussel life.

Along with pesticides and ammonia, other factors, such as sedimentation and disease, need to be evaluated systematically, at large scales, and in environmentally relevant contexts. The frequent assertion that mussel declines result from the sum of multiple, disparate impacts is accurate for the fauna as a whole but is surely inaccurate on a case-by-case basis, where specific factors have likely played inordinately large roles. Uncritical acceptance of the multiple-cause hypothesis can lead to adoption of broad conservation strategies that may not effectively address specific causal factors. Remedial and preventative measures to address specific factors will likely be similar to existing strategies such as reducing agricultural runoff. However, knowledge of specific causal factors is needed to effectively monitor success of these measures and to assess the potential for stream rehabilitation.

Not long ago, large-scale restoration of North American rivers seemed an impossibility and the fragmentation of river systems a permanent feature of the landscape. Today, we are on the cusp of a revolution in societal attitudes toward the value and management of aquatic ecosystems. As loss of essential ecosystem services and attributes accelerates, restoration efforts in turn will accelerate by necessity. Since 1990, the number of river restoration projects increased exponentially, and more than $1 billion annually was spent on these efforts (Bernhardt et al. 2005). Restoration goals from a purely ecological perspective will be tempered and modified by practical limitations (McDonald et al. 2004). Even with aggressive habitat restoration, the original connectivity of river systems will never be achieved. In some cases, restored dispersal corridors will allow mussels to recolonize historically occupied habitats. However, many populations will remain isolated, and many restored stream reaches will remain inaccessible to immigration. Furthermore, for critically imperiled species, natural dispersal may be too slow to save them from extinction. Human assistance will therefore be necessary to establish additional populations necessary for species survival and to restore mussel assemblages in many streams.

11.4. Reintroduction and population augmentation

Two common approaches to restoring populations of wild organisms are to transplant individuals from one place to another (translocation) and to propagate individuals in captivity and release them to the wild. Carefully and thoughtfully implemented, these approaches are powerful conservation tools and have successfully restored many plants or animals to healthy levels (e.g., white-tailed deer, wild turkey). However, translocation and release of captive-bred individuals can result in a wide range of catastrophic, if unintended, ecological consequences. Introductions of nonindigenous species are classic examples (Section 10.6.C). Nonindigenous species are typically thought of as originating in a foreign country, but even native species introduced beyond their natural range can wreak ecological havoc. Well-known examples in North American freshwater ecosystems are rainbow trout (*Oncorhynchus mykiss*), largemouth bass (*Micropterus salmoides*), and rusty crayfish (*Orconectes rusticus*). Intentional and unintentional translocation of these species has caused severe declines of native species, including extinction of several fishes. Introductions of captive-bred individuals also pose the risks of loss of genetic variation, introgressive hybridization, outbreeding depression, and loss of distinct, local genetic stocks, all of which can decrease fitness in wild populations (Ryman and Laikre 1991; Utter 2003). Because of the risks involved, translocation of wild individuals or stocking captive-bred individuals should be considered an option of last resort. For many mussel species, such desperate efforts are clearly warranted.

Translocation and captive propagation have been used in mussel conservation for more than 100 years but have accelerated recently along with the growing conservation crisis and advances in propagation techniques. These efforts fall mostly into two categories: (1) *reintroduction*, the attempt to establish additional populations of a species into habitats where it occurred formerly; and (2) *stocking* translocated or captively propagated individuals into existing populations in an attempt to increase population size. Stocking is typically referred to as *augmentation*, likely to avoid negative connotations associated with the former term. A third approach, *assisted colonization*, is the intentional movement of a species beyond its native range (Ricciardi and Simberloff 2009; Shirey and Lamberti 2010). Assisted colonization is proposed to prevent species extinction due to climate change or unavailability of suitable introduction sites within the native range, but this approach has not yet been advocated explicitly for mussels. Reintroduction and augmentation represent some of the most promising opportunities for restoration of the North American mussel fauna but also pose potentially serious threats to the integrity of remaining populations and assemblages. In the following sections, I review the history of these efforts and provide a critical examination of their application.

11.4.A. Translocation

In the early 1900s, mussels were translocated widely to bolster populations decimated by commercial harvest and, in some cases, to introduce commercially valuable species into regions where they did not occur naturally. The success of these attempts or their effects on natural assemblages is mostly unknown, but in some cases, they may have resulted in local establishment of nonnative populations (e.g., Wilson and Clark 1914).

The most common use of translocation today is to remove mussels from impacts of construction (e.g., replacement of bridge pilings) or channel dredging. These efforts typically relocate mussels to similar, unimpacted habitats nearby, and most are mandated as mitigation for destruction of habitat for federally endangered species (Cope and Waller 1995). Many such relocation projects have not been monitored carefully, and the success of others has been widely variable; 30 percent of translocation projects completed before 1995 had mortality of more than 70 percent (Cope and Waller 1995). However, other projects had much higher survival and provided guidelines to maximize success (Havlik 1997; Cope et al. 2003).

Although this strategy may reduce short-term mussel mortality, its value as mitigation for habitat destruction is dubious. Relocation sites are typically selected on the basis of having existing populations (Cosgrove and Hastie 2001; Bolden and Brown 2002; Miller and Payne 2006). Because mussel abundance at recipient sites is controlled to a large extent by local conditions, relocation of additional individuals is unlikely to result in a net gain in population size over time. Furthermore, this strategy does not reduce extinction risk by increasing the number of existing populations.

Translocation also has been used to reintroduce mussels into streams previously affected by water pollution or other impacts. The lower North Fork Holston River, Virginia, lost its mussel fauna due to discharge of mercury and chloride salts from a chemical plant in operation from 1894 to 1972. After closure of the plant and site remediation, 17 species were translocated from other populations between 1975 and 1985 (Ahlstedt 1979; Sheehan et al. 1989). Two years after a 1981 reintroduction, recapture of live individuals varied among species from 17 to 41 percent, but recaptures declined to 1 to 11 percent after 4 years (Sheehan et al. 1989). However, surveys in 1995 found nine species and documented recruitment for four, suggesting that some earlier reintroductions were successful (Henley and Neves 1999). In 1982, TVA translocated 1,000 birdwing pearlymussels, *Lemiox rimosus*, from the Duck River, Tennessee, to each of four other sites within the species' historical range. By 1995, all translocated populations had declined to very low levels, but one or two juveniles were found at two of the sites (J. Jenkinson, personal communication). In 2003, a pilot reintroduction of 80 individuals each of the endangered species *Dromus dromas*, *Epioblasma ahlstedti*, and *L. rimosus* took place in the Wilson Dam tailwaters on the Tennessee River, Alabama. The short-lived *E. ahlstedti* disappeared after 2–3 years, but *D. dromas* and *L. rimosus* continue to survive 8 years later, and gravid females have been found. No evidence of recruitment has been seen, possibly because of a low number of darters (hosts for all three species) in the impounded tailwaters, but also because of the huge extent of available habitat and small size of reintroduced populations (J. Garner, personal communication).

The apparent poor success of these efforts may be due to several factors. First, repeated introductions of large numbers of individuals may be needed to compensate for natural and handling mortality. Second, success is difficult to evaluate because estimating survival requires intensive sampling, and evidence of recruitment may not be detectable for many years. Third, factors that led to initial mussel disappearance may continue to limit survival and reproduction. However, even if translocated individuals do not reproduce, this strategy may be a useful temporary measure to reduce extinction risk of species reduced to single populations.

Translocation may be a viable conservation strategy to establish additional populations of species that remain abundant at other sites. However, translocation of individuals into existing populations poses the risk of mixing distinct genetic stocks, resulting in outbreeding depression or loss of local adaptations (see Section 11.4.B). The most practical problem is that many imperiled species exist at such low abundance that source populations likely cannot sustain the removal of large numbers of individuals necessary to ensure successful translocation to other streams.

11.4.B. Captive propagation

Perhaps the most exciting development in mussel conservation is the recent advance in techniques for propagating mussels in captivity. Captive propagation has been a goal of mussel conservation for more than 100 years and was viewed as a solution to overharvest for the button industry in the early 1900s (e.g., Coker et al. 1921; Section 9.4). Development of propagation techniques was a main focus of research at the Fairport Biological Station (Section 2.2.B). These efforts elucidated host relationships and other aspects of mussel reproduction and developed methods for artificially infecting fishes with glochidia. Large numbers of juveniles could be produced easily on fishes, but raising juveniles to a larger size in captivity proved difficult. Release of larger juveniles was and continues to be considered desirable because of the high natural mortality of newly transformed juveniles (Jones et al. 2006b). Because of the difficulty of culturing juveniles, most efforts to increase stocks of commercial species involved release of fishes artificially infected with glochidia. Fairport scientists reported release of 183 million glochidia artificially infected on fishes in 1920 and release of 5 million infected fishes in 1921 (Coker 1921). However, success of these massive efforts was difficult to assess, and mussel propagation largely ceased with closure of the Fairport laboratory in 1933.

Shortly before closure of the Fairport laboratory, Max Ellis claimed to have perfected a method for bypassing the host stage by metamorphosing glochidia on artificial culture media (Ellis and Ellis 1926). However, his methods were not reported, and the promise of this technique was not fulfilled (Section 2.2.B). Artificial media culture was revisited in the early 1980s and facilitated metamorphosis of several species in vitro (Isom and Hudson 1982). Artificially metamorphosed individuals were cultured for at least 74 days, but juveniles had low growth rates, and culture success varied widely among species (Hudson and Isom 1984). In vitro methods have been simplified but still require stringent laboratory technique, including incubation at elevated CO_2 concentration (Keller and Zam 1990; Roberts and Barnhart 1999). In addition to methodological difficulties, artificial culture was unsuccessful for several species (Milam et al. 2000). More seriously, artificial culture requires use of antibiotics to inhibit fungal or microbial infections, and sensitivity of juveniles to contaminants can differ from juveniles propagated on fishes (Bishop et al. 2007). Because of these factors, along with bypassing the natural host stage, in vitro culture has strong potential for laboratory selection of juveniles with lower probability of survival in the wild. Despite its negative aspects, in vitro culture has the distinct advantage of potentially allowing propagation of critically imperiled species for which hosts are unknown, and for maximizing yield and efficiency in those cases. In vitro culture is currently used in a minority of propagation programs, but efforts to refine these techniques continue (e.g., Owens et al. 2010).

After a hiatus of more than 50 years, captive propagation using natural metamorphosis on fishes began again in earnest in the 1990s and is now commonplace. These efforts use the same basic techniques developed in the early 1900s, and initial work faced similar problems culturing juveniles past the settlement stage. However, extensive research addressing problems of diet, culture conditions, and predator control has now nearly perfected propagation such that large numbers of juveniles of many species can be reared in captivity for more than 1 year (e.g., Gatenby et al. 1997; Henley et al. 2001; Zimmerman et al. 2003; Jones et al. 2005; Barnhart 2006; Figure 11.4). Release of newly metamorphosed juveniles or fishes infected with glochidia is still used in some cases, including attempts to bolster stocks of commercially valuable species (Hubbs 2000; Milam et al. 2000), but capturing, maintaining, and transporting large numbers of infected fishes is difficult, and juveniles produced by these methods cannot be marked to monitor success. In addition to their higher survival, larger juveniles cultured in the laboratory can be uniquely tagged (Eads and Layzer 2002), making release of large, cultured juveniles the method of choice for reintroduction or augmentation.

The ability to produce large numbers of juvenile mussels in captivity opens new possibilities for restoring mussel populations (Figure 11.5). Captive propagation reduces limitations of sufficient source stock associated with translocation. Even

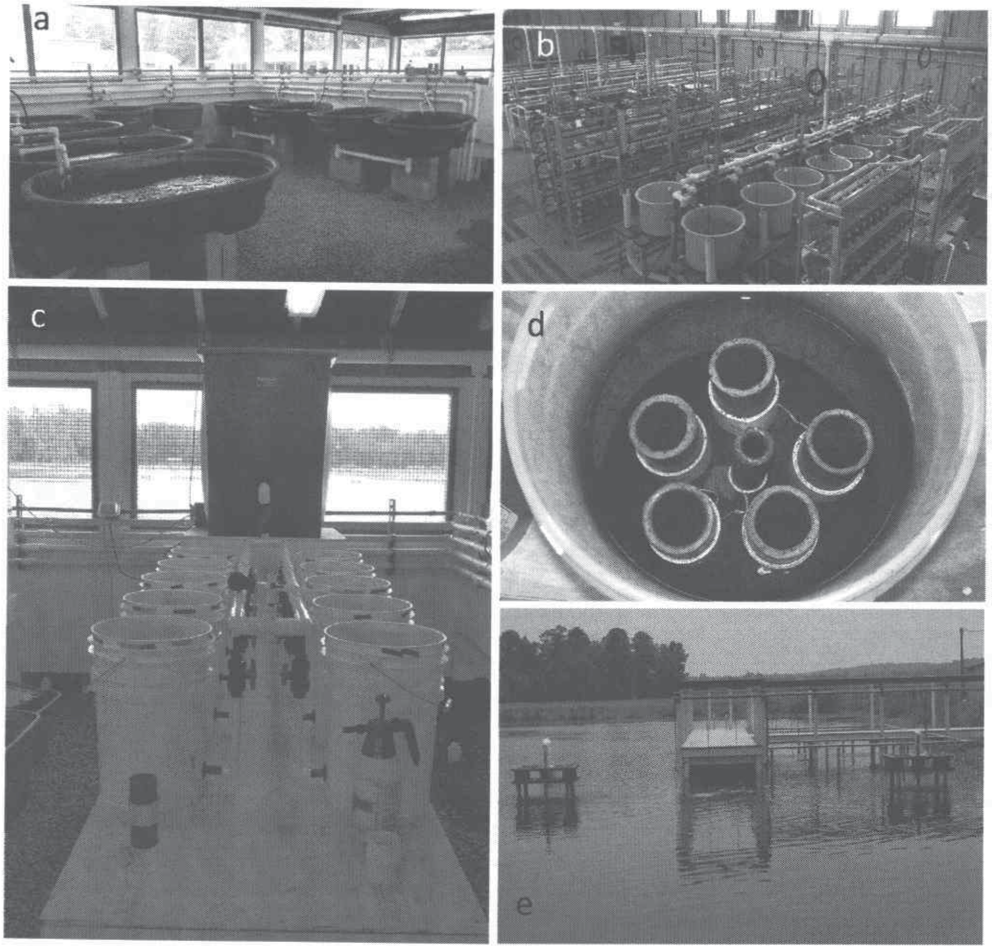

Figure 11.4. Mussel propagation facilities at the Alabama Aquatic Biodiversity Center (AABC), Marion, Alabama. (a) Flow-through holding troughs for adult broodstock. (b) Array of tank sizes used for infecting large numbers of fishes with glochidia. (c) Upwelling, flow-through bucket culture system for newly metamorphosed juvenile mussels, with water supply tank in background. (d) Inside view of bucket culture system showing individual, screened culture chambers. (e) Pond used for juvenile mussel grow-out. Culture buckets are suspended from the dock (AABC, photos, courtesy Paul Johnson).

for the rarest species, glochidia from a single gravid female can produce thousands of juveniles, and the donor female can be returned to the source population. With readily available source stock, reintroductions can be repeated annually, producing large reintroduced populations. Captive propagation also allows release of mussels that more closely match local genetic stocks. In contrast, translocation projects often introduced animals from distant populations because of a lack of sufficient sources nearby (e.g., Layzer and Scott 2006). In addition to its benefits in population restoration, propagation also makes available large numbers of juvenile mussels for toxicity testing and other experimental uses.

Figure 11.5. Propagated juvenile mussels. (a) Approximately 4,000 20-month-old juvenile wavy-rayed lampmussels, *Lampsilis fasciola*, propagated from a single adult female. (b) One-year-old juveniles of the endangered Alabama lampmussel, *Lampsilis virescens*, ready for reintroduction. (c) Placing individually tagged 5-month-old juvenile *L. virescens* in the Paint Rock River, Alabama (AABC, photos, courtesy Paul Johnson).

Captive propagation is now under way on a large scale at laboratories and hatcheries in at least 12 U.S. states and Canada and represents the majority of population restoration efforts. From 1998 to 2001, about 330,000 juvenile mussels of 16 endangered mussel species were produced and released in seven U.S. states (Neves 2004). This number has grown exponentially with advances in propagation methods. In 2004, more than 1 million juveniles were produced and released by a single facility in Missouri and more than 600,000 by a single facility in Virginia in 2010 (Barnhart 2004; Virginia Department of Game and Inland Fisheries 2010). In some cases, propagated juveniles are being used for reintroductions. The long-term success of these efforts is unknown, but some show encouraging signs. From 2003 to 2005, 7,400 juvenile Higgins eye, *Lampsilis higginsii*, were reintroduced into a section of the upper

Mississippi River. At some sites, recovery of propagated individuals was high, and most showed good growth (Davis 2005). In 1999 and 2000, juvenile Neosho muckets, *L. rafinesqueana*, were reintroduced into the Fall River, Missouri. Individuals 42–64 mm in length were recovered in 2002, indicating that propagated juveniles had nearly reached reproductive maturity (Barnhart 2002). However, the majority of propagated juveniles are now being used to augment existing populations rather than to establish additional populations (e.g., Barnhart 2004; Neves 2004).

The most important advantages of captive propagation also present serious risks. Although culturing juveniles to large size may improve survival, an extended period in captivity could select for traits that are nonadaptive in the wild. Culturing and releasing thousands of juveniles from a single female mussel would result in a reintroduced population with extremely low genetic variability. Even large reintroductions derived from multiple females could represent a small proportion of genetic variability present in the source population, resulting in low genetic effective population size (Ryman and Laikre 1991).

The potential for negative genetic effects is most serious with augmentation of existing populations. Large numbers of propagated individuals originating from few females could rapidly swamp and greatly lower genetic variation in the existing population. For example, 50,000 propagated juveniles of the mucket, *Actinonaias ligamentina*, from a single female from the Bourbeuse River were released into an existing population in the Meramec River, Missouri (Barnhart 2002). This sudden influx of huge numbers of individuals of a single genotype contrasts with natural recruitment, in which individual females produce on average fewer than one offspring each year after larval and juvenile mortality (Chapter 7). Multiple paternity, in which several males fertilize eggs of a single female, has been documented in mussels and reduces somewhat the potential for reduction of genetic variability, but the extent of this phenomenon remains poorly known (Section 1.4.C). Augmentation also could result in outbreeding depression or loss of among-population genetic structure by mixing distinct genetic stocks. In the mid-1990s, augmentation of a declining population of the inflated heelsplitter, *Potamilus inflatus*, in the Amite River, Louisiana, was proposed using stock from the Black Warrior River, Alabama, but subsequent studies showed that these two populations represented distinct, cryptic species (Lydeard and Roe 1998; Roe and Lydeard 1998a). Cryptic variation has been discovered within several North American mussel taxa (Serb 2006; Jones and Neves 2010) and is likely widespread, but it has not been examined for most of the fauna.

Several measures have addressed the genetic risks associated with captive propagation. In 2000, a policy providing guidelines for captive propagation was adopted jointly by the U.S. Fish and Wildlife Service and the National Marine Fisheries Service (USFWS and NMFS 2000) and was elaborated on extensively by Jones et al. (2006b). These guidelines aim to (1) minimize loss of within-population genetic variation by use of multiple broodstock females that are rotated frequently and long-term propagation efforts to increase genetic variation over many year-classes; (2) minimize outbreeding depression and loss of among-population genetic variation by not mixing evolutionary significant units or other distinctive genetic stocks; (3) reduce hatchery selection and domestication by mimicking as closely as possible natural conditions such as fish hosts, diet, temperature regimes, and habitat and by release of cultured juveniles at the earliest age that maximizes survival in the wild; and (4) prevent overcollection of broodstock from small donor populations. Accordant with the risks of captive propagation, this policy further states that the first priority is to recover populations in their natural habitats without resorting to captive propagation (USFWS and NMFS 2000; Neves 2004). Other guidelines stipulate that augmentation should be used only when a population is experiencing recruitment failure (Davis 2005). Because of limited resources and ecological concerns, mussel recovery efforts in the Tennessee–Cumberland and Mobile basins now emphasize reintroduction of populations into historically occupied habitats over augmentation of existing populations (R. Butler and P. Johnson, personal communication).

These genetic guidelines have raised awareness of the potential negative effects of captive propagation and have been widely adopted by hatchery managers. For example, Grobler et al. (2006) provided a comprehensive assessment of range-wide genetic structure in the slabside pearlymussel, *Pleuronaia dolabelloides*, for the express purpose of assessing the appropriateness of existing populations as source stock for reintroduction or augmentation in other streams; studies of this nature should be a prerequisite for any reintroduction or augmentation project. In contrast, the charge that captive propagation be used only as a last resort has been heeded to a lesser extent, and the technique is now used routinely and, in some cases, perhaps indiscriminately. Furthermore, despite the greater risks of augmentation, this remains the most common destination for captively propagated individuals in many places.

Captive propagation is clearly justified and necessary for critically imperiled species and should be used aggressively for restoring mussel assemblages in isolated streams that have recovered from past impacts. In some cases, saving a species will warrant relaxation of genetic guidelines because geographic or among population genetic variation has already been lost. For example, reintroduction of the cracking pearlymussel, *Hemistena lata*, into other streams within its historical range is needed to lessen extinction risk, but all future populations will necessarily be derived from the Tennessee River system, which supports the only remaining populations. Similarly, the only remaining population of the catspaw, *Epioblasma o. obliquata*, in Killbuck Creek, Ohio, is declining rapidly due to unknown impacts. If gravid females can still be found, it is urgent that juveniles be propagated and distributed to other suitable sites, even though offspring may have low genetic variability. Although mixing of genetic stocks is a principal danger of augmentation, in some situations it may be desirable to mix populations that do not represent separate evolutionarily significant units.

In populations that have undergone a severe bottleneck and are experiencing reduced individual fitness as a consequence, augmentation with propagated or translocated individuals from other populations may be necessary to increase genetic variation and prevent further fragmentation of the species' gene pool (Grobler et al. 2006; see also Johnson et al. 2010). However, the level of genetic variability needed to ensure population viability in mussels is unknown and likely varies widely among species, and this concern has not yet been used as a basis for augmentation or translocation.

Augmentation may be warranted in isolated populations that have declined to such low levels that their disappearance is imminent. Even with recent improvements in flow regime, the population of *Obovaria retusa* in the Green River may be too small to reproduce or recover naturally and is highly vulnerable to stochastic effects. Because few opportunities currently exist for establishment of this species elsewhere, augmentation with captively propagated individuals may be needed to prevent global extinction of the species. However, in many cases, augmentation can and should be avoided. In addition to the genetic risks of augmentation, this conservation strategy suffers from a lack of clear guidelines on when augmentation is necessary, how much is necessary, and specific goals (e.g., population size) to evaluate when augmentation should cease. These guidelines are difficult to set given our poor knowledge of mussel population dynamics, and even justified augmentation efforts will need to be conducted by trial and error (Jones et al. 2006b). Nevertheless, the lack of clear guidelines and goals for augmentation underscores the haphazard and risky nature of this strategy.

Augmentation has proliferated unnecessarily for several related reasons. First, hatcheries often produce large numbers of juveniles of nonimperiled species during pilot studies to perfect propagation techniques. Rather than dispose of these hard-won juveniles in a responsible, if unsatisfying and perhaps distasteful, way (e.g., preservation or euthanasia), they have frequently been released into existing, natural populations. Second, advances in captive propagation techniques have occurred much more rapidly than habitat restoration, with the result that opportunities for releasing propagated individuals are largely limited to existing populations. Third, the dire nature of the mussel conservation crisis has prompted people who care deeply about this resource to take direct action, and raising mussels in captivity is a compelling and tangible channel for this energy. These reasons are understandable, but I argue that our ability to propagate large numbers of juveniles is alone insufficient to justify doing so when objective and defensible justification does not exist.

11.4.C. Maintaining the integrity of existing and reintroduced assemblages

Equally important to saving imperiled species is maintenance of the ecological integrity of the few remaining healthy mussel assemblages and the emulation of this integrity in reintroduced assemblages. The value of any wild creature is inseparable from its context within the ecosystem of which it is an integral component. Divorced from this context, a creature becomes little more than a curiosity in a zoo or botanical garden. From a more practical perspective, a growing body of research shows that mussel assemblages are dynamic entities that interact extensively among themselves and with other components of the ecosystem. For example, optimal mussel growth and survival may depend on feeding interactions between dominant, keystone species and subordinate species, and these processes in turn may have positive, cascading effects on overall ecosystem health (Spooner and Vaughn 2008). This suggests that successful reintroduction of imperiled species into rehabilitated streams also may require simultaneous reintroduction of nonimperiled species to create an assemblage that provides a full range of ecosystem services. Far from being an abstract conceit, maintenance and restoration of overall mussel assemblage integrity may be necessary to save imperiled species.

Maintenance of ecological integrity is emphasized in propagation guidelines to ensure genetic integrity of individual species and populations (Jones et al. 2006b). In contrast, maintenance of overall assemblage integrity has received little attention, and there are numerous examples of conservation programs that could damage this integrity.

The most obvious examples are introductions of species beyond their native range or in habitats for which they are clearly unadapted. Between 1992 and 1995, more than 2,000 adult individuals of 22 mussel species were translocated from other streams to the upper reaches of Shoal Creek, Alabama (average width = 8 m), which had earlier lost its mussel fauna to water pollution (Morgan et al. 1997). However, 15 were large-river species not reported historically from the creek, and two were not native to the region (*Fusconaia flava* and *Quadrula nodulata*). Similarly, attempts to reestablish mussel populations in tailwater reaches of the French Broad River, Tennessee, included several species not known from the river historically (*Reginaia ebena*, *Megalonaias nervosa*, *Obliquaria reflexa*) and two that are not native to the upper Tennessee River system (*Arcidens confragosus* and *F. flava*) (Layzer and Scott 2006). In both cases, translocated species were apparently a random collection of readily available species obtained without assessment of their ecological or biogeographical suitability for the recipient habitat.

The potential for ecological harm is greatest in streams that continue to support diverse and important mussel assemblages. The upper Big South Fork Cumberland River, Kentucky and Tennessee, supports the best remaining representation of the unique Cumberland River system mussel fauna, including the largest remaining populations worldwide of the little-wing pearlymussel, *Pegias fabula*, and Cumberland bean, *Villosa trabalis*, and the only known population of the tan riffleshell, *Epioblasma florentina walkeri* (Ahlstedt et al. 2003–2004; Jones and Neves 2010). The lower Big South Fork near its confluence with the Cumberland River supported higher diversity historically, including several large-river species, but this fauna was lost to impoundment and coal mining impacts by the 1950s. The upper river was not surveyed historically, but the present fauna is typical of historical assemblages in mid-sized streams elsewhere in the Cumberland River system, and recruitment is occurring for most species. This suggests that the assemblage is relatively intact and has lost few, if any, species. Nevertheless, a program is now under way to introduce several large-river species reported historically from the lower river into the upper river (Bakaletz and Neves 2004). The program also includes augmentation of existing populations of endangered species with captively propagated individuals, despite abundant evidence of natural recruitment. The rationale for augmenting these healthy populations is hard to fathom. The choice of the upper river for introduction of large-river species is one of desperation because there are currently few or no options for creating additional populations of these species in more suitable habitats. Consequently, these efforts could be considered akin to assisted colonization, in which species are introduced into novel habitats without full consideration of the effects on existing assemblages (e.g., Ricciardi and Simberloff 2009). The vital importance and apparently intact nature of the present fauna, coupled with the low likelihood that the upper river will provide a suitable habitat for large-river species, seem to make the Big South Fork a dangerous place to gamble with untested conservation strategies.

Because of our poor knowledge of mussel population dynamics, assessing when a species' abundance is too low is difficult. Consequently, decisions to augment a population typically are made based on value-laden, personal perceptions. A population occurring at low abundance can be stable and recruiting. If the species is not currently imperiled, low abundance is usually acceptable to managers, if it is even noticed. Conversely, if the species is of conservation concern, the immediate assumption often is that its abundance must be increased by stocking. Indeed, stocking has been conducted even in reproducing populations of endangered species that occur at relatively high abundance (see the previous discussion of Big South Fork, for example). These actions are based on legitimate concern for species' survival, but they also illustrate a lack of consideration for overall assemblage integrity and an unwillingness to accept that natural assemblages are structured by ecological forces that should not, and ultimately cannot, be subverted.

Rare species are a natural feature of all ecological assemblages (Section 8.1). Although many mussel species have declined dramatically in the last century, the rarity of many species was a characteristic of assemblages even prior to human impacts. Rafinesque (1820, 70) wrote, "Some of these shells are so very rare, that I have only met them once in 4,000 miles of travels and explorations," and Coker (1919, 42) said, "Some species are nearly always rare, or at least, are never the dominant species of mussel beds." Even in prehistoric shell middens, the majority of species individually composed less than 1 percent of the assemblage (Parmalee et al. 1980; Ahlstedt and McDonough 1995–1996). Prior to widespread stream alteration, *Lampsilis abrupta* was widely distributed but apparently always rare. In the Cumberland River in 1911, only "1 to 3 examples [were] found on each bed," and "this is a very good button species, but so uncommon that it is not much of an item in the trade" (Wilson and Clark 1914, 49). Similarly, Ortmann (1918b) found only two individuals of *L. abrupta* in his survey of the upper Tennessee River system. The rarity of this species even historically is not surprising given its host specialization on top predators such as black bass and walleye and the potential for strong host competition with other species with similar host use (Section 8.3.B). Presently, populations of *L. abrupta* and the ecologically similar *L. higginsii* are being augmented aggressively because of their endangered status. The natural rarity of these species calls into question the necessity and effectiveness of attempting to increase their population size artificially. If hosts are limiting, does this mean we should consider reducing populations of nonendangered species, such as the plain pocketbook, *L. cardium*, and fatmucket, *L. siliquoidea*, that are host competitors? This example may seem extreme (at least I hope so), but it illustrates the type of sticky issues that will arise when we attempt to increase the abundance of certain species beyond the natural capacity of the ecosystem to support them.

Assessment of population viability and stability and hence the need for augmentation or other management actions are dependent on better information about population dynamics. Optimal levels of recruitment, survival, and population size should be expected to differ widely among habitats, life history strategies, and even among populations of species with plastic life history traits (e.g., Bauer 1991). For opportunistic and periodic life history strategists, low annual recruitment may be a sign of a declining population in need of management but is likely a sustainable and natural characteristic (to a point) of many equilibrium strategists (Chapter 7). The large, high density populations seen in large river mussel beds are likely unattainable in small streams or for species that use numerically rare hosts (Chapter 8). Consideration of these factors also may be useful in identifying desired attributes of restored habitats. For example, increased disturbance or habitat variability in regulated, impounded streams may reduce the potential for dominance by a single species by creating temporal and spatial niches for a wider variety of species (see Section 10.5.A).

The coexistence of ecologically similar species is dependent on a delicate balance of many factors, and natural variation in abundance of species over time and space is essential for maintaining diversity. We currently have almost no knowledge of the effects of intentional mussel assemblage alteration, but the human-assisted spread of the Asian unionid *Sinanodonta woodiana* appears to be negatively affecting native bivalve assemblages worldwide (Pou-Rovira et al. 2009). Tinkering with existing assemblages could cause harm in several ways. First, artificially increasing the abundance of certain species could disrupt feeding interactions that are potentially vital for assemblage health and function. Second, changing assemblage structure by augmentation or addition of other species could alter dynamics of host use and availability. Modeling studies show that increasing the abundance of one species could result in extirpation or decline of other species with similar host use by reducing host availability (Rashleigh and DeAngelis 2007). Third, despite the most stringent safeguards, captive propagation and translocation still pose the risks of negative genetic effects and introduction of disease.

One could argue that augmentation or translocation in existing assemblages is unlikely to cause harm simply because they are doomed to failure; that is, the ecological processes that structure assemblages will supersede stocking efforts by, for instance, preventing subordinate species from becoming dominant and displacing keystone species or by limiting the ability of large-river species to persist in small streams. If so, it is imperative to avoid wasted efforts given the limited resources available for mussel conservation. More important, outcomes of these actions are impossible to predict given our rudimentary knowledge of mussel assemblage dynamics. Efforts to save imperiled species unavoidably include an element of risk. But, as in medicine, a fundamental charge for conservation should be "first, do no harm."

11.5. A prognosis

We are in little danger of losing the North American mussel fauna completely, but the extent of remaining diversity that can be conserved is unknown. Ironically, mussel assemblages in some of the most highly altered habitats have the greatest chance of long-term survival. Many species that have adapted to impounded rivers or reservoirs are thriving and occupy extensive areas of contiguous habitat, reducing their vulnerability to localized, stochastic events. The outlook for other species is dire. Species that now exist only in small, isolated populations have a low probability of survival in the future without human intervention. In addition, a large number of other species that are now more widespread could quickly become critically imperiled by loss of one or two important populations.

It is hard to avoid pessimism about our ability to save these species and the unique assemblages they make up. As human populations grow, pressures on natural resources will intensify. Demand for water and power will represent particularly serious threats to the health of aquatic ecosystems, including the viability of mussel populations (e.g., Peterson et al. 2011). Conservation of aquatic ecosystems poses exceptional challenges because they are affected by human activities throughout their watersheds, in contrast to terrestrial systems, which can often be managed in relative isolation (Strayer 2006). Invasive species continue to arrive at an alarming rate, and expansion of aquaculture and global commerce may accelerate the unintentional or intentional introduction of nonnative organisms. Of particular concern is the black carp (*Mylopharyngodon piceus*), a native of eastern Asia. This fish is a specialized molluscivore with large pharyngeal teeth adapted for crushing, and its large size (more than 150 cm) allows it to eat even adults of most North American mussel species (Nico et al. 2005). Ostensibly triploid (and hence sterile) black carp were imported by fish farmers in Arkansas, Mississippi, and Missouri in the 1980s to control snails (the intermediate host of a fish parasite) in aquaculture ponds, but wild, reproducing populations of diploid individuals are now established in Louisiana and perhaps elsewhere. Another pressing issue is that we still do not understand the causes of enigmatic mussel declines and have minimal ability to prevent future declines or to remediate past declines. Pervading all these threats is the specter of global climate change. The effects of climate change on mussels remain to be seen, but they could significantly alter habitats and ecological relationships on which remaining assemblages depend (e.g., Spooner and Vaughn 2008). Any of these factors could represent the last nail in the coffin for a large percentage of mussel diversity.

More specific realities of mussel conservation also are discouraging. Funding for mussel conservation is pitifully low, even compared to the relatively scant funding for conservation of more charismatic organisms, and resources are not available to enact aggressive conservation measures for all imperiled species. Even with increased funding, some species are now so rare that obtaining broodstock for propagation may be impossible. Furthermore, hosts of these species are largely unknown, and suitable sites for reintroduction often do not currently exist. Although habitat restoration holds great promise, it is much more difficult and expensive than propagation, and restoration will not occur fast enough to provide additional habitat for some species that now teeter on the brink of extinction. It is likely that some of these species have already slipped away.

The traditional emphasis on single-species management will need to remain a focus of mussel conservation for several reasons. Regionally endemic species are the most unique elements of the North American fauna and represent the majority of endangered species targeted for management. The primary danger in mussel conservation is that we could ultimately be left with a homogeneous fauna of species adaptable to highly altered habitats, and a shift in focus from endangered species could promote this outcome. Furthermore, the Endangered Species Act is the most powerful regulatory tool to protect and restore aquatic habitats, and the protective umbrella afforded by this legislation benefits many other organisms that co-occur with endangered species.

Nevertheless, mussel conservation must also embrace a broader emphasis on maintenance and enhancement of overall assemblage integrity and ecosystem health. Sole focus on single-species management has the potential to cloud a broader conservation vision. Conservation actions spurred by desperation to save a single species could degrade other elements of assemblage integrity and ultimately compromise the ecosystem functions on which all species depend. Similarly, despite its vital importance, unnecessary propagation efforts could siphon scarce resources from equally vital, if less immediately tangible, strategies. Exercising restraint in captive propagation, particularly with regard to population augmentation, and relying instead on natural recovery *when appropriate* – as mandated by policy guidelines – should not be considered “fiddling while Rome burns” or a “do-nothing” strategy but rather should be accompanied by aggressive habitat protection and restoration. Without these efforts, captive propagation will be needed in perpetuity to support small, isolated populations. Many elements of an assemblage-focused approach are already embodied in current conservation plans, especially watershed-scale initiatives. However, more explicit focus on assemblage integrity would lessen the potential for unintended harm and concentrate efforts on outcomes that increase the chances of creating self-sustaining populations that have a high probability of survival in the future without human intervention.

An assemblage-focused approach would contain the following elements: (1) emphasis on habitat restoration and improvement and subsequent reintroduction of extirpated species or entire mussel assemblages (including "common" species); reintroduction of common species could be accomplished largely by translocation, lessening the strain on scarce resources for propagation; (2) increased attention to protection of healthy assemblages that do not contain threatened or endangered species; (3) adherence to policy guidelines stating that first priority is given to recovering existing populations in their natural habitats without resorting to captive propagation, augmentation, or translocation. As an example, an assemblage-focused approach for conservation of the Cumberland River system fauna would concentrate on aggressive efforts to identify and remediate factors responsible for recent declines in remnant assemblages (e.g., Horse Lick Creek, Little South Fork; Section 10.4.C), followed by reintroduction of the full assemblage that formerly inhabited these streams. Remaining healthy assemblages, such as the Big South Fork, would provide broodstock for reintroduction efforts elsewhere, but equal focus would be given to maintaining the integrity and natural structure of this assemblage.

Such an approach would have several specific benefits. First, healthy and intact mussel assemblages currently receive little protection or attention if they do not include threatened or endangered species. Increased focus on these assemblages could prevent other species from becoming critically imperiled. Second, reintroduction of assemblages of "common" species in formerly degraded streams could hasten recovery and increase the ability of these habitats to support rare species by restoring facilitative feeding interactions and other ecosystem services and would provide valuable, low-risk lessons for future reintroductions. Third, a broader approach to restoring assemblage integrity and ecosystem services could be more politically palatable and feasible than single-species efforts, especially if tied directly to tangible water quality and quantity issues (Strayer 2006).

Despite the bleak outlook I painted at the beginning of this section, there are many reasons to be optimistic about the future of the North American mussel fauna. Even with a growing human population, many streams and lakes have seen dramatic improvements in water quality in the 40 years since passage of the U.S. Clean Water Act and other legislation. Accordingly, mussel populations have rebounded in many places. The ability of mussels to persist at extremely low densities for long periods gives hope that at least some species currently considered extremely rare or even extinct will surprise us by also responding to these improvements. Stream restoration efforts will continue to grow as the tangible and essential services provided by healthy ecosystems are acknowledged more fully. I believe that now-unimaginable opportunities for stream restoration will become available, if not necessary, due to factors not directly related to mussel conservation (e.g., dam safety, water quality for human use). These opportunities will allow us to directly address the fundamental threat to the mussel fauna: habitat fragmentation and isolation. Along with the building mussel conservation crisis has come wide media coverage and increased public awareness of the plight of this formerly unsung resource. This awareness will help accelerate habitat restoration efforts and increase support for mussel conservation. Perhaps most important, the number of people who have dedicated themselves to saving freshwater mussels is growing every year. As a result, new discoveries about mussel ecology and innovative and bold conservation approaches are revealed with increasing frequency. My impression of these talented and committed people is that they will accept nothing less than to pass on stewardship of the treasures of our streams with the resource in better shape than they found it.

A prognosis for the North American fauna must include a mixture of optimism and realism. Aspirations to leave the resource in better shape for future generations will be limited by practical realities, and we should be prepared for the loss of additional species despite our efforts. Nevertheless, it is possible that the building momentum for mussel conservation means that we have already seen the darkest days for the North American fauna. Mussels are a unique part of our natural heritage, and they hold many more surprises and doubtlessly provide important benefits of which we remain unaware. My hope is that – as in the past – mussels will once again become a conspicuous part of our cultural landscape, not because of their dire predicament but because of their abundance and ubiquity.

Appendix A

Values for life history traits of representative North American mussel species

Species	Max. life span (years)	Mean annual fecundity	Age at maturity (year of life)	Glochidia length (μm)	Max. adult size (mm)	Sources[a]
Actinonaias ligamentina	50	820,920	5*	244	140	Moles and Layzer (2008); 2
Alasmidonta heterodon	10	2,661	3*	300	45	Michaelson and Neves (1995); R. Mair (unpublished data)
Alasmidonta marginata	12	47,298	2*	356	102	R. Mair (unpublished data); 2
Alasmidonta viridis	18	6,914	2*	278	38	2,3
Amblema plicata (mean)	31	277,855	6*	205	178	1,2
A. plicata, L. Tallahatchie R.	18	325,709	4	205	101	1,2
A. plicata, Sipsey R.	54	229,738	10*	205	115	1,2
Cumberlandia monodonta	56	5,136,667	10	60	203	Baird (2000)
Cyprogenia stegaria	26	43,494	7	192	75	Jones and Neves (2002); 2
Dromus dromas	25	108,381	8	158	79	Jones et al. (2004)
Ellipsaria lineolata	19	97,833	3*	280	66	2,3
Elliptio arca	34	130,114	3	231	88	1,2
Elliptio crassidens	57	651,250	5*	146	152	2,3

(*continued*)

(*continued*)

Species	Max. life span (years)	Mean annual fecundity	Age at maturity (year of life)	Glochidia length (μm)	Max. adult size (mm)	Sources[a]
Epioblasma capsaeformis	9	13,589	3*	240	49	Jones and Neves (2011); 3
Fusconaia cerina	45	23,922	5	153	62	1,2
Hamiota altilis	15	91,800[2]	3*	288	65	2,3
Lampsilis ornata	18	281,709	2	223	95	1,2
Lampsilis straminea	25	256,500	3*	234	88	2,3
Lampsilis teres	13	2,813,300	1	213	126	2,3,4
Lemiox rimosus	11	16,596	2*	240	39	Jones et al. (2010)
Leptodea fragilis	6	8,319,975	1	80	128	2,3,4
Ligumia recta	13	1,537,964	2*	243	149	2,3
Ligumia subrostrata	9	137,500	1	300	95	3,4
Margaritifera margaritifera	71	7,560,533	12	69	120	Smith (1979); Bauer (1982); Young and Williams (1984a); Hastie et al. (2000b)
Medionidus acutissimus	5	16,258	1	223	34	2,3,4
Megalonaias nervosa	41	607,455	11*	307	207	Coon et al. (1977); 2,3
Obliquaria reflexa	23	37,914	3	214	54	1,2,3
Obovaria unicolor	20	56,390	4	196	42	2,3,4
Plectomerus dombeyanus	33	553,500	5*	236	144	2,3
Pleurobema collina	19	12,423	6*	180	75	Hove and Neves (1994)
Pleurobema decisum	45	33,975	5	170	67	1,2,3
Potamilus ohiensis	5	1,062,768	1	140	140	Coker et al. (1921); 3,4
Potamilus purpuratus	9	416,729	1	276	130	2,3,4
Ptychobranchus fasciolaris	32	247,000[3]	7*	180	157	2
Pyganodon grandis	11	412,300	1	378	134	2,3,4
Quadrula asperata	27	8,308	5	261	56	1,2
Quadrula pustulosa	48	30,220	7	259	80	1,2
Quadrula rumphiana	28	26,275	4*	82	71	2,3
Strophitus subvexus	18	23,214	3*	333	95	2,3

Species	Max. life span (years)	Mean annual fecundity	Age at maturity (year of life)	Glochidia length (μm)	Max. adult size (mm)	Sources[a]
Toxolasma parva	5	11,000	1	175	27	2,3,4
Toxolasma texasensis	11	32,988	2*	185	36	2,3
Truncilla donaciformis	8	351,900	2*	62	47	2,3
Truncilla truncata	10	805,408	3*	65	58	2,3
Utterbackia imbecillis	5	50,265	1	301	82	Harmon and Joy (1990); 2,3
Venustaconcha ellipsiformis	12	138,700	3*	256	76	van der Schalie and van der Schalie (1963); 2,3
Villosa lienosa	6	143,833	1*	240	63	2,3
Villosa nebulosa	6	140,000	2*	262	44	2,3

Note: Age at maturity values marked with an asterisk are estimated based on growth rate (see Section 6.2.B); first year of life = age 0, etc. Maximum adult size from Nico et al. (2005); glochidial size from Barnhart et al. (2008).

[a] Other sources: 1, Haag and Staton (2003); 2, Haag and Rypel (2011); 3, W.R. Haag (in press); 4, W.R. Haag (unpublished data).

[b] Estimated from data on *H. australis* (Blalock-Herod et al. 2002).

[c] Estimated from data on *P. subtentum* (V. Mengel and J. Layzer, unpublished data).

Appendix B

Sources for mussel assemblage data

Stream	Source
Large Rivers, Mississippian region	
Green River, Warren Co., Kentucky	Cochran and Layzer (1993)
Ohio River, Ballard Co., Kentucky	Miller et al. (1986)
Ohio River, Campbell Co., Kentucky	Miller and Payne (1993)
Ouachita River (ORM 344.9), Ouachita Co., Arkansas	Posey (1997)
Ouachita River (ORM 249.0), Bradley Co., Arkansas	Posey (1997)
St. Croix River, Interstate Park, Minnesota	Hornbach and Deneka (1996)
St. Croix River, Lakeland, Minnesota	Hornbach and Deneka (1996)
St. Francis River, Cross Co., Arkansas	Posey (1997)
Tennessee River, Marshall Co., Kentucky	Miller et al. (1992)
Tennessee River, Marshall Co., Kentucky	Layzer and Madison (1997)
Tennessee River, Hardin Co., Tennessee	Layzer and Madison (1997)
Tennessee River, Marshall Co., Alabama	Ahlstedt and McDonough (1993)
Tennessee River, Meigs Co., Tennessee	Ahlstedt and McDonough (1995–1996)
Mississippi River, Crawford Co., Wisconsin	Holland-Bartels (1990)
Mississippi River, Ralls Co., Missouri	Koch (1990)
Mid-sized Streams, Mississippian region	
Allegheny River, Forest Co., Pennsylvania	Smith et al. (2001)
Barren River, Warren Co., Kentucky	Weiss and Layzer (1995)
Big Sunflower River, Sharkey Co., Mississippi	Miller et al. (1992a)
Black River, Sanilac Co., Michigan	Trdan and Hoeh (1993)
Cache River, Monroe Co., Arkansas	Christian and Harris (2005)
Caddo River, Pike Co., Arkansas	Harris and Gordon (1988)
Clinch River, Hancock Co., Tennessee	Ahlstedt and Tuberville (1997)
Clinch River, Russell Co., Virginia	Ahlstedt and Tuberville (1997)
Clinch River, Scott Co., Virginia	Ahlstedt and Tuberville (1997)
Clinton River, Oakland Co., Michigan	Trdan and Hoeh (1993)
Duck River, Maury Co., Tennessee	Ahlstedt (1991)

Stream	Source
Elk River, Lincoln Co., Tennessee	Ahlstedt (1983)
Green River, Hart Co., Kentucky	J. Layzer and D. Crigger (unpublished data)
Licking River, Bath Co., Kentucky	Smathers (1990)
Little Tallahatchie River, Panola Co., Mississippi	Haag and Warren (2007)
North Fork Holston River, Smyth Co., Virginia	Neves and Widlak (1988)
Ouachita River, Montgomery Co., Arkansas	Harris and Gordon (1988)
Paint Rock River, Jackson Co., Alabama	Barr et al. (1995)
Powell River, Claiborne Co., Tennessee	Ahlstedt and Tuberville (1997)
Powell River, Lee Co., Virginia	Ahlstedt (1991)
Saline River, Bradley Co., Arkansas	Davidson and Clem (2004)
Saline River, Saline Co., Arkansas	Harris and Gordon (1988)
Sangamon River, Champaign Co., Illinois	Shanzle and Cummings (1991)
Sipsey Fork Black Warrior River, Winston Co., Alabama	Haag and Warren (2008)
Sipsey River, Greene Co., Alabama	Haag and Warren (2010)
Sipsey River, Pickens Co., Alabama	Haag and Warren (2010)
Sipsey River, Pickens Co., Alabama	Haag and Warren (2010)
South Fork Sangamon River, Macon Co., Illinois	Shanzle and Cummings (1991)
St. Francis River, Wayne Co., Arkansas	Ahlstedt and Jenkinson (1991)
Strawberry River, Sharp Co., Arkansas	J. Harris (unpublished data)
Tippecanoe River, Pulaski Co., Indiana	Cummings and Berlocher (1990)
Tyronza River, Crittenden Co., Arkansas	Jenkinson and Ahlstedt (1993–1994)
Wolf River, Shewano Co., Wisconsin	Havlik (1997)
Small Streams, Mississippian region	
Alum Fork Saline River, Saline Co., Arkansas	Harris and Gordon (1988)
Ausable River, Ontario	DiMaio and Corkum (1995)
Big Moccasin Creek, Russell Co., Virginia	Zale and Neves (1982a)
Blanchard River, Hancock Co., Ohio	Hoggarth et al. (2000)
Blanchard River, Hancock Co., Ohio	Hoggarth et al. (2000)
Borden Creek, Lawrence Co., Alabama	Haag and Warren (2008)
Brown Creek, Winston Co., Alabama	Haag and Warren (2008)
Catfish Creek, Ontario	DiMaio and Corkum (1995)
Copper Creek, Scott Co., Virginia	Ahlstedt (1981)
Copper Creek, Scott Co., Virginia	Barr et al. (1995)
Estill Fork Paint Rock River, Jackson Co., Alabama	McGregor and Shelton (1995)
Flannagin Creek, Lawrence Co., Alabama	Haag and Warren (2008)
Fowler Creek, Madison Co., Alabama	McGregor and Shelton (1995)
Horse Lick, Jackson Co., Kentucky	Houslet and Layzer (1997)
Horse Lick, Jackson Co., Kentucky	Houslet and Layzer (1997)
Hurricane Creek, Jackson Co., Alabama	McGregor and Shelton (1995)
Iatt Creek, Winn Parish, Louisiana	W. R. Haag and M. L. Warren (unpublished data)
Jordan Creek, Vermillion Co., Illinois	Szafoni et al. (2000)

(*continued*)

(*continued*)

Stream	Source
Kickapoo Creek, McLean Co., Illinois	Shanzle and Cummings (1991)
Kinniconick Creek, Lewis Co., Kentucky	W. R. Haag and R. R. Cicerello (unpublished data)
Laurel Fork, Rockcastle Co., Kentucky	Cicerello (1993)
Lick Fork, Jackson Co., Alabama	McGregor and Shelton (1995)
Little Paint Creek, Jackson Co., Alabama	McGregor and Shelton (1995)
Lonetree Creek, Champaign Co., Illinois	Shanzle and Cummings (1991)
Middle Branch, Vermilion Co., Illinois	Szafoni et al. (2000)
North Fork Saline River, Saline Co., Arkansas	Harris and Gordon (1988)
Red River, Powell Co., Kentucky	Houp (1993)
Redbird River, Clay Co., Kentucky	Cicerello (1996a)
Rock Creek, McCreary Co., Kentucky	Cicerello (1996b)
Rush Creek, Winston Co., Alabama	Haag and Warren (2008)
Saugeen River, Ontario	DiMaio and Corkum (1995)
Shoal Creek, Cleburne Co., Alabama	W. R. Haag and M. L. Warren (unpublished data)
South Fork Ouachita River, Montgomery Co., Arkansas	Harris and Gordon (1988)
Sugar Creek, Logan Co., Illinois	Shanzle and Cummings (1991)
Atlantic region	
Asheulot River, New Hampshire	Strayer et al. (1996a)
Crooked Creek, North Carolina	Strayer et al. (1996a)
Hudson River, New York	Strayer et al. (1994)
Little River, North Carolina	Strayer et al. (1996a)
Moccasin Creek, North Carolina	Strayer et al. (1996a)
Neversink River, Orange Co., New York	Strayer and Ralley (1993)
Tar River, North Carolina	Strayer et al. (1996a)
Eastern Gulf region	
Big Creek, Houston Co., Alabama	Garner et al. (2009)
Cowart's Creek, Houston Co., Alabama	Garner et al. (2009)
East Fork Choctawhatchee River, Henry Co., Alabama	Pilarczyk et al. (2006)
Eightmile Creek, Geneva Co., Alabama	Pilarczyk et al. (2006)
Flat Creek, Geneva Co., Alabama	Pilarczyk et al. (2006)
Pea Creek, Barbour Co., Alabama	Pilarczyk et al. (2006)
Pea River, Barbour Co., Alabama	Pilarczyk et al. (2006)
West Fork Choctawhatchee River, Dale Co., Alabama	Pilarczyk et al. (2006)
Yellow River, Covington Co., Alabama	Pilarczyk et al. (2006)

Note: See Chapter 8.

Bibliography

Abell, R.A., et al. 2000. *Freshwater ecoregions of North America: A conservation assessment.* Island Press, Washington, D.C., USA.

Adams, C.C. 1892. Mollusks as cat-fish food. *Nautilus* 5:127–128.

Adams, C.C. 1905. The postglacial dispersal of the North American biota. *Biological Bulletin (Woods Hole)* 9:53–71.

Agassiz, L. 1862. Observations on the rate of increase and other characters of freshwater shells, Unios. *Proceedings of the Boston Society of Natural History* 8:100–101.

Agrell, I. 1948. The shell morphology of some Swedish Unionidae as affected by ecological conditions. *Arkiv for Zoologi* 41:1–30.

Ahlstedt, S.A. 1979. Recent mollusk transplants into the North Fork Holston River in southwestern Virginia. *Bulletin of the American Malacological Union* 1979:21–23.

Ahlstedt, S.A. 1981. The molluscan fauna of Copper Creek (Clinch River system) in southwestern Virginia. *Bulletin of the American Malacological Union* 1981:4–6.

Ahlstedt, S.A. 1983. The molluscan fauna of the Elk River in Tennessee and Alabama. *American Malacological Bulletin* 1:43–50.

Ahlstedt, S.A. 1991. Cumberlandian Mollusk Conservation Program: Mussel surveys in six Tennessee Valley streams. *Walkerana* 5:123–160.

Ahlstedt, S.A., et al. 2003–2004. Current status of freshwater mussels (Bivalvia: Unionidae) in the Big South Fork National River and Recreation Areas of the Cumberland River, Tennessee and Kentucky (1999–2002). *Walkerana* 14:33–77.

Ahlstedt, S.A., et al. 2004. Historical and current examination of freshwater mussels (Bivalvia: Margaritiferidae, Unionidae) in the Duck River basin, Tennessee. Report to Tennessee Wildlife Resources Agency, Nashville, USA.

Ahlstedt, S.A., and J.J. Jenkinson. 1991. Distribution and abundance of *Potamilus capax* and other freshwater mussels in the St. Francis River system, Arkansas and Missouri, USA. *Walkerana* 5:225–261.

Ahlstedt, S.A., and T.A. McDonough. 1993. Quantitative evaluation of commercial mussel populations in the Tennessee River portion of Wheeler Reservoir, Alabama. Pages 38–49 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels. Upper Mississippi River Conservation Committee*, Rock Island, Illinois, USA.

Ahlstedt, S.A., and T.A. McDonough. 1995–1996. Summary of pre-operational monitoring of the mussel fauna in the upper Chickamauga reservoir (Tennessee River) in the vicinity of TVA's Watts Bar Nuclear Plant, 1983–1993. *Walkerana* 8:107–126.

Ahlstedt, S.A., and C. Saylor. 1998. Status survey of the little-wing pearly mussel, *Pegias fabula* (Lea, 1838). *Walkerana* 8:81–105.

Ahlstedt, S.A., and J. Tuberville. 1997. Quantitative reassessment of the freshwater mussel fauna in the Clinch and Powell rivers, Tennessee and Virginia. Pages 72–97 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Alabama Power. 2010. Biological assessment for threatened and endangered species for the Coosa River, Mitchell, and Jordan projects. Alabama Power Company, Birmingham (http://www.alabamapower.com/hydro/coosa_application/ Biological_031307.pdf).

Alderman, J.M., and W.F. Adams. 1993. Conservation of critical habitat for freshwater mussels in North Carolina. Pages 81–82 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Aldridge, D.C., and A.L. McIvor. 2003. Gill evacuation and release of glochidia by *Unio pictorum* and *Unio tumidus* (Bivalvia: Unionidae) under thermal and hypoxic stress. *Journal of Molluscan Studies* 63:55–59.

Aldridge, D.W., B.S. Payne, and A.C. Miller. 1987. The effects of intermittent exposure to suspended solids and turbulence on three species of freshwater mussels. *Environmental Pollution* 45:17–28.

Alexander, R.R., and G.P. Dietl. 2005. Non-predatory shell damage in Neogene western Atlantic deep-burrowing bivalves. *Palaios* 20:280–295.

Allam, B., et al. 2006. Effects of the pathogenic *Vibrio tapetis* on defence factors of susceptible and non-susceptible bivalve species: II. Cellular and biochemical changes following in vivo challenge. *Fish and Shellfish Immunology* 20:384–397.

Allan, J.D. 1995. *Stream ecology: Structure and function of running waters*. Chapman and Hall, London, UK.

Allen, D.C., et al. 2007. Early life-history and conservation status of *Venustaconcha ellipsiformis* (Bivalvia, Unionidae) in Minnesota. *American Midland Naturalist* 157:74–91.

Allen, D.C., and C.C. Vaughn. 2009. Burrowing behavior of freshwater mussels in experimentally manipulated communities. *Journal of the North American Benthological Society* 28:93–101.

Allen, D.C., and C.C. Vaughn. 2010. Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. *Journal of the North American Benthological Society* 29:383–394.

Allen, D.E. 2001. *Naturalists and society: The culture of natural history in Britain, 1700–1900*. Ashgate, Aldershot, UK.

Allen, E. 1924. The existence of a short reproductive cycle in *Anodonta imbecillis*. *Biological Bulletin (Woods Hole)* 46:88–94.

Allen, W.R. 1914. The food and feeding habits of freshwater mussels. *Biological Bulletin (Woods Hole)* 27:127–147.

Allen, W.R. 1921. Studies of the biology of freshwater mussels. I. Experimental studies of the food relations of certain Unionidae. *Biological Bulletin (Woods Hole)* 40:210–241.

Allen, W.R. 1923. Studies of the biology of freshwater mussels. II. The nature and degree of response to certain physical and chemical stimuli. *Ohio Journal of Science* 23:57–82.

Allen, Y.C., and C.W. Ramcharan. 2001. *Dreissena* distribution in commercial waterways of the US: Using failed invasions to identify limiting factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58:898–907.

Allen, Y.C., et al. 1999. Growth and mortality rates of the zebra mussel, *Dreissena polymorpha*, in the lower Mississippi River. *Canadian Journal of Fisheries and Aquatic Sciences* 56:748–759.

Allran, J.W., and W.H. Karasov. 2000. Effects of atrazine and nitrate on northern leopard frog (*Rana pipiens*) larvae exposed in the laboratory from posthatch through metamorphosis. *Environmental Toxicology and Chemistry* 19:2850–2855.

Amyot, J.-P., and J.A. Downing. 1991. Endo- and epibenthic distribution of the unionid mollusc *Elliptio complanata*. *Journal of the North American Benthological Society* 10:280–285.

Amyot, J.-P., and J.A. Downing. 1997. Seasonal variation in vertical and horizontal movement of the freshwater bivalve *Elliptio complanata* (Mollusca:Unionidae). *Freshwater Biology* 37:345–354.

Amyot, J.-P., and J.A. Downing. 1998. Locomotion in *Elliptio complanata* (Mollusca: Unionidae): A reproductive function? *Freshwater Biology* 39:351–358.

Anders, K., and B. Wiese. 1993. Glochidia of the freshwater mussel, *Anodonta anatine*, affecting the anadromous European smelt (*Osmerus eperlanus*) from the Eider Estuary, Germany. *Journal of Fish Biology* 42:411–419.

Anderson, R.M., et al. 1993. Why did Indiana halt commercial mussel harvest in 1991? Pages 19–24 *in* K.S. Cummings, A.C. Buchanan, and L.M. Koch, editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Anfinson, J.O. 2003. *The river we have wrought: A history of the upper Mississippi*. University of Minnesota Press, Minneapolis, USA.

Angelo, R.T., et al. 2007. Residual effects of lead and zinc mining on freshwater mussels in the Spring River Basin (Kansas, Missouri, and Oklahoma, USA). *Science for the Total Environment* 384:467–496.

Angermeier, P.L., and I.J. Schlosser. 1989. Species-area relationships for stream fishes. *Ecology* 70:1450–1462.

Angermeier, P.L., and M.R. Winston. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* 79:911–927.

Anthony, J.L., and J.A. Downing. 2001. Exploitation trajectory of a declining fauna: A century of freshwater mussel fisheries in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2071–2090.

Anthony, J. L., et al. 2001. Length-specific growth rates in freshwater mussels (Bivalvia: Unionidae): Extreme longevity or generalized growth cessation? *Freshwater Biology* 46:1349–1359.

Antunes, F., et al. 2010. Association between environmental microbiota and indigenous bacteria found in hemolymph, extrapallial fluid and mucus of *Anodonta cygnea* (Linnaeus, 1758). *Microbial Ecology* 60:304–309.

Apgar, A.C. 1887. The muskrat and the Unio. *The Zoologist* 11:425–426.

Arbuckle, K.E., and J.A. Downing. 2002. Freshwater mussel abundance and species richness: GIS relationships with watershed land use and geology. *Canadian Journal of Fisheries and Aquatic Sciences* 59:310–316.

Arey, L.B. 1921. An experimental study on glochidia and the factors underlying encystment. *Journal of Experimental Zoology* 33:463–499.

Arey, L.B. 1923. Observations on an acquired immunity to a metazoan parasite. *Journal of Experimental Zoology* 38:377–381.

Arey, L.B. 1932a. The formation and structure of the glochidial cyst. *Biological Bulletin (Woods Hole)* 62:212–221.

Arey, L.B. 1932b. The nutrition of glochidia during metamorphosis. *Journal of Morphology* 53:201–221.

Arter, H.E. 1989. Effect of eutrophication on species composition and growth of freshwater mussels (Mollusca:Unionidae) in Lake Hallwil (Aargau, Switzerland). *Aquatic Science* 51:87–99.

Aspelin, A.L. 2003. Pesticide usage in the United States: Trends during the 20th century. Technical Bulletin 105. Center for Integrated Pest Management, North Carolina State University, Raleigh, USA.

Athearn, H.D. 1967. Changes and reductions in our freshwater molluscan populations (Abstract). American Malacological Union Annual Reports 1967:44–45.

Audubon, M.R. 1899. The eccentric naturalist. Pages 473–480 *in Audubon and his journals*. Scribner's, New York, USA [reprinted in 1972 by Peter Smith, Gloucester, Massachusetts, USA].

Augspurger, T., et al. 2003. Water quality guidance for protection of freshwater mussels (Unionidae) from ammonia exposure. *Environmental Toxicology and Chemistry* 22:2569–2575.

Babbitt B. 2002. What goes up, may come down. *Bioscience* 52:656–658.

Bailey, R.C., and R.H. Green. 1988. Within-basin variation in the shell morphology and growth rate of a freshwater mussel. *Canadian Journal of Zoology* 66:1704–1708.

Bailey, R.M., et al. 1970. *A list of common and scientific names of fishes from the United States and Canada*. Special Publication Number 6. American Fisheries Society, Bethesda, Maryland, USA.

Bain, M.B., and N.J. Stephenson, editors. 1999. *Aquatic habitat assessment: Common methods*. American Fisheries Society, Bethesda, Maryland, USA.

Baird, M.S. 2000. Life history of the spectaclecase, *Cumberlandia monodonta* Say, 1829 (Bivalvia, Unionoidea, Margaritiferidae). Thesis, Southwest Missouri State University, Springfield, USA.

Bakaletz, S., and R.J. Neves. 2004. Big South Fork restores endangered mussels. Natural Resource Year in Review – 2004, U.S. National Park Service (http://www.nature.nps.gov/yearinreview/yir2004/03_E.html).

Baker, F.C. 1898. The Mollusca of the Chicago area, Part I: The Pelecypoda. *Bulletin of the Chicago Academy of Science* 3:1–130.

Baker, F.C. 1926. The naiad fauna of the Rock River system: A study of the law of stream distribution. *Transactions of the Illinois State Academy of Science* 19:103–112.

Baker, F.C. 1928. The fresh water Mollusca of Wisconsin. Part II. Pelecypoda. *Bulletin of the Wisconsin Geological and Natural History Survey* 70:1–495.

Baker, F.C. 1941. Part II. A study in ethnozoology of the prehistoric Indians of Illinois. *Transactions of the American Philosophical Society* 32:51–77.

Baker, J.A., and S.T. Ross. 1981. Spatial and temporal resource utilization by southeastern cyprinids. *Copeia* 1981:178–189.

Baker, S.M., and D.J. Hornbach. 2001. Seasonal metabolism and biochemical composition of two unionid mussels, *Actinonaias ligamentina* and *Amblema plicata*. *Journal of Molluscan Studies* 67:407–416.

Baker, S.M., and J.S. Levinton. 2003. Selective feeding by three native North American freshwater mussels implies food competition with zebra mussels. *Hydrobiologia* 505:97–105.

Baldigo, B.P., et al. 2003–2004. Effects of environmental and spatial features on mussel populations and communities in a North American river. *Walkerana* 14:1–32.

Balfour, D.L., and L.A. Smock. 1995. Distribution, age structure, and movements of the freshwater mussel *Elliptio complanata* (Mollusca:Unionidae) in a headwater stream. *Journal of Freshwater Ecology* 10:255–268.

Ball, G.H. 1922. Variation in fresh-water mussels. *Ecology* 3:93–121.

Balla, S.A., and K.F. Walker. 1991. Shape variation in the Australian freshwater mussel *Alathyria jacksoni* Iredale (Bivalvia, Hyriidae). *Hydrobiologia* 220:89–98.

Barfield, M., and G.T. Watters. 1998. Non-parasitic life cycle in the green floater, *Lasmigona subviridis* (Conrad, 1835). *Triannual Unionid Report* 16:22 (http://ellipse.inhs.uiuc.edu/FMCS/TUR/default.html).

Bärlocher, F., and H. Brendelberger. 2004. Filtration of aquatic hyphomycete spores by a benthic suspension feeder. *Limnology and Oceanography* 49:2292–2296.

Barnes, G.E. 1962. The behaviour of unrestrained *Anodonta*. *Animal Behaviour* 10:174–176.

Barnhart, M.C. 1997. Fertilization success in freshwater mussels. Report to Missouri Department of Conservation, Columbia, USA (http://biology.missouristate.edu/faculty_pages/Barnhart%20pubs/barnhart_pubs.htm).

Barnhart, M.C. 2001. Fish hosts and culture of mussel species of special concern. Report to U.S. Fish and Wildlife Service and Missouri Department of Conservation, Columbia, USA (http://biology.missouristate.edu/faculty_pages/ Barnhart%20pubs/barnhart_pubs.htm).

Barnhart, M.C. 2002. Propagation and culture of mussel species of special concern. Report to U.S. Fish and Wildlife Service and Missouri Department of Conservation, Columbia, USA (http://biology.missouristate.edu/faculty_pages/Barnhart%20pubs/barnhart_pubs.htm).

Barnhart, M.C. 2004. Propagation and restoration of mussel species of concern. Report to the Missouri Department of Conservation, Columbia, USA (http://biology.missouristate.edu/faculty_pages/Barnhart%20pubs/barnhart_pubs.htm).

Barnhart, M.C. 2006. Buckets of muckets: A compact system for rearing juvenile freshwater mussels. *Aquaculture* 254:227–233.

Barnhart, M.C. 2010. Unio gallery (http://unionid.missouristate.edu).

Barnhart, M.C., and M.S. Baird. 2000. Fish hosts and culture of mussel species of special concern: Annual report for 1999. Report to U.S. Fish and Wildlife Service and Missouri Department of Conservation, Columbia, USA (http://biology.missouristate.edu/faculty_pages/Barnhart%20pubs/barnhart_pubs.htm).

Barnhart, M.C., and A. Roberts. 1997. Reproduction and fish hosts of unionids from the Ozark uplifts. Pages 16–20 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Barnhart, M.C., et al. 2008. Adaptations to larval parasitism in the Unionoida. *Journal of the North American Benthological Society* 27:370–394.

Barr, W.C., et al. 1995. Cumberlandian mollusk conservation program. Activity 8: Analysis of macrofauna factors. *Walkerana* 7:159–224.

Barton, D.R., et al. 2000. The effects of carp (*Cyprinus carpio* L.) on sediment export from a small urban impoundment. *Journal of Aquatic Ecosystem Stress and Recovery* 8:155–159.

Bartsch, M.R., et al. 2005. Strong effects of predation by fishes on an invasive macroinvertebrate in a large floodplain river. *Journal of the North American Benthological Society* 24:168–177.

Bartsch, M.R., et al. 2010. Influence of shell morphology on distributions of unionids in the upper Mississippi River. *Journal of Molluscan Studies* 76:67–76.

Bartsch, P. 1916. The Missouri River as a faunal barrier. *Nautilus* 30:92.

Bates, J.M. 1962. The impact of impoundment on the mussel fauna of Kentucky Reservoir, Tennessee River. *American Midland Naturalist* 68:232–236.

Bauer, G. 1983. Age structure, age-specific mortality rates and population trend of the freshwater pearl mussel (*Margaritifera margaritifera*) in North Bavaria. *Archives für Hydrobiologie* 98:523–531.

Bauer, G. 1987. Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *Journal of Animal Ecology* 56:691–704.

Bauer, G. 1988. Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in central Europe. *Biological Conservation* 45:239–253.

Bauer, G. 1991. Plasticity of life history traits of the freshwater pearl mussel – consequences for the danger of extinction and for conservation measures. Pages 103–120 *in* A. Seitz and V. Loeschcke, editors. *Species conservation. A population-biological approach*. Birkhauser Verlag, Basel, Switzerland.

Bauer, G. 1992. Variation in the life span and size of the freshwater pearl mussel. *Journal of Animal Ecology* 61:425–436.

Bauer, G. 1994. The adaptive value of offspring size among freshwater mussels (Bivalvia: Unionoidea). *Journal of Animal Ecology* 63:933–944.

Bauer, G. 1998. Allocation policy of female freshwater pearl mussels. *Oecologia (Berlin)* 117:90–94.

Bauer, G. 2001. Life-history variation on different taxonomic levels of naiads. Pages 83–91 *in* G. Bauer and K. Wächtler, editors. *Ecology and evolution of the freshwater mussels Unionoida*. Ecological Studies 145. Springer, Heidelberg, Germany.

Bauer, G., and C. Vogel. 1987. The parasitic stage of the freshwater pearl mussel (*Margaritifera margaritifera* L.) I. Host response to glochidiosis. *Archiv für Hydrobiologie Supplement* 76:393–402.

Bauer, G., et al. 1991. Spatial distribution of freshwater mussels: The role of host fish and metabolic rate. *Freshwater Biology* 26:377–386.

Beaz-Hidalgo, R., et al. 2010. Diversity and pathogenecity of *Vibrio* species in cultured bivalve mollusks. *Environmental Microbiology Reports* 2:34–43.

Beckman, K.B., and B.N. Ames. 1998. The free radical theory of ageing matures. *Physiological Review* 78:547–581.

Bednarek, A.T., and D.D. Hart. 2005. Modifying dam operations to restore rivers: Ecological responses to Tennessee River dam mitigation. *Ecological Applications* 15:997–1008.

Beebee, T.J.C., and R.A. Griffiths. 2005. The amphibian decline crisis: A watershed for conservation biology? *Biological Conservation* 125:271–285.

Beeton, A.M. 1965. Eutrophication of the St. Lawrence Great Lakes. *Limnology and Oceanography* 10:240–254.

Belanger, T.V., et al. 1990. Growth rates of the Asiatic clam, *Corbicula fluminea*, in the upper and middle St. Johns River, Florida. *Nautilus* 104:4–9.

Benjamini, Y., and D. Yekutieli. 2001. The control of false discovery rate under dependency. *Annals of Statistics* 29: 1165–1188.

Benke, A.C. 1990. A perspective on America's vanishing streams. *Journal of the North American Benthological Society* 9:77–88.

Benke, A.C., and C.E. Cushing. 2005. *Rivers of North America*. Elsevier, Burlington, Massachusetts, USA.

Benke, A.C., et al. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308–343.

Berg, D.J., et al. 1998. Genetic structure of *Quadrula quadrula* (Bivalvia: Unionidae): Little variation across large distances. *Journal of Shellfish Research* 17:1365–1373.

Berg, D.J., et al. 2007. Population genetic structure of three freshwater mussel (Unionidae) species within a small stream system: Significant variation at local spatial scales. *Freshwater Biology* 52:1427–1439.

Bernhardt, E.S., et al. 2005. Synthesizing U.S. river restoration efforts. *Science* 308:636–637.

Beussink, Z.S. 2007. The effects of suspended sediment on the attachment and metamorphosis success of freshwater mussel parasitic life stages. Thesis, Missouri State University, Springfield, USA.

Billington, D.P., et al. 2005. The history of large federal dams: Planning, design, and construction. U.S. Bureau of Reclamation, National Park Service, and Army Corps of Engineers, Washington, D.C., USA.

Bisbee, G.D. 1984. Ingestion of phytoplankton by two species of freshwater mussels, the black sandshell, *Ligumia recta*, and the three ridger, *Amblema plicata*, from the Wisconsin River in Oneida County, Wisconsin. *Bios* 58:219–225.

Bishop, C.D., et al. 2007. Propagation and culture of freshwater mussels. Pages 65–94 *in* J.L. Farris and J.H. Van Hassel, editors. *Freshwater bivalve ecotoxicology*. CRC Press, Boca Raton, Florida, USA.

Bishop, J.D.D., and A. J. Pemberton. 2006. The third way: spermcast mating in sessile marine invertebrates. *Integrative and Comparative Biology* 46:398–406.

Black, B.A., et al. 2010. Spatial variability in growth-increment chronologies of long-lived freshwater mussels: Implications for climate impacts and reconstructions. *Ecoscience* 17:240–250.

Blalock, H.N., and J.B. Sickel. 1996. Changes in the mussel (Bivalvia: Unionidae) fauna within the Kentucky portion of Lake Barkley since impoundment of the lower Cumberland River. *American Malacological Bulletin* 13:111–116.

Blalock-Herod, H.N., et al. 2002. Evaluation of conservation status, distribution, and reproductive characteristics of an endemic Gulf Coast freshwater mussel, *Lampsilis australis* (Bivalvia: Unionidae). *Biodiversity and Conservation* 11:1877–1887.

Blalock-Herod, H.N., et al. 2005. A historical and current perspective of the freshwater mussel fauna (Bivalvia: Unionidae) from the Choctawhatchee River drainage in Alabama and Florida. *Bulletin of the Alabama Museum of Natural History* 24:1–26.

Blevins, R.L., and W.W. Frye. 1993. Conservation tillage: An ecological approach to soil management. Pages 33–78 *in* D.L. Sparks, editor. *Advances in agronomy*. Volume 51. Academic Press, San Diego, California, USA.

Bloomer, H.H. 1934. On the sex, and sex-modification of the gill of *Anodonta cygnea*. *Proceedings of the Malacological Society, London* 21:21–28.

Blumentritt, D.J., et al. 2009. Formation and early history of Lakes Pepin and St. Croix of the upper Mississippi River. *Journal of Paleolimnology* 41:545–562.

Boepple, J.F., and R.E. Coker. 1912. Mussel resources of the Holston and Clinch rivers of eastern Tennessee. *U.S. Bureau of Fisheries Document* 765:1–13.

Boewe, C. 1988. Rafinesque among the field naturalists. *Bartonia* 54:48–58.

Bogan, A.E. 1993. Freshwater bivalve extinctions (Mollusca: Unionoida): A search for causes. *American Zoologist* 33:599–609.

Bogan, A.E. 2002. *Workbook and key to the freshwater bivalves of North Carolina*. North Carolina Museum of Natural Sciences, Raleigh, USA.

Bogan, A.E. 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. *Hydrobiologia* 595:139–147.

Bolden, S.R., and K.M. Brown. 2002. Role of stream, habitat, and density in predicting translocation success in the threatened Louisiana pearlshell, *Margaritifera hembeli* (Conrad). *Journal of the North American Benthological Society* 21:89–96.

Bonsall, M.B. 2005. Longevity and ageing: Appraising the evolutionary consequences of growing old. *Philosophical Transactions of the Royal Society of London, Series B* 361:119–135.

Borah, D.K., et al. 2003. Water, sediment, nutrient, and pesticide measurements in an agricultural watershed in Illinois during storm events. *Transactions of the American Society of Agricultural Engineers* 46:657–674.

Borcherding, J. 1991. The annual reproductive cycle of the freshwater mussel *Dreissena polymorpha* (Pallas) in lakes. *Oecologia (Berlin)* 87:208–218.

Boschung, H.T., and R.L. Mayden. 2004. *Fishes of Alabama*. Smithsonian Books, Washington, D.C., USA.

Bowers, R.W., and F.A. de Szalay. 2007. Fish predation of zebra mussels attached to *Quadrula quadrula* (Bivalvia: Unionidae) and benthic molluscs in a Great Lakes coastal wetland. *Wetlands* 27:203–208.

Boyer, S.L., et al. 2011. A DNA-barcoding approach to identifying juvenile freshwater mussels (Bivalvia:Unionidae) recovered from naturally infested fishes. *Journal of the North American Benthological Society* 30:182–194.

Brainwood, M., et al. 2008. The role of geomorphology in substratum patch selection by freshwater mussels in the Hawkesbury-Nepean River (New South Wales) Australia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18:1285–1301.

Brann, W.P. 1947. Fresh-water mussel shells, the basis for an Arkansas industry. *University of Arkansas Bureau of Research, Research Series* 9:1–37.

Braun, E.L. 1950. *Deciduous forests of eastern North America*. Blakiston, Philadelphia, Pennsylvania, USA.

Bravard, J.P., et al. 1999. Environmental and societal effects of channel incision and remedial strategies. Pages 304–341 *in* S.E. Darby and A. Simon, editors. *Incised river channels*. John Wiley, Chichester, UK.

Brendelberger, H., and C. Klauke. 2009. Pedal feeding in freshwater unionid mussels: Particle-size selectivity. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 30:1082–1086.

Briggs, J.C. 1986. Introduction to the biogeography of North American fishes. Pages 1–16 *in* C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley, New York, USA.

Bright, W. 2004. *Native American place names of the United States*. University of Oklahoma Press, Norman, USA.

Brim Box, J., and J. Mossa. 1999. Sediment, land use, and freshwater mussels: Prospects and problems. *Journal of the North American Benthological Society* 18:99–117.

Brim Box, J., and J.D. Williams. 2000. Unionid mollusks of the Apalachicola Basin in Alabama, Florida, and Georgia. *Bulletin of the Alabama Museum of Natural History* 21:1–143.

Brim Box, J., et al. 2002. Relationships between streambed substrate characteristics and freshwater mussels (Bivalvia: Unionidae) in coastal plain streams. *Journal of the North American Benthological Society* 21:253–260.

Brim-Box, J., et al. 2006. Freshwater mussels (Bivalvia: Unionidae) of the Umatilla and Middle Fork John Day rivers in eastern Oregon. *Northwest Science* 80:95–107.

Bringolf, R.B., et al. 2007a. Acute and chronic toxicity of pesticide formulations (atrazine, chlorpyrifos, and permethrin) to glochidia and juveniles of *Lampsilis siliquoidea*. *Environmental Toxicology and Chemistry* 26:2101–2107.

Bringolf, R.B., et al. 2007b. Acute and chronic toxicity of technical-grade pesticides to glochidia and juveniles of freshwater mussels (Unionidae). *Environmental Toxicology and Chemistry* 26:2086–2093.

Bringolf, R.B., et al. 2010. Environmental occurrence and reproductive effects of the pharmaceutical fluoxetine in native freshwater mussels. *Environmental Toxicology and Chemistry* 29:1311–1318.

Britton, J.C., and B. Morton. 1979. *Corbicula* in North America: The evidence reviewed and evaluated. Pages 250–287 *in* J.C. Britton, editor. *First International Corbicula Symposium*. Texas Christian University Research Foundation, Fort Worth, USA.

Brodniewicz, I. 1968. On glochidia of the genera *Unio* and *Anodonta* from the Quaternary freshwater sediments of Poland. *Acta Palaeontologica Polonica* 13:619–628.

Brönmark, C., and B. Malmqvist. 1982. Resource partitioning between unionid mussels in a Swedish lake outlet. *Holarctic Ecology* 5:389–395.

Brown, A.V., et al. 2005. Lower Mississippi River and its tributaries. Pages 230–281 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America*. Elsevier, Burlington, Massachusetts, USA.

Brown, C.J.D., et al. 1938. The size of certain naiades from western Lake Erie in relation to shoal exposure. *American Midland Naturalist* 19:682–701.

Brown, K.M., and P.D. Banks. 2001. The conservation of unionid mussels in Louisiana rivers: Diversity assemblage composition and substrate use. *Aquatic Conservation: Marine and Freshwater Ecosystems* 11:189–198.

Brown, K.M., and J.P. Curole. 1997. Longitudinal changes in the mussels of the Amite River: Endangered species, effects of gravel mining, and shell morphology. Pages 236–246 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II:*

Initiatives for the future. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Brown, K.M., et al. 2010. The effect of Hurricane Katrina on the mussel assemblage of the Pearl River, Louisiana. *Aquatic Ecology* 44:223–231.

Bruenderman, S.A., and R.J. Neves. 1993. Life history of the endangered fine-rayed pigtoe, *Fusconaia cuneolus* (Bivalvia: Unionidae) in the Clinch River, Virginia. *American Malacological Bulletin* 10:83–91.

Bruenderman, S.A., et al. 2001. Survey for the Curtis pearlymussel, *Epioblasma florentina curtisii* (Utterback 1914) and other mussel species in Little Black River, Missouri. Report to the U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA.

Buchanan, A.C. 1980. Mussels (Naiades) of the Meramec River basin, Missouri. *Missouri Department of Conservation Aquatic Series* 17:1–68.

Buchanan, A.C. 1987. Die-off impacts on the mussel fauna of selected reaches of the Bourbeuse and Meramec rivers, Missouri. Pages 44–54 *in* R.J. Neves, editor. *Proceedings of the workshop on die-offs of freshwater mussels in the United States*. Upper Mississippi River Conservation Committee, Davenport, Iowa, USA.

Bur, M.T. 1982. Food of freshwater drum in western Lake Erie. *Journal of Great Lakes Research* 8:672–675.

Burdick, R.C., and M.M. White. 2007. Phylogeography of the Wabash pigtoe, *Fusconaia flava* (Rafinesque, 1820) (Bivalvia:Unionidae). *Journal of Molluscan Studies* 73:367–375.

Burlakova, L.E., et al. 1998. Field and laboratory studies of zebra mussel (*Dreissena polymorpha*) infection by the ciliate *Conchophthirus acuminatus* in the Republic of Belarus. *Journal of Invertebrate Pathology* 71:251–257.

Burr, B.M., and M.L. Warren. 1986. *A distributional atlas of Kentucky fishes*. Scientific and Technical Series 4. Kentucky State Nature Preserves Commission, Frankfort, USA.

Busby, W.H., and G. Horak. 1993. Unionid mussels in Kansas: Overview of conservation efforts and harvest regulations. Pages 50–55 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Butler, A.W. 1885. Observations on the muskrat. *American Naturalist* 19:1044–1055.

Butler, R.S. 1989. Distributional records for freshwater mussels (Bivalvia: Unionidae) in Florida and South Alabama, with zoogeographic and taxonomic notes. *Walkerana* 3:239–261.

Butler, R.S., and R.L. Mayden. 2003. Cryptic biodiversity. *Endangered Species Bulletin* 28:24–26.

Cahoon, L.B., and D.A. Owen. 1996. Can suspension feeding by bivalves regulate phytoplankton biomass in Lake Waccamaw, North Carolina? *Hydrobiologia* 315:193–200.

Cain, A.J. 1988. The colours of marine bivalve shells with special reference to *Macoma balthica*. *Malacologia* 28:289–318.

Cairns, J., et al. 1975. The effects of temperature upon the toxicity of chemicals to aquatic organisms. *Hydrobiologia* 47:135–171.

Call, R.E. 1878. Mode of distribution of fresh-water mussels. *American Naturalist* 12:472–473.

Call, R.E. 1900. A descriptive illustrated catalogue of the Mollusca of Indiana. *24th Annual Report, Indiana Department of Geology and Natural Resources* 1899:335–535.

Camargo, J.A., and A. Alonso. 2006. Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: A global assessment. *Environment International* 32:831–849.

Campbell, D.C., and C. Lydeard. 2012a. The genera of Pleurobemini (Bivalvia: Unionidae: Ambleminae). *American Malacological Bulletin* 30:19–38.

Campbell, D.C., and C. Lydeard. 2012b. Molecular systematics of *Fusconaia* (Bivalvia: Unionidae: Ambleminae). *American Malacological Bulletin* 30:1–17.

Campbell, D.C., et al. 2005. Phylogeny of North American amblemines (Bivalvia, Unionida): Prodigious polyphyly proves pervasive across genera. *Invertebrate Biology* 124:131–164.

Campbell, D.C., et al. 2008. Identification of "extinct" freshwater mussel species using DNA barcoding. *Molecular Ecology Resources* 8:711–724.

Caraco, N.F., et al. 1997. Zebra mussel invasion in a large, turbid river: Phytoplankton response to increased grazing. *Ecology* 78:588–602.

Caraco, N.F., et al. 2006. Top-down control from the bottom: Regulation of eutrophication in a large river by benthis grazing. *Limnology and Oceanography* 51:664–670.

Carling, P.M. 1992. In-stream hydraulics and sediment transport. Pages 101–125 *in* P. Calow and G.E. Petts, editors. *The rivers handbook*. Vol. I. Blackwell, Oxford, UK.

Carman, S.M. 2007. Texas hornshell recovery plan. New Mexico Department of Fish and Game, Conservation Services Division, Sante Fe, USA (http://www.wildlife.state.nm.us/conservation/threatened_endangered_species/).

Carson, R. 1962. *Silent spring*. Houghton Mifflin, New York, USA.

Cartwright, C. 2003. Unusual use of freshwater mussel (*Unio* sp.) shells during the Early Bronze Age at Tell es-Sa'idiyeh, Jordan. *Environmental Archaeology* 8:85–89.

Casagrandi, R., et al. 2007. Modelling the local dynamics of the zebra mussel (*Dreissena polymorpha*). *Freshwater Biology* 52:1223–1238.

Casey, J. 1987. Aboriginal and modern mussel assemblages of the lower Cumberland River. *Southeastern Archaeology* 6:115–124.

Caswell, H. 1976. Community structure: A neutral model analysis. *Ecological Monographs* 46:327–354.

Ceas, P.A., and L.M. Page. 1997. Systematic studies of the *Etheostoma spectabile* complex (Percidae; subgenus *Oligocephalus*), with descriptions of four new species. *Copeia* 1997:496–522.

Chamberlain, T.K. 1934. The glochidial conglutinates of the Arkansas fanshell, *Cyprogenia aberti* (Conrad). *Biological Bulletin* 66:55–61.

Charlesworth, B. 1994. *Evolution in age-structured populations*. Cambridge University Press, Cambridge, UK.

Charnov, E.L. 1982. *The theory of sex allocation*. Princeton University Press, Princeton, New Jersey, USA.

Charnov, E.L., et al. 2007. Lifetime reproductive effort. *The American Naturalist* 170:E129–E142.

Chen, L. 1998. The respiratory physiology and energy metabolism of freshwater mussels and their responses to lack of oxygen. Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, USA.

Chen, L.-Y., et al. 2001. Comparison of oxygen consumption in freshwater mussels (Unionidae) from different habitats during declining dissolved oxygen concentration. *Hydrobiologia* 450:209–214.

Cherry, D.S., et al. 2005. Potential effects of Asian clam (*Corbicula fluminea*) die-offs on native freshwater mussels (Unionidae) I: Water-column ammonia levels and ammonia toxicity. *Journal of North American Benthological Society* 24:369–380.

Chesney, H.C.G., et al. 1993. *Margaritifera durrovensis* Phillips, 1928: Taxonomic status, ecology and conservation. *Journal of Conchology* 34:267–300.

Chichon, M. 1997. Evolution of longevity through optimal resource allocation. *Philosophical Transactions of the Royal Society of London, Series B* 264:1383–1388.

Chong, J.P., et al. 2008. Three deeply divided lineages of the freshwater mussel genus *Anodonta* in western North America. *Conservation Genetics* 9:1303–1309.

Christian, A.D., and J.L. Harris. 2005. Development and assessment of a sampling design for mussel assemblages in large streams. *American Midland Naturalist* 153:284–292.

Christian, A.D., et al. 2004. Trophic position and potential food sources of 2 species of unionid bivalves (Mollusca: Unionidae) in 2 small Ohio streams. *Journal of the North American Benthological Society* 23:101–113.

Christian, A.D., et al. 2005. Freshwater mussel (Bivalvia: Unionidae) assemblages of the Lower Cache River, Arkansas. *Southeastern Naturalist* 4:487–512.

Christian, A.D., et al. 2007. Methods of DNA extraction and PCR amplification for individual freshwater mussel (Bivalvia: Unionidae) glochidia, with the first report of multiple paternity in these organisms. *Molecular Ecology Notes* 7:570–573.

Church, M. 1992. Channel morphology and typology. Pages 126–143 *in* P. Calow and G. E. Petts, editors. *The rivers handbook*. Vol. I. Blackwell, Oxford, UK.

Churchill, E.P., and S.I. Lewis. 1924. Food and feeding in fresh-water mussels. *Bulletin of the Bureau of Fisheries* 39:439–471 [issued separately as U.S. Bureau of Fisheries Document 963].

Cicerello, R.R. 1993. A survey of the unionids (Bivalvia:Unionidae) of the Rockcastle River, Middle Fork to Billows, Kentucky. Report to U.S. Forest Service, Daniel Boone National Forest. Kentucky State Nature Preserves Commission, Frankfort, USA.

Cicerello, R.R. 1994. A survey of the unionids (Bivalvia:Unionidae) of the Rockcastle River, Billows, Kentucky, to the Cumberland River. Report to the U.S. Forest Service, Daniel Boone National Forest. Kentucky State Nature Preserves Commission, Frankfort, USA.

Cicerello, R.R. 1996a. A survey of the unionids of the Redbird River, Clay and Leslie counties, Kentucky. Unpublished report. Kentucky Nature Preserves Commission, Frankfort, USA.

Cicerello, R.R. 1996b. A survey of the unionids of Rock Creek, McCreary County Kentucky. Unpublished report. Kentucky Nature Preserves Commission, Frankfort, USA.

Cicerello, R.R., and G.A. Schuster. 2003. *A guide to the freshwater mussels of Kentucky*. Scientific and Technical Series 7. Kentucky State Nature Preserves Commission, Frankfort, USA.

Cicerello, R.R., et al. 1991. A distributional checklist of the freshwater unionids (Bivalvia: Unionidea) of Kentucky. *American Malacological Bulletin* 8:113–129.

Claassen, C. 1986. Shellfishing seasons in the prehistoric southeastern United States. *American Antiquity* 51:21–37.

Claassen, C. 1994. Washboards, pigtoes, and muckets: Historic musseling in the Mississippi watershed. *Historical Archaeology* 28:1–145.

Clabaugh, J.P., et al. 1996. Systematics and biogeography of snubnose darters, genus *Etheostoma* (Teleostei:Percidae) from the Black Warrior River system, Alabama. *Biochemical Systematics and Ecology* 24:119–134.

Clark, H.W., and C.B. Wilson. 1912. The mussel fauna of the Maumee River. Report and Special Papers of the U.S. Fish Commission 1911:1–72 [issued separately as U.S. Bureau of Fisheries Document 757].

Clark, T.D. 1984. *The greening of the South*. University Press of Kentucky, Lexington, USA.

Clarke, A.H. 1973. The freshwater molluscs of the Canadian Interior Basin. *Malacologia* 13:1–509.

Clarke, A.H. 1981a. *The freshwater mollusks of Canada*. National Museum of Natural Sciences, National Museums of Canada, Ottawa.

Clarke, A.H. 1981b. The tribe Alasmidontini (Unionidae: Anodontinae), Part I. *Pegias*, *Alasmidonta*, and *Arcidens*. Smithsonian Contributions to Zoology 326. Smithsonian Institution, Washington, D.C., USA.

Clarke, A.H. 1985. The tribe Alasmidontini (Unionidae: Anodontinae), Part II: *Lasmigona* and *Simpsonaias*. Smithsonian Contributions to Zoology 399. Smithsonian Institution, Washington, D.C., USA.

Clarke, A.H., and C.O. Berg. 1959. The freshwater mussels of central New York. *Memoirs of the Cornell University Agricultural Experiment Station, New York State College of Agriculture* 367:1–79.

Clarke, A.H., and D.H. Stansbery. 1988. Are some Lake Erie molluska products of post-Pleistocene evolution? Pages 85–274 *in* J.F. Downhower, editor. *The biogeography of the island region of western Lake Erie*. Ohio State University Press, Columbus, USA.

Clayton, J.L., et al. 2001. Status of and potential impacts to the freshwater bivalves (Unionidae) in Patterson Creek, West Virginia. *Northeastern Naturalist* 8:179–188.

Clayton, L.A., et al. 1994. *The De Soto Chronicles: The expedition of Hernando De Soto to North America 1539–1543*. University of Alabama Press, Tuscaloosa, USA.

Clebsch, E.E.C., and R.T. Busing. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. *Ecology* 70:728–735.

Clench, W.J. 1925. Collecting in Kentucky. *Nautilus* 39:71–72.

Clench, W.J. 1926. Some notes and a list of shells of Rio, Kentucky. *Nautilus* 40:7–12.

Clench, W.J., and R.D. Turner. 1956. Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River. *Bulletin of the Florida State Museum, Biological Sciences* 1:97–239.

Cobb, W.D. 1939. The pearl of Allah. *Natural History Magazine*, November.

Cochran, T.G., and J.B. Layzer. 1993. Effects of commercial harvest on unionid habitat use in the Green and Barren rivers, Kentucky. Pages 61–65 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Coe, W.R. 1931. Spermatogenesis in the California oyster (*Ostrea lurida*). *Biological Bulletin* 61:309–315.

Cohen, R.R.H., et al. 1984. The effect of the Asiatic clam, *Corbicula fluminea* on phytoplankton of the Potomac River, Maryland. *Limnology and Oceanography* 29:170–180.

Coker, R.E. 1914a. The Fairport Fisheries Biological Station: Its equipment, organization, and functions. *Bulletin of the Bureau of Fisheries* 34:383–405.

Coker, R.E. 1914b. The Fairport Biological Station. *Science* 39:457–458.

Coker, R.E. 1914c. The protection of fresh-water mussels. *Report and Special Papers of the U.S. Bureau of Fisheries 1912:1–23* [issued separately as U.S. Bureau of Fisheries Document 793].

Coker, R.E. 1914d. Water-power development in relation to fishes and mussels of the Mississippi. *Report of the US Commissioner of Fisheries for 1913 Appendix* 8:1–28 [issued separately as U.S. Bureau of Fisheries Document 805].

Coker, R.E. 1915. Mussel resources of the Tensas River of Louisiana. *U.S. Bureau of Fisheries Economic Circular* 14:1–7.

Coker, R.E. 1916. The utilization and preservation of fresh-water mussels. *Transactions of the American Fisheries Society* 46:39–49.

Coker, R.E. 1919. Fresh-water mussels and mussel industries of the U.S. *Bulletin of the Bureau of Fisheries* 36:13–89 [issued separately as U.S. Bureau of Fisheries Document 865].

Coker, R.E. 1921. The Fisheries Biological Station at Fairport, Iowa. *U.S. Bureau of Fisheries Document* 895:1–12.

Coker, R.E., and J.B. Southall. 1915. Mussel resources in tributaries of the upper Missouri River. *U.S. Bureau of Fisheries Document* 812.

Coker, R.E., and T. Surber. 1911. A note on the metamorphosis of the mussel *Lampsilis laevissimus*. *Biological Bulletin (Woods Hole)* 20:179–182.

Coker, R.E., et al. 1921. Natural history and propagation of freshwater mussels. *Bulletin of the Bureau of Fisheries* 37:75–181 [issued separately as U.S. Bureau of Fisheries Document 893].

Colburn, T., et al. 1993. Developmental effects of endocrine-disrupting chemicals in wildlife and humans. *Environmental Health Perspectives* 101:378–384.

Comfort, A. 1951. The pigmentation of molluscan shells. *Biological Review* 26:285–301.

Conner, C.H. 1909. Supplementary notes on the breeding seasons of the Unionidae. *Nautilus* 22:111–112.

Conner, J.V., and R.D. Suttkus. 1986. Zoogeography of freshwater fishes of the Western Gulf Slope of North American. Pages 413–456 *in* C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley, New York, USA.

Conners, D.E., and M.C. Black. 2004. Evaluation of lethality and genotoxicity in the freshwater mussel *Utterbackia imbecillis* (Bivalvia: Unionidae) exposed singly and in combination to chemicals used in lawn care. *Archives of Environmental Contamination and Toxicology* 46:362–371.

Conrad, T.A. 1834. *New freshwater shells of the United States, with coloured illustrations; and a monograph of the genus Anculotus of Say; also a synopsis of the American naiades*. J. Dobson, Philadelphia, Pennsylvania, USA.

Convey, L.E., et al. 1989. Size-selective predation on unionid clams by muskrats. *Journal of Wildlife Management* 53:654–657.

Coon, T.G., et al. 1977. Relative abundance and growth of mussels (Mollusca: Eulamellibranchia) in Pools 8, 9, and 10 of the Mississippi River. *Freshwater Biology* 7:279–285.

Cooper, C.M. 1984. The freshwater mussels of Lake Chicot, an oxbow of the Mississippi in Arkansas. *Nautilus* 98:142–145.

Cooper, C.M. 1987. Benthos of Bear Creek, Mississippi: Effects of habitat variation and agricultural sediments. *Journal of Freshwater Biology* 4:101–113.

Cooper, N.L., et al. 2005. Potential effects of Asian clam (*Corbicula fluminea*) die-offs on native freshwater mussels (Unionidae) II: Porewater ammonia. *Journal of the North American Benthological Society* 24:381–394.

Cope, W.G., and D.L. Waller. 1995. Evaluation of freshwater mussel relocation as a conservation and management strategy. *Regulated Rivers: Research and Management* 11:147–155.

Cope, W.G., et al. 2003. Evaluation of relocation of unionid mussels to in situ refugia. *Journal of Molluscan Studies* 69:27–34.

Corey, C.A., et al. 2006. Display behavior of *Ligumia* (Bivalvia: Unionidae). *Northeastern Naturalist* 13:319–332.

Cosgrove, P.J., and L.C. Hastie. 2001. Conservation of threatened freshwater pearl mussel populations: River management, mussel translocation and conflict resolution. *Biological Conservation* 99:183–190.

Costa, J. 1975. Effects of agriculture on erosion and sedimentation in the Piedmont Province, Maryland. *Bulletin of the Geological Society of America* 86:1281–1286.

Cottam, C. 1936. Food of the limpkin. *Wilson Bulletin* 48:11–13.

Counts, C.L. 1981. *Corbicula fluminea* (Bivalvia: Corbiculidae) in British Columbia. *Nautilus* 95:12–13.

Counts, C.L. 1986. The zoogeography and history of the invasion of the United States by *Corbicula fluminea* (Bivalvia: Corbiculidae). *American Malacological Bulletin, Special Edition* 2:7–39.

Covich, A.P., et al. 1981. Crayfish predation on *Corbicula* under laboratory conditions. *American Midland Naturalist* 105:181–188.

Cox, L.R. 1969. Mollusca 6. Pages 1–489 *in* R.C. Moore and C. Teichert, editors. *Treatise on invertebrate paleontology*. Vol. 1. Geological Society of America and University of Kansas Press, Lawrence, USA.

Crabtree, D.L., and T.A. Smith. 2009. Population attributes of an endangered mussel, *Epioblasma torulosa rangiana* (Northern Riffleshell), in French Creek and implications for its recovery. *Northeastern Naturalist* 16:339–354.

Crane, A.L., et al. 2011. Do gill parasites influence the foraging and antipredator behaviour of rainbow darters, *Etheostoma caeruleum*? *Animal Behaviour* 82:817–823.

Crawford, B. 1994. *Kentucky stories*. Turner, Paducah, Kentucky, USA.

Crivelli, A.J. 1983. The destruction of aquatic vegetation by carp: A comparison between southern France and the United States. *Hydrobiologia* 106:37–41.

Crowell, E.F., and B.T. Kinman. 1993. Musseling in Kentucky: The first 200 years. Pages 25–31 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Culp, J.J., et al. 2009. Fish hosts and conglutinates of the pyramid pigtoe (*Pleurobema rubrum*). *Southeastern Naturalist* 8:19–22.

Culp, J.J., et al. 2011. Seasonal and species-specific patterns in abundance of freshwater mussel glochidia in stream drift. *Journal of the North American Benthological Society* 30:436–445.

Cummings, K.S., and J.M.K. Berlocher. 1990. The naiades or freshwater mussels (Bivalvia: Unionidae) of the Tippecanoe River, Indiana. *Malacological Review* 23:83–98.

Cummings, K.S., and D.L. Graf. 2009. Mollusca: Bivalvia. Pages 309–384 *in* J.H. Thorp and A.P. Covich, editors. *Ecology and classification of North American freshwater invertebrates*. 3rd ed. Academic Press, San Diego, California, USA.

Cummings, K.S., and C.A. Mayer. 1992. *Field guide to freshwater mussels of the Midwest*. Manual 5, Illinois Natural Survey, Champaign, USA.

Cummings, K.S., and C.A. Mayer. 1993. Distribution and host species of the federally endangered freshwater mussel, *Potamilus capax* (Green, 1832) in the lower Wabash River, Illinois and Indiana. Illinois Natural History Survey Technical Report 1993:1–29.

Cummings, K.S., and G.T. Watters. 2010. Mussel/host database (http://128.146.250. 235/MusselHost/).

Cummings, K.S., et al. 1988. The freshwater mussels (Mollusca:Bivalvia) of the Embarras River in Illinois: Thirty years of stream change. Illinois Natural History Survey Technical Report 1988.

Cummings, K.S., et al. 2010. Freshwater mollusk bibliography (http://ellipse.inhs.uiuc.edu: 591/mollusk/).

Cvancara, A.M. 1970. Mussels (Unionidae) of the Red River valley in North Dakota and Minnesota, USA. *Malacologia* 10:57–92.

Cvancara, A.M. 1972. Lake mussel distribution as determined with SCUBA. *Ecology* 53:154–157.

Cvancara, A.M., and S.S. Harrison. 1965. Distribution and ecology of mussels in the Turtle River, North Dakota. *Proceedings of the North Dakota Academy of Science* 19:128–146.

Cyr, F., et al. 2007. Cryptic lineages and hybridization in freshwater mussels of the genus *Pyganodon* (Unionidae) in northeastern North America. *Canadian Journal of Zoology* 85:1216–1227.

Cyr, H. 2008. Physical forces constrain the depth distribution of the abundant native mussel *Elliptio complanata* in lakes. *Freshwater Biology* 53:2414–2425.

Cyr, H. 2009. Substrate and fetch affect the emergence of freshwater mussels from lake sediments. *Journal of the North American Benthological Society* 28:319–330.

Dahm, C.N., et al. 2005. Gulf coast rivers of the southwestern United States. Pages 180–228 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America*. Elsevier, Burlington, Massachusetts, USA.

Dame, R.F. 1996. *Ecology of marine bivalves: An ecosystem approach*. CRC Press, Boca Raton, Florida, USA.

Dance, S.P. 1958. Drought resistance in an African freshwater bivalve. *Journal of Conchology* 24:281–283.

Danglade, E. 1914. The mussel resources of the Illinois River. *Report of the U.S. Commissioner of Fisheries for 1913 Appendix* 6:1–48 [issued separately as U.S. Bureau of Fisheries Document 804].

Darnell, R.M. 1961. Trophic spectrum of an estuarine community based on studies of Lake Pontchartrain, Louisiana. *Ecology* 42:553–568.

Dartnall, H.J.G., and M. Walkey. 1979. The distribution of glochidia of the Swan mussel, *Anodonta cygnea* (Mollusca) on the three-spined stickleback *Gasterosteus aculeatus* (Pisces). *Journal of Zoology, London* 189:31–37.

Davenport, D., and M. Warmuth. 1965. Notes on the relationship between the freshwater mussel *Anodonta implicata* Say and the alewife *Pomolobus pseudoharengus* (Wilson). *Limnology and Oceanography* 10(Supplement):R74–R78.

David, M.B., et al. 2002. Transport of herbicides in the upper Embarras River watershed. Illinois Department of Natural Resources, Waste Management and Research Center Report RR-91.

Davidson, C.L., and S.A. Clem. 2004. The freshwater mussel (Bivalvia:Unionacea) resources in a selected segment of the Saline River: Location, species composition, and status of mussel beds. Addendum 2: Arkansas highway 15 to Felsenthal National Wildlife Refuge. Report to The Nature Conservancy, Arkansas Chapter, and the Arkansas Game and Fish Commission, Little Rock, USA.

Davidson, D. 1946. *The Tennessee – the old river: Frontier to secession.* University of Tennessee Press, Knoxville, USA.

Davis, M. 2005. Clam chronicles: An account of activities associated with efforts to propagate and repatriate Lampsilis higginsii in the Mississippi River, Minnesota. Minnesota Department of Natural Resources, Minneapolis, USA (http://www.fws.gov/midwest/mussel/documents/clam_chronicles_2005.pdf).

Day, M.E. 1984. The shell as a recording device: Growth record and shell ultrastructure of *Lampsilis radiata radiata* (Pelecypoda: Unionidae). *Canadian Journal of Zoology* 62:2495–2504.

de Kroon, H., et al. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427–1431.

Death, R.G. 1995. Spatial patterns in lotic invertebrate community composition: Is substrate disturbance actually important? *Canadian Journal of Fisheries and Aquatic Sciences* 60:603–611.

Delcourt, H.R. 1987. The impact of pre-Columbian agriculture and land occupation on natural vegetation. *Trends in Ecology and Evolution* 2:39–44.

d'Eliscu, P.N. 1972. Observation of the glochidium, metamorphosis, and juvenile of *Anodonta californiensis* Lea, 1857. *Veliger* 15:57–58.

Delong, M.D. 2005. Upper Mississippi River basin. Pages 326–373 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America.* Elsevier, Burlington, Massachusetts, USA.

Dettman, D.L., et al. 1999. Controls on the stable isotope composition of seasonal growth bands in aragonitic fresh-water bivalves (Unionidae). *Geochimica et Cosmochimica Acta* 63:1049–1057.

Dettmers, J.M., et al. 2001. Patterns of abundance of fishes in main channels of the upper Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences* 58:933–942.

Dexter, R.W. 1961. Mussel Shoals vs. Muscle Shoals. *Sterkiana* 4:29–31.

Diamond, J.M., et al. 2002. Assessing relationships between human land uses and the decline of native mussels, fish, and macroinvertebrates in the Clinch and Powell River watershed, USA. *Environmental Toxicology and Chemistry* 21:1147–1155.

Dickenson, B.D., and B.E. Sietman. 2008. Recent observation of metamorphosis without parasitism in *Utterbackia imbecillis. Ellipsaria* 10:7–8.

Dickerson, W.H., and B.E. Dethier. 1970. *Drought frequency in the northeastern United States.* West Virginia University Agricultural Experiment Station Bulletin 595.

Diggins, T.P., and K.M. Stewart. 2000. Evidence of large change in unionid mussel abundance from selective muskrat predation, as inferred by shell remains left on shore. *International Review of Hydrobiology* 85:505–520.

Dillon, R.T. 2000. *The ecology of freshwater molluscs*. Cambridge University Press, Cambridge, UK.

Di Maio, J., and L.D. Corkum. 1995. Relationship between the spatial distribution of freshwater mussels (Bivalvia:Unionidae) and the hydrological variability of rivers. *Canadian Journal of Zoology* 73:663–671.

Di Maio, J., and L.D. Corkum. 1997. Patterns of orientation in unionids as a function of rivers with differing hydrological variability. *Journal of Molluscan Studies* 63:531–539.

DiStefano, R.J. 1984. Freshwater mussels (Bivalvia:Unionidae) of Horse Lick Creek, Rockcastle River, Kentucky. *Nautilus* 98:110–113.

Distler, D.A., and D.E. Bleam. 1995. Decline in the diversity of Bivalvia, Ninnescah River, Kansas. *Transactions of the Kansas Academy of Science* 98:156–159.

Dodd, B.J., et al. 2005. Cross-resistance of largemouth bass to glochidia of unionid mussels. *Journal of Parasitology* 91:1064–1072.

Dodd, B.J., et al. 2006. Persistence of host response against glochidia larvae in *Micropterus salmoides*. *Fish and Shellfish Immunology* 21:473–484.

Dolgov, L.V. 1991. Sexual structure of a *Tridacna squamosa* population: Relative advantages of sequential and simultaneous hermaphroditism. *Journal of Molluscan Studies* 58:21–27.

Donald, D.B., et al. 1999. Agricultural pesticides threaten the ecological integrity of northern prairie wetlands. *Science of the Total Environment* 231:173–181.

Doran, W.J., et al. 2001. Acetylcholinesterase inhibition in the three ridge mussel (*Amblema plicata*) by chlorpyrifos: Implications for biomonitoring. *Ecotoxicology and Environmental Safety* 49:91–98.

Downing, D.M., et al. 2003. Navigating through clean water act jurisdiction: A legal review. *Wetlands* 23:475–493.

Downing, J.A., and W.L. Downing. 1992. Spatial aggregation, precision, and power in surveys of freshwater mussel populations. *Canadian Journal of Fisheries and Aquatic Sciences* 49:985–991.

Downing, J.A., et al. 1989. Visceral sex, hermaphroditism, and protandry in a population of the freshwater bivalve *Elliptio complanata*. *Journal of the North American Benthological Society* 8:92–99.

Downing, J.A., et al. 1993. Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanata*. *Journal of the North American Benthological Society* 12:148–156.

Downing, J.A., et al. 2000. Substratum patch selection in the lacustrine mussels *Ellipitio complanata* and *Pyganodon grandis grandis*. *Freshwater Biology* 44:641–648.

Downing, J.A., et al. 2010. Suspects and evidence: A review of the causes of extirpation and decline in freshwater mussels. *Animal Biodiversity and Conservation* 33:151–185.

Downing, W.L., et al. 1992. Non-annual external annuli in the freshwater mussels *Anodonta grandis grandis* and *Lampsilis radiata siliquoidea*. *Freshwater Biology* 28:309–317.

Doyle, M.W., et al. 2003. Dam removal in the United States: Emerging needs for science and policy. *Eos Transactions of the American Geophysical Union* 84:29–36.

Drake, J.M., and J.M. Bossenbroek. 2004. The potential distribution of zebra mussels in the United States. *BioScience* 54:931–941.

Dudgeon, D., and B. Morton. 1983. The population dynamics and sexual strategy of *Anodonta woodiana* (Bivalve: Unionacea) in Plover Cove Reservoir, Hong Kong. *Journal of Zoology* 201:161–183.

Dunca, E., and H. Mutvei. 2001. Comparison of microgrowth pattern in *Margaritifera margaritifera* shells from south and north Sweden. *American Malacological Bulletin* 16:239–250.

Dynesius, M., and C. Nilsson. 1994. Fragmentation and flow regulation of river systems in the northern third of the World. *Science* 266:753–762.

Eads, C.B., et al. 2010. Fish hosts of the Carolina heelsplitter (*Lasmigona decorata*), a federally endangered freshwater mussel (Bivalvia:Unionidae). *American Malacological Bulletin* 28:151–158.

Eads, C.B., and J.B. Layzer. 2002. How to pick your mussels out of a crowd: Using fluorescence to mark juvenile freshwater mussels. *Journal of the North American Benthological Society* 21:476–486.

Eagar, R.M.C. 1978. Shape and function of the shell: A comparison of some living and fossil bivalve molluscs. *Biological Review* 53:169–210.

Eans, K. 2007. Manuscripts and folklife archives, FA finding aid 119, Paper 57. Western Kentucky University, Bowling Green, USA (http://digitalcommons.wku.edu/dlsc_fa_fin_aid/57).

Ebert, T.A. 1999. *Plant and animal populations: Methods in demography*. Academic Press, San Diego, California, USA.

Eckert, N.L. 2003. Reproductive biology and host requirement differences among isolated populations of *Cyprogenia aberti* (Conrad, 1850). Thesis, Missouri State University, Springfield, USA.

Edgar, A.L. 1965. Observations on sperm of the pelecypod *Anodontoides ferussacinanus* (Lea). *Transactions of the American Microscopical Society* 84:228–230.

Ekdahl, E.J., et al. 2004. Prehistorical record of cultural eutrophication from Crawford Lake, Canada. *Geology* 32:745–748.

Elderkin, C.L., and P.L. Klerks. 2005. Variation in thermal tolerance among three Mississippi River populations of the zebra mussel, *Dreissena polymorpha*. *Journal of Shellfish Research* 24:221–226.

Elderkin, C.L., et al. 2007. Population genetics of the freshwater mussel, *Amblema plicata* (Say 1817) (Bivalvia:Unionidae): Evidence of high dispersal and post-glacial colonization. *Conservation Genetics* 8:355–372.

Elderkin, C.L., et al. 2008. Population genetics and phylogeography of freshwater mussels in North America, *Elliptio dilatata* and *Actinonaias ligamentina* (Bivalvia: Unionidae). *Molecular Ecology* 17:2149–2163.

Ellis, M.M. 1931. Some factors affecting the replacement of the commercial fresh-water mussels. *U.S. Bureau of Fisheries Fishery Circular* 7:1–10.

Ellis, M.M. 1936. Erosion silt as a factor in aquatic environments. *Ecology* 17:29–42.

Ellis, M.M., and M.D. Ellis. 1926. Growth and transformation of parasitic glochidia in physiological nutrient solutions. *Science* 64:579–580.

Eng, L. 1979. Population dynamics of the Asiatic clam, *Corbicula fluminea* (Müller), in the concrete-lined Delta-Mendota canal of central California. Pages 39–68 *in* J.C. Britton, editor. *Proceedings of the First International Corbicula Symposium*. Texas Christian University Research Foundation, Ft. Worth, USA.

Engel, H. 1990. Untersuchungen zur Autökologie von *Unio crassus* (Philippson) in Norddeutschland. Dissertation, University of Hannover, Germany (in German).

Englund, V., and M. Heino. 1994a. Valve movement of *Anodonta anatina* and *Unio tumidus* (Bivalvia, Unionidae) in a eutrophic lake. *Annales Zoologici Fennici* 31:257–262.

Englund, V., and M. Heino. 1994b. Valve movement of freshwater mussel *Anodonta anatina*: A reciprocal transplant experiment between two lakes. *Annales Zoologici Fennici* 31:417–423.

Etnier, D.A., and W.C. Starnes. 1993. *The fishes of Tennessee*. University of Tennessee Press, Knoxville, USA.

Evans, R.R. 2001. Historical and contemporary distributions of aquatic mollusks in the Upper Conasauga River system of Georgia and Tennessee. Thesis, University of Tennessee, Chattanooga, USA.

Evans, S., et al. 2009. Heritability of shell pigmentation in the Pacific oyster, *Crassostrea gigas*. *Aquaculture* 286:211–216.

Evermann, B.W., and H.W. Clark. 1918. The Unionidae of Lake Maxinkukee. *Proceedings of the Indiana Academy of Science* 1917:251–285.

Fagan, W.F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83:3243–3249.

Falese, L.E., et al. 2011. Spermcasting of spermatozeugmata by the bivalves *Nutricola confusa* and *N. tantilla*. *Invertebrate Biology* 130:334–343.

Fassler, C.R. 1997. The American mussel crisis: Effects on the world pearl industry. Pages 265–277 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Fausch, K.D., et al. 1984. Regional application of an index of biotic integrity based on stream fish communities. *Transactions of the American Fisheries Society* 113:39–55.

Fenneman, N.M. 1938. *Physiography of the Eastern United States*. McGraw-Hill, New York, USA.

Fent, K., et al. 2006. Ecotoxicology of human pharmaceuticals. *Aquatic Toxicology* 76:122–159.

Ferriter, A., et al. 2005. Invasive exotic species in the south Florida environment. Chapter 9 *in 2005 South Florida Environmental Report*. South Florida Water Management District, West Palm Beach, USA.

Fikes, M.A., and R.A. Tubb. 1971. *Amblema plicata* as a pesticide monitor. Pages 34–37 *in* S.E. Jorgensen and R.E. Sharp, editors. *Proceedings of a symposium on rare and endangered mollusks (naiads) of the US*. U.S. Fish and Wildlife Service, Twin Cities, Minnesota, USA.

Fisher, G.R., and R.V. Dimock. 2000. Viability of glochidia of *Utterbackia imbecillis* (Bivalvia:Unionidae) following their removal from the parental mussel. Pages 185–188 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Fisher, G.R., and R.V. Dimock. 2002a. Morphological and molecular changes during metamorphosis in *Utterbackia imbecillis* (Bivalvia:Unionidae). *Journal of Molluscan Studies* 68:159–164.

Fisher, G.R., and R.V. Dimock. 2002b. Ultrastructure of the mushroom body: Digestion during metamorphosis of *Utterbackia imbecillis* (Bivalvia:Unionidae). *Invertebrate Biology* 121:126–135.

Fisher, R.A. 1930. *The genetical theory of natural selection*. Clarendon Press, London, UK.

Fitzpatrick, F.A., J.C. Knox, and H.E. Whitman. 1999. Effects of historical land-cover changes on flooding and sedimentation, North Fish Creek, Wisconsin. Water-Resources Investigations Report 99-4083. U.S. Geological Survey, Middleton, Wisconsin, USA.

Fleming, W.J., et al. 1995. Freshwater mussel die-off attributed to anticholinesterase poisoning. *Environmental Toxicology and Chemistry* 14:877–879.

Flory, M.B. 1988. Pearls for Venus. *Historia: Zeitschrift für Alte Geschichte* 37:498–504.

Flynn, K., and T. Spellman. 2009. Environmental levels of atrazine decrease spatial aggregation in the freshwater mussel, *Elliptio complanata*. *Ecotoxicology and Environmental Safety* 72:1228–1233.

Fobian, T.B. 2007. Reproductive biology of the rabbitsfoot mussel (*Quadrula cylindrica*) (Say, 1817) in the Upper Arkansas River system, White River system, and the Red River system. Thesis, Missouri State University, Springfield, USA.

Forbes, S.A. 1888. On the food relationships of freshwater fishes: A summary and discussion. *Bulletin of the Illinois State Laboratory of Natural History* 2:475–538.

Forbes, S.A., and R.E. Richardson. 1913. Studies on the biology of the upper Illinois River. *Bulletin of the Illinois State Natural History Survey* 9:481–574.

Fox, D.L. 1983. Biochromy of the Mollusca. Pages 281–303 *in* P.W. Hochachka, editor. The Mollusca. Vol. 2. *Environmental Biochemistry and Physiology*. Academic Press, New York, USA.

Franklin, I.A. 1980. Evolutionary changes in small populations. Pages 135–150 *in* M. Soulé and B.A. Wilcox, editors. *Conservation biology: An evolutionary and ecological perspective*. Sinauer Associates, Sunderland, Massachusetts, USA.

Frazier, B.E., et al. 1996. Temporal and vertical distribution of total ammonia nitrogen and un-ionized ammonia nitrogen in sediment pore water from the Upper Mississippi River. *Environmental Toxicology and Chemistry* 15:92–99.

Freed, D. 1978. *Possum living: How to live well without a job and with (almost) no money.* Tin House Books, Portland, Oregon, USA.

Freeman, M.C., et al. 2005. Status and conservation of the fish fauna of the Alabama River system. Pages 557–585 *in* J.N. Rinne, et al., editors. *Historical changes in large river fish assemblages of the Americas.* American Fisheries Society Symposium 45, Bethesda, Maryland, USA.

Frierson, L.S. 1899. How uniones emigrate. *Nautilus* 12:139–140.

Frierson, L.S. 1903a. Observations on the bysus of Unionidae. *Nautilus* 17:76–77.

Frierson, L.S. 1903b. The specific value of *Unio declivus*, Say. *Nautilus* 17:49–51.

Fritts, A.K., et al. In press. Early life history and conservation status of *Quadrula metanevra* (Mollusca: Bivalvia) in Minnesota and Wisconsin. *Walkerana.*

Fritz, A.W. 1987. Commercial fishing for carp. Pages 17–30 *in* E.L. Cooper, editor. *Carp in North America.* American Fisheries Society, Bethesda, Maryland, USA.

Fuller, K., et al. 1995. *The Great Lakes: An environmental atlas and resource book.* Environment Canada and US Environmental Protection Agency, Chicago, Illinois, USA.

Fuller, S.L.H. 1974. Clams and mussels (Mollusca: Bivalvia). Pages 215–273 *in* C.W. Hart and S.L.H. Fuller, editors. *Pollution ecology of freshwater invertebrates.* Academic Press, New York, USA.

Fuller, S.L.H. 1980. Historical and current distributions of fresh-water mussels (Mollusca:Bivalvia:Unionidae) in the upper Mississippi River. Pages 72–119 *in* J.L. Rasmussen, editor. *Proceedings of the Symposium on Upper Mississippi River bivalve mollusks.* Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Gagné, F., and C. Blaise. 2003. Effects of municipal effluents on serotonin and dopamine levels in the freshwater mussel *Elliptio complanata. Comparative Biochemistry and Physiology C* 136:117–125.

Gagné, F., et al. 2001. Occurrence of compounds estrogenic to freshwater mussels in surface waters in an urban area. *Environmental Toxicology* 16:260–268.

Gagné, F., et al. 2004. Serotonergic effects of municipal effluents: Induced spawning activity in freshwater mussels. *Fresenius Environmental Bulletin* 13:1099–1103.

Gagné, F., et al. 2011. Evidence of feminization in wild *Elliptio complanata* mussels in the receiving waters downstream of a municipal effluent outfall. *Comparative Biochemistry and Physiology C* 153:99–106.

Gagnon, P., et al. 2004. Drought responses of freshwater mussels (Unionidae) in coastal plain tributaries of the Flint River Basin, Georgia. *Journal of Freshwater Ecology* 19:667–679.

Galat, D.L., et al. 2005. Missouri River basin. Pages 426–480 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America.* Elsevier, Burlington, Massachusetts, USA.

Galbraith, H.S., et al. 2009. Comparison of gill surface morphology across a guild of suspension-feeding unionid bivalves. *Journal of Molluscan Studies* 75:103–107.

Galbraith, H.S., and C.C. Vaughn. 2009. Temperature and food interact to influence gamete development in freshwater mussels. *Hydrobiologia* 636:35–47.

Galloway, W.E., et al. 2011. History of Cenozoic North American drainage basin evolution, sediment yield, and accumulation in the Gulf of Mexico basin. *Geosphere* 7:938–973.

Gangloff, M.M., and J.W. Feminella. 2007. Stream channel geomorphology influences mussel abundance in southern Appalachian streams, USA. *Freshwater Biology* 52:64–74.

Gangloff, M.M., and D.L. Gustafson. 2000. The freshwater mussels (Bivalvia: Unionoida) of Montana. *Central Plains Archeology* 8:121–130.

Gangloff, M.M., et al. 2006. A new species of freshwater mussel (Bivalvia: Unionidae), *Pleurobema athearni*, from the Coosa River Drainage of Alabama, *USA. Zootaxa* 1118:43–56.

Gangloff, M.M., et al. 2008. Parasitic mite and trematode abundance are associated with reduced reproductive output and physiological condition of freshwater mussels. *Hydrobiologia* 610:25–31.

Gardner, J.A., et al. 1976. The invasion of the Asiatic clam (*Corbicula manilensis* Philippi) in the Altamaha River, Georgia. *Nautilus* 90:117–125.

Garner, J.T., and S.W. McGregor. 2001. Current status of freshwater mussels (Unionidae, Margaritiferidae) in the Muscle Shoals area of Tennessee River in Alabama (Muscle Shoals revisited again). *American Malacological Bulletin* 16:155–170.

Garner, J.T., et al. 1999. Reproductive cycle of *Quadrula metanevra* (Bivalvia: Unionidae) in the Pickwick Dam tailwater of the Tennessee River. *American Midland Naturalist* 141:277–283.

Garner, J.T., et al. 2009. Freshwater mussels (Unionidae) in the headwaters of the Chipola River, Houston County, Alabama. *Southeastern Naturalist* 8:687–694.

Gascho-Landis, A.M., et al. In press. Effects of temperature and photoperiod on lure display and glochidial release in freshwater mussels. *Freshwater Science*.

Gatenby, C.M., et al. 1996. Influence of sediment and algal food on cultured juvenile freshwater mussels. *Journal of the North American Benthological Society* 15:597–609.

Gatenby, C.M., et al. 1997. Growth and survival of juvenile rainbow mussels, *Villosa iris* (Lea, 1829) (Bivalvia: Unionidae), reared on algal diets and sediment. *American Malacological Bulletin* 14:57–66.

Geist, J., et al. 2006. The status of host fish populations and fish species richness in European freshwater pearl mussel (*Margaritifera margaritifera*) streams. *Aquatic Conservation: Marine and Freshwater Ecosystems* 16:251–266.

George, A.L., et al. 2006. Conservation genetics of an imperiled riverine fish from eastern North America, the blotchside logperch, *Percina burtoni* (Teleostei:Percidae). *Copeia* 2006:585–594.

George, J.L., and D.E.H. Frear. 1966. Pesticides in the Antarctic. *Journal of Applied Ecology* 3:155–167.

George, S.G., and M.F. Vidrine. 1993. New Louisiana records for freshwater mussels (Unionidae) and a snail (Pleuroceridae). *Texas Journal of Science* 45:363–366.

Ghent, A.W., et al. 1978. Depth distributions determined with SCUBA, and associated studies of the freshwater unionid clams *Elliptio complanata* and *Anodonta grandis* in Lake Bernard, Ontario. *Canadian Journal of Zoology* 56:1654–1663.

Ghiselin, M.T. 1969. The evolution of hermaphroditism among animals. *Quarterly Review of Biology* 44:189–208.

Gillette, R. 1972. Stream channelization: Conflict between ditchers, conservationists. *Science* 176:890–894.

Gillies, R.R., et al. 2003. Effects of urbanization on the aquatic fauna of the Line Creek watershed, Atlanta – a satellite perspective. *Remote Sensing of Environment* 86: 411–422.

Gilpin, M.E., and M.E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pages 19–34 *in* M.E. Soulé, editor. *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, USA.

Giribet, G. 2008. Bivalvia. Pages 105–141 *in* W.F. Ponder and D.R. Lindberg, editors. *Phylogeny and evolution of the Mollusca*. University of California Press, Berkeley, USA.

Glen Canyon Institute. 2011. The restoration of Glen Canyon (http://www.glencanyon.org/library/glenrestoration.php).

Godman, J. 1842. Rambles of a naturalist, number III. Pages 297–301 *in American Natural History, Volume 2*. 3rd ed. R.W. Pomeroy, Philadelphia, Pennsylvania, USA.

Goewert, A., et al. 2007. Oxygen and carbon isotope ratios of *Lampsilis cardium* (Unionidae) from two streams in agricultural watersheds of Iowa, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252:637–648.

Golladay, S.W., et al. 2004. Response of freshwater mussel assemblages (Bivalvia: Unionidae) to a record drought in the Gulf Coastal Plain of southwestern Georgia. *Journal of the North American Benthological Society* 23:494–506.

Goodrich, C. 1922. The Anculosae of the Alabama River drainage. *Miscellaneous Publications of the University of Michigan Museum of Zoology* 7:1–57.

Goodrich, C. 1931a. Some conchological beginnings. *Nautilus* 45:41–47.

Goodrich, C. 1931b. *Pleurobema aldrichianum,* a new naiad. *Occasional Papers of the University of Michigan Museum of Zoology* 229:1–4.

Goodrich, C., and H. van der Schalie. 1944. A revision of the Mollusca of Indiana. *American Midland Naturalist* 32:257–326.

Gordon, J., and M.R. Carriker. 1978. Growth lines in a bivalve mollusk: Subdaily patterns and dissolution of the shell. *Science* 202:519–521.

Gordon, M.E. 1995. *Venustaconcha sima* (Lea), an overlooked freshwater mussel (Bivalvia: Unionoidea) from the Cumberland River basin of central Tennessee. *Nautilus* 108:55–60.

Gordon, M.E., and J.B. Layzer. 1993. Glochidial host of *Alasmidonta atropurpurea* (Bivalvia: Unionoidea, Unionidae). *Transactions of the American Microscopical Society* 112:145–150.

Gordon, M.E., and D.G. Smith. 1990. Autumnal reproduction in *Cumberlandia monodonta* (Unionoidea: Margaritiferidae). *Transactions of the American Microscopical Society* 109:407–411.

Gordon, N.D., et al. 1992. *Stream hydrology: An introduction for ecologists.* John Wiley, Chichester, UK.

Gore, J.A., and F.D. Shields. 1995. Can large rivers be restored? A focus on rehabilitation. *Bioscience* 45:142–152.

Gore, J.A., et al. 1989. Instream flow predictions and management options for biota affected by peaking hydropower releases. *Regulated Rivers: Research and Management* 3:35–48.

Gotelli, N.J., and G.L. Entsminger. 2004. *EcoSim: Null models software for ecology.* Version 7. Acquired Intelligence Inc. and Kesey-Bear, Jericho, Vermont, USA.

Gotelli, N.J., and G.R. Graves. 1996. *Null models in ecology.* Smithsonian Institution Press, Washington, D.C., USA.

Gould, R.M., and G.A. Cottrell. 1974. Putrescine in molluscs: Identification and occurrence in neurones and other tissues. *Comparative Biochemistry and Physiology* 48B: 591–597.

Gould, S.J. 1971. Precise but fortuitous convergence in Pleistocene land snails from Bermuda. *Journal of Paleontology* 45:409–418.

Gould, S.J., and R.C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B* 205:581–598.

Grace, J.B. 1991. A clarification of the debate between Grime and Tilman. *Functional Ecology* 5:583–587.

Graf, D.L. 1997. Northern redistribution of freshwater pearly mussels (Bivalvia: Unionoidea) during Wisconsin deglaciation in the southern glacial Lake Agassiz region: A review. *American Midland Naturalist* 138:37–47.

Graf, D.L. 2002. Molecular phylogenetic analysis of two problematic freshwater mussel genera (*Unio* and *Gonidea*) and a re-evaluation of the classification of nearctic Unionidae (Bivalvia: Paleoheterodonta:Unionoida). *Journal of Molluscan Studies* 68:65–71.

Graf, D.L., and K.S. Cummings. 2006. Palaeoheterodonta diversity (Mollusca: Trigonioida + Unionoida): What we know and what we wish we knew about freshwater mussel evolution. *Zoological Journal of the Linnean Society* 148:343–394.

Graf, D.L., and K.S. Cummings. 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia:Unionoida). *Journal of Molluscan Studies* 73:291–314.

Graf, D.L., and K.S. Cummings. 2008. The MUSSEL project (http://www. mussel-project .net/).

Graf, W.L. 1999. Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. *Water Resources Research* 35:1305–1311.

Graf, W.L. 2001. Damage control: Restoring the physical integrity of America's rivers. *Annals of the Association of American Geographers* 91:1–27.

Grande, C., et al. 2001. The gonads of *Margaritifera auricularia* (Spengler, 1793) and *M. margaritifera* (Linnaeus, 1758) (Bivalvia:Unionoidea). *Journal of Molluscan Studies* 67:27–35.

Graney, R.L., et al. 1980. The influence of thermal discharges and substrate composition on the population structure and distribution of the Asiatic clam, *Corbicula fluminea*, in the New River, Virginia. *Nautilus* 64:130–135.

Graymore, M., et al. 2001. Impacts of atrazine in aquatic ecosystems. *Environment International* 26:483–495.

Green, R.H. 1972. Distribution and morphological variation of *Lampsilis radiata* (Pelecypoda, Unionidae) in some central Canadian Lakes: A multivariate statistical approach. *Journal of the Fisheries Research Board of Canada* 29:1565–1570.

Green, R.H. 1980. Role of a unionid clam population in the calcium budget of a small arctic lake. *Canadian Journal of Fisheries and Aquatic Sciences* 37:219–224.

Greenburg, L.A. 1991. Habitat use and feeding behavior of thirteen species of benthic stream fishes. *Environmental Biology of Fishes* 31:389–401.

Greenburg, L.A., and D.A. Holtzman. 1987. Microhabitat utilization, feeding periodicity, home range and population size of the banded sculpin, *Cottus carolinae*. *Copeia* 1987:19–25.

Griffiths, N.A., and H. Cyr. 2006. Are there hot spots for *Elliptio complanata* in the shallow littoral zone of a large Canadian Shield lake? *Canadian Journal of Fisheries and Aquatic Sciences* 63:2137–2147.

Grime, J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley, Chichester, UK.

Grinnell, G.B. 1913. Some Indian stream names. *American Anthropologist* 15:327–331.

Grizzle, J.M., and C.J. Brunner. 2009. Infectious diseases of freshwater mussels and other freshwater bivalve mollusks. *Reviews in Fisheries Science* 17:425–467.

Grobler, P.J., et al. 2006. Patterns of genetic differentiation and conservation of the slabside pearlymussel, *Lexingtonia dolabelloides* (Lea, 1840) in the Tennessee River drainage. *Journal of Molluscan Studies* 72:65–75.

Grobler, P.J., et al. 2011. Homogeneity at nuclear microsatellite loci masks mitochondrial haplotype diversity in the endangered fanshell pearlymussel (*Cyprogenia stegaria*). *Journal of Heredity* 102:196–206.

Gutiérrez, J.L., et al. 2003. Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos* 101:79–90.

Haag, W.R. 2002. Spatial, temporal, and taxonomic variation in population dynamics and community structure of freshwater mussels. Dissertation, University of Mississippi, Oxford, USA.

Haag, W.R. 2004. Alabama spike *Elliptio arca*. Page 44 *in* R. Mirarchi et al., editors. *Alabama wildlife*. Vol. 2. *Imperiled aquatic mollusks and fishes*. University of Alabama Press, Tuscaloosa, USA.

Haag, W.R. 2009a. Extreme longevity in freshwater mussels revisited: Sources of bias in age estimates derived from mark-recapture experiments. *Freshwater Biology* 54:1474–1486.

Haag, W.R. 2009b. Past and future patterns of freshwater mussel extinctions in North America during the Holocene. Pages 107–128 *in* S. Turvey, editor. *Holocene extinctions*. Oxford University Press, Oxford, UK.

Haag, W.R. 2010. A hierarchical classification of freshwater mussel diversity in North America. *Journal of Biogeography* 37:12–26.

Haag, W.R. In press. The role of fecundity and reproductive effort in defining life history strategies of North American freshwater mussels. *Biological Reviews.*

Haag, W.R., and A.M. Commens-Carson. 2008. Testing the assumption of annual shell ring deposition in freshwater mussels. *Canadian Journal of Fisheries and Aquatic Sciences* 65:493–508.

Haag, W.R., and A.L. Rypel. 2011. Growth and longevity in freshwater mussels: Evolutionary and conservation implications. *Biological Reviews* 86:225–247.

Haag, W.R., and J.L. Staton. 2003. Variation in fecundity and other reproductive traits in freshwater mussels. *Freshwater Biology* 48:2218–2130.

Haag, W.R., and M.L. Warren. 1997. Host fishes and reproductive biology of 6 freshwater mussel species from the Mobile Basin, USA. *Journal of the North American Benthological Society* 16:576–585.

Haag, W.R., and M.L. Warren. 1998. Role of ecological factors and reproductive strategies in structuring freshwater mussel communities. *Canadian Journal of Fisheries and Aquatic Sciences* 55:297–306.

Haag, W.R., and M.L. Warren. 1999. Mantle displays of freshwater mussels elicit attacks from fish. *Freshwater Biology* 42:35–40.

Haag, W.R., and M.L. Warren. 2000. Effects of light and presence of fish on lure display and larval release behaviours in two species of freshwater mussels. *Animal Behaviour* 60:879–886.

Haag, W.R., and M.L. Warren. 2003. Host fishes and infection strategies of freshwater mussels in large Mobile Basin streams, USA. *Journal of the North American Benthological Society* 22:78–91.

Haag, W.R., and M.L. Warren. 2004. Species richness and total population size of freshwater mussels in Horse Lick Creek, Kentucky in 2003. Unpublished report, USDA Forest Service, Oxford, Mississippi, USA.

Haag, W.R., and M.L. Warren. 2006. Seasonal feeding specialization on snails by river darters (*Percina shumardi*) with a review of snail feeding by other darter species. *Copeia* 2006:604–612.

Haag, W.R., and M.L. Warren Jr. 2007. Freshwater mussel assemblage structure in a regulated river in the Lower Mississippi River Alluvial Basin, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 17:25–36.

Haag, W.R., and M.L. Warren. 2008. Effects of severe drought on freshwater mussel assemblages. *Transactions of the American Fisheries Society* 137:1165–1178.

Haag, W.R., and M.L. Warren. 2010. Diversity, abundance, and size structure of bivalve assemblages in the Sipsey River, Alabama. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20:655–667.

Haag, W.R., et al. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 50:13–19.

Haag, W.R., et al. 1995. An extraordinary reproductive strategy in freshwater bivalves: Prey mimicry to facilitate larval dispersal. *Freshwater Biology* 34:471–476.

Haag, W.R., et al. 1999. Host fishes and host-attracting behavior of *Lampsilis altilis* and *Villosa vibex* (Bivalvia:Unionidae). *American Midland Naturalist* 141:149–157.

Haddon, M. 2001. *Modelling and quantitative methods in fisheries*. Chapman and Hall, Boca Raton, Florida, USA.

Haggerty, T.M., and J.T. Garner. 2000. Seasonal timing of gametogenesis, spawning, brooding and glochidia discharge in *Potamilus alatus* (Bivalvia:Unionidae) in the Wheeler Reservoir, Tennessee River, Alabama, USA. *Invertebrate Reproduction and Development* 38:35–41.

Haggerty, T.M., et al. 1995. A quantitative assessment of the reproductive biology of *Cyclonaias tuberculata* (Bivalvia:Unionidae). *Canadian Journal of Zoology* 73:83–88.

Haggerty, T.M., et al. 2005. Reproductive phenology in *Megalonaias nervosa* (Bivalvia: Unionidae) in Wheeler Reservoir, Tennessee River, Alabama, USA. *Hydrobiologia* 539:131–136.

Haggerty, T.M., et al. 2011. Reproductive seasonality and annual fecundity in *Arcidens confragosus* (Unionidae: Unioninae: Anodontini) from Tennessee River, Alabama, USA. *Invertebrate Reproduction & Development* 55:230–235.

Haley, L., et al. 2007. Reproductive timing of freshwater mussels and potential impacts of pulsed flows on reproductive success. Report to Pulsed Flow Program, Center of Aquatic Biology and Aquaculture, University of California, Davis, USA (http://animalscience.ucdavis.edu/Pulsedflow/CEC-500-2007-097.pdf).

Hamilton, D.J., et al. 1994. Predation of zebra mussels by diving ducks: An enclosure study. *Ecology* 75:521–531.

Hanlon, S.D., and R.J. Neves. 2006. Seasonal growth and mortality of juveniles of *Lampsilis fasciola* (Bivalvia: Unionidae) released to a fish hatchery raceway. *American Malacological Bulletin* 21:45–49.

Hanlon, S.D., et al. 2009. Status of native freshwater mussels in Copper Creek, Virginia. *Southeastern Naturalist* 8:1–18.

Hanson, J.M., et al. 1988. Population size, growth, and production of a unionid clam, *Anodonta grandis simpsoniana*, in a small, deep boreal forest lake in Central Alberta. *Canadian Journal of Zoology* 66:247–253.

Hanson, J.M., et al. 1989. Effect of size-selective predation by muskrats (*Ondatra zibethicus*) on a population of unionid clams (*Anodonta grandis simpsoniana*). *Journal of Animal Ecology* 58:15–28.

Harker, D.F., et al. 1979. Aquatic biota and water quality survey of the Appalachian Province, Eastern Kentucky. Vol. 1. Kentucky Nature Preserves Commission, Frankfort, USA.

Harman, W.N. 1969. The effect of changing pH on the Unionidae. *Nautilus* 83:69–70.

Harman, W.N. 1970. New distribution records and ecological notes on central New York Unionacea. *American Midland Naturalist* 84:46–58.

Harman, W.N. 1974. The effects of reservoir construction and canalization on the mollusks of the Upper Delaware watershed. *Bulletin of the American Malacological Union* 1973:12–14.

Harmon, J.L., and J.E. Joy. 1990. Growth rates of the freshwater mussel, *Anodonta imbecillis* Say 1829, in five West Virginia Wildlife Station ponds. *American Midland Naturalist* 124:372–378.

Harris, J.L., and M.E. Gordon. 1988. Status survey of *Lampsilis powelli* (Lea, 1852). Final Report Number 14-16-0004-87-066. U.S. Fish and Wildlife Service, Jackson, Mississippi, USA.

Harris, J.L., and M.E. Gordon. 1990. *Arkansas mussels*. Arkansas Game and Fish Commission, Little Rock, USA.

Harris, J.L., et al. 2009. Unionoida (Mollusca:Margaritiferidae, Unionidae) in Arkansas, third status review. *Journal of the Arkansas Academy of Science* 63:50–86.

Harrison, S., and A.D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 *in* I. Hanski and M.E. Gilpin, editors. *Metapopulation biology*. Academic Press, San Diego, California, USA.

Hart, D.D., et al. 2002. Dam removal: Challenges and opportunities for ecological research and river restoration. *Bioscience* 52:669–681.

Hart, R.A. 1999. Population dynamics of unionid mussels in Lake Pepin, upper Mississippi River, Minnesota and Wisconsin. Dissertation, North Dakota State University, Fargo, USA.

Hart, R.A., et al. 2001. Empirically derived survival rates of a native mussel, *Amblema plicata*, in the Mississippi and Otter Tail Rivers, Minnesota. *American Midland Naturalist* 146:254–263.

Hart, R.A., et al. 2002. Changes in the freshwater mussel communities of Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin, 1990–1997. *American Malacological Bulletin* 17:109–122.

Hartfield, P. 1993. Headcuts and their effect on freshwater mussels. Pages 131–141 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Hartfield, P.D., and R.S. Butler. 1997. Observations on release of superconglutinates by *Lampsilis perovalis* (Conrad 1834). Pages 11–13 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Hartfield, P.D., and D. Ebert. 1986. The mussels of southwest Mississippi streams. *American Malacological Bulletin* 4:21–23.

Hartfield, P.D., and E. Hartfield. 1996. Observations on the conglutinates of *Ptychobranchus greeni* (Conrad, 1834) (Mollusca:Bivalvia:Unionoidea). *American Midland Naturalist* 135:370–375.

Hartfield, P.D., and R.G. Rummel. 1985. Freshwater mussels (Unionidae) of the Big Black River, Mississippi. *Nautilus* 99:116–119.

Hastie, L.C. 2006. Determination of mortality in exploited freshwater pearl mussel (*Margaritifera margaritifera*) populations. *Fisheries Research* 80:305–311.

Hastie, L.C., and M.R. Young. 2003. Timing of spawning and glochidial release in Scottish freshwater pearl mussel (*Margaritifera margaritifera*) populations. *Freshwater Biology* 48:2107–2117.

Hastie, L.C., et al. 2000a. Physical microhabitat requirements of freshwater pearl mussels, *Margaritifera margaritifera* (L.). *Hydrobiologia* 429:59–71.

Hastie, L.C., et al. 2000b. Sizes, densities, and age structures of Scottish *Margaritifera margaritifera* (L.) populations. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10:229–247.

Hastie, L.C., et al. 2001. The effects of a major flood on an endangered freshwater mussel population. *Biological Conservation* 98:107–115.

Haszprunar, G., et al. 2008. Relationships of higher molluscan taxa. Pages 19–32 *in* W.F. Ponder and D.R. Lindberg, editors. *Phylogeny and evolution of the Mollusca*. University of California Press, Berkeley, USA.

Haukioja, E., and T. Hakala. 1978. Life-history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda). *Oecologia (Berlin)* 35:253–266.

Havlik, M.E. 1997. Are unionid translocations a viable mitigation technique? The Wolf River, Wisconsin, experience, 1992–1995. Pages 184–195 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Havlik, M.E. 1983. Naiad mollusk populations (Bivalvia:Unionidae) in Pools 7 and 8 of the Mississippi River near La Crosse, Wisconsin. *American Malacological Bulletin* 1:51–60.

Havlik, M.E., and D.H. Stansbery. 1978. The naiad mollusks of the Mississippi River in the vicinity of Prairie Du Chien, Wisconsin. *Bulletin of the American Malacological Union* 1977:9–12.

Hayes, T.B., et al. 2002. Hermaphroditic, demasculinized frogs after exposure to the herbicide atrazine at low ecologically relevant doses. *Proceedings of the National Academy of Science* 99:5476–5480.

He, J.X., and D.J. Stewart. 2002. A stage-explicit expression of the von Bertalanffy growth model for understanding age at first reproduction of Great Lakes fishes. *Canadian Journal of Fisheries and Aquatic Science* 59:250–261.

Headlee, T.J. 1906. Ecological notes on the mussels of Winona, Pike, and Center lakes of Kosciusko County, Indiana. *Biological Bulletin (Woods Hole)* 11:305–319.

Headlee, T.J., and J. Simonton. 1904. Ecological notes on the mussels of Winona Lake. *Proceedings of the Indiana Academy of Science* 1903:173–179.

Heard, W.H. 1970. Hermaphroditism in *Margaritifera falcata* (Gould) (Pelecypoda: Margaritiferidae). *Nautilus* 83:113–114.

Heard, W.H. 1975. Sexuality and other aspects of reproduction in *Anodonta* (Pelecypoda: Unionidae). *Malacologia* 15:81–103.

Heard, W.H. 1979. Hermaphroditism in *Elliptio* (Pelecypoda:Unionidae). *Malacological Review* 12:21–28.

Heard, W.H. 1998. A history of the study of generation of unionoidean bivalves: Aristotle to Houghton (1862). *Malacological Review – Bivalvia I Supplement* 7:123–136.

Heard, W.H. 1999. Glochidial larvae of freshwater mussels and their fish hosts: Early discoveries and interpretations of the association. *Malacological Review – Freshwater Mollusca I Supplement* 8:83–88.

Heard, W.H., and G. Dinesen. 1999. A history of the controversy about *Glochidium parasiticum* Rathke, 1797 (Palaeoheterodonta:Unionoida:Unionidea). *Malacological Review – Freshwater Mollusca I Supplement* 8:89–106.

Heath, D.J., et al. 2000. Determination of basic reproductive characteristics of the winged mapleleaf mussel (*Quadrula fragosa*) relevant to recovery. Job 1: Determination of gravidity period. Report to Wisconsin Department of Natural Resources, Madison, USA (http://dnr.wi.gov/fish/reports/final/stcroixmapleleafrepro2000.pdf).

Hebert, P.D.N., et al. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): A new mollusc in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1587–1591.

Hebert, P.D.N., et al. 1991. Demography and ecological impacts of the invading mollusc *Dreissena polymorpha*. *Canadian Journal of Zoology* 69:405–409.

Hedegaard, C., et al. 2006. Molluscan shell pigments: An *in situ* resonance raman study. *Journal of Molluscan Studies* 72:157–162.

Heege, K.V. 1998. "They're pretty, but they're work": Shell-decorated graves as community art. *Folklore Forum* 29:65–98.

Heino, M., and V. Kaitala. 1997. Should ecological factors affect the evolution of age at maturity in freshwater clams? *Evolutionary Ecology* 11:67–81.

Heinricher, J.R., and J.B. Layzer. 1999. Reproduction by individuals of a nonreproducing population of *Megalonaias nervosa* (Mollusca:Unionidae) following translocation. *American Midland Naturalist* 141:140–148.

Helama, S., and I. Valovirta. 2008. Ontogenetic morphometrics of individual freshwater pearl mussels (*Margaritifera margaritifera* (L.)) reconstructed from geometric and trigometric sclerochronology. *Hydrobiologia* 610:43–53.

Helama, S., et al. 2007. Conchology of endangered freshwater pearl mussel: Conservation palaeobiology applied to museum shells originating from northern Finland. *Bollettino Malacologico* 43:161–170.

Heming, T.A., et al. 1988. Acid base regulation in the freshwater pearl mussel *Margaritifera margaritifera* effects of emersion and low water pH. *Journal of Experimental Biology* 137:501–512.

Henley, W.F., and R.J. Neves. 1999. Recovery status of freshwater mussels (Bivalvia: Unionidae) in the North Fork Holston River, Virginia. *American Malacological Bulletin* 15:65–73.

Henley, W.F., et al. 2001. Design and evaluation of recirculating water systems for maintenance and propagation of freshwater mussels. *North American Journal of Aquaculture* 63:144–155.

Herman, S.G. 2002. Wildlife biology and natural history: Time for a reunion. *Journal of Wildlife Management* 66:933–946.

Hiestand, W.A. 1938. Respiration studies with fresh-water mollusks: I. Oxygen consumption in relation to oxygen tension. *Proceedings of the Indiana Academy of Science* 47:287–292.

Higgins, F. 1858. A catalogue of the shell-bearing species of Mollusca, inhabiting the vicinity of Columbus, Ohio, with some remarks thereon. Ohio State Board of Agriculture with an

Abstract of the Proceedings of the County Agricultural Societies 12 Annual Report for 1857:548–555.

Hildreth, S.P. 1828. Observations on, and descriptions of the shells found in the waters of the Muskingum River, Little Muskingum, and Duck Creek, in the vicinity of Marietta, Ohio. *American Journal of Science and Arts* 14:276–291 [reprinted in *Sterkiana* 8:39–48, 1962].

Hill, D.M. 1986. Cumberlandian mollusks conservation program, activity 3: Identification of fish hosts. Office of Natural Resources and Economic Development, Tennessee Valley Authority, Knoxville, USA.

Hinch, S.G., et al. 1986. Growth of *Lampsilis radiata* (Bivalvia: Unionidae) in sand and mud: A reciprocal transplant experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 43:548–552.

Hinch, S.G., et al. 1989. Morphological variation of *Elliptio complanata* (Bivalvia: Unionidae) in differing sediments of soft-water lakes exposed to acidic deposition. *Canadian Journal of Zoology* 67:1895–1899.

Hinkley, A.A. 1906. Some shells from Mississippi and Alabama. *Nautilus* 20:52–55.

Hoagland, K.E. 1978. Protandry and the evolution of environmentally-mediated sex change: A study of the Mollusca. *Malacologia* 17:365–391.

Hochwald, S. 2001. Plasticity of life-history traits in *Unio crassus*. Pages 127–141 *in* G. Bauer and K. Wächtler, editors. *Ecology and evolution of the freshwater mussels Unionoida*. Ecological Studies 145. Springer, Berlin, Germany.

Hocutt, C.H., and E.O. Wiley, editors. 1986. *The zoogeography of North American freshwater fishes*. Wiley-Interscience, New York, USA.

Hocutt, C.H., et al. 1986. Zoogeography of fishes of the Central Appalachians and Central Atlantic Coastal Plain. Pages 161–121 *in* C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley, New York, USA.

Hoeh, W.R., et al. 1995. A phylogenetic perspective on the evolution of simultaneous hermaphroditism in a freshwater mussel clade (Bivalvia:Unionidae:*Utterbackia*). *Malacological Review* 28:25–42.

Hoeh, W.R., et al. 1996. Multiple origins of gender-associated mitochondrial DNA lineages in bivalves (Mollusca: Bivalvia). *Evolution* 50:2276–2286.

Hoeh, W.R., et al. 1998. Correlation between mating system and distribution of genetic variation in *Utterbackia* (Bivalvia:Unionidae). *Journal of Shellfish Research* 17:1383–1393.

Hoggarth, M.A. 1988. The use of glochidia in the systematics of the Unionidae (Mollusca: Bivalvia). Dissertation, Ohio State University, Columbus, USA.

Hoggarth, M.A. 1999. Descriptions of some of the glochidia of the Unionidae (Mollusca: Bivalvia). *Malacologia* 41:1–118.

Hoggarth, M.A., and A.S. Gaunt. 1988. Mechanics of glochidial attachment (Mollusca: Bivalvia: Unionidae). *Journal of Morphology* 198:71–81.

Hoggarth, M.A., et al. 1995. Discovery of the federally endangered freshwater mussel, *Epioblasma obliquata obliquata* (Rafinesque, 1820) (Unionidae), in Ohio. *Ohio Journal of Science* 95:298–299.

Hoggarth, M.A., et al. 2000. The correlation of mussels with fish in the upper Blanchard River in Hardin and Hancock counties, Ohio, with special regard to the rayed bean (*Villosa fabalis*). Pages 19–26 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Hoke, E. 2005. The freshwater mussels (Mollusca:Bivalvia:Unionidae) of northern Nebraska: The Missouri, Niobrara, and White river basins. *American Malacological Bulletin* 20:27–35.

Holland, D.F. 1991. Prolonged emersion tolerance in freshwater mussels (Bivalvia:Unionidae): Interspecific comparison of behavioral strategies and water loss rates. Thesis, University of Texas at Arlington, USA.

Holland-Bartels, L.E. 1990. Physical factors and their influence on the mussel fauna of a main channel border habitat of the Upper Mississippi River. *Journal of the North American Benthological Society* 9:327–335.

Holland-Bartels, L.E., and T.W. Kammer. 1989. Seasonal reproductive development of *Lampsilis cardium, Amblema plicata plicata* and *Potamilus alatus* (Pelecypoda:Unionidae) in the upper Mississippi River. *Journal of Freshwater Ecology* 5:87–92.

Hoos, A.B. et al. 2002. Water quality of the Flint River Basin, Alabama and Tennessee, 1999–2000. Water-Resources Investigations Report 01-4185. U.S. Geological Survey, Nashville, Tennessee, USA.

Hopkins, S.H. 1934. The parasite inducing pearl formation in American freshwater Unionidae. *Science* 79:385–386.

Hornbach, D.J. 2001. Macrohabitat factors influencing the distribution of naiads in the St. Croix River, Minnesota and Wisconsin, USA. Pages 213–230 *in* G. Bauer and K. Wätchler, editors. *Ecology and evolution of the freshwater mussels Unionoida. Ecological Studies* 145. Springer, Berlin, Germany.

Hornbach, D.J., and T. Deneka. 1996. A comparison of a qualitative and a quantitative collection method for examining freshwater mussel assemblages. *Journal of the North American Benthological Society* 15:587–596.

Hornbach, D.J., et al. 2010. Variation in freshwater mussel shell sculpture and shape along a river gradient. *American Midland Naturalist* 164:22–36.

Horwitz, R.J. 1978. Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs* 48:307–321.

Hough, W. 1926. Fire as an agent in human culture. Bulletin 139. Smithsonian Institution, Washington, D.C., USA.

Houp, R.E. 1993. Observations on long-term effects of sedimentation on freshwater mussels (Mollusca:Unionidae) in the North Fork of Red River, Kentucky. *Transactions of the Kentucky Academy of Science* 54:93–97.

Houslet, B.S., and J.B. Layzer. 1997. Difference in growth between two populations of *Villosa taeniata* in Horse Lick Creek, Kentucky. Pages 37–44 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Hove, M.C., and R.J. Neves. 1994. Life history of the endangered James spinymussel *Pleurobema collina* (Conrad, 1837) (Mollusca:Unionidae). *American Malacological Bulletin* 11:29–40.

Hove, M.C., et al. 1997. Suitable fish hosts for glochidia of four freshwater mussels. Pages 21–25 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Hove, M.C., et al. 2011. Early life history and distribution of pistolgrip (*Tritogonia verrucosa* (Rafinesque, 1820)) in Minnesota and Wisconsin. *American Midland Naturalist* 165:338–354.

Hove, M.C., et al. 2012. Early life history of the winged mapleleaf mussel (*Quadrula fragosa*). *American Malacological Bulletin* 30:47–57.

Howard, A.D. 1913. The catfish as a host for fresh-water mussels. *Transactions of the American Fisheries Society* 42:65–70.

Howard, A.D. 1914. Some cases of narrowly restricted parasitism among commercial species of fresh water mussels. *Transactions of the American Fisheries Society* 44:41–44.

Howard, A.D. 1915. Some exceptional cases of breeding among the Unionidae. *Nautilus* 29:4–11.

Howard, A.D. 1922. Experiments in the culture of fresh-water mussels. *Bulletin of the U.S. Bureau of Fisheries* 38:63–89 [issued separately as U.S. Bureau of Fisheries Document 916].

Howard, A.D. 1951. A river mussel parasitic on a salamander. *Natural History Miscellanea* 77:1–6.

Howard, A.D., and B.J. Anson. 1922. Phases in the parasitism of the Unionidae. *Journal of Parasitology* 9:68–82.

Howard, J.K., and K.M. Cuffey. 2003. Freshwater mussels in a California North Coast Rangeriver: Occurrence, distribution, and controls. *Journal of the North American Benthological Society* 22:63–77.

Howard, J.K., and K.M. Cuffey. 2006a. The functional role of native freshwater mussels in the fluvial benthic environment. *Freshwater Biology* 51:460–474.

Howard, J.K., and K.M. Cuffey. 2006b. Factors controlling the age structure of *Margaritifera falcata* in 2 northern California streams. *Journal of the North American Benthological Society* 25:677–690.

Howard, P.H. 1991. *Handbook of environmental fate and exposure data for organic chemicals*. Vol. III. *Pesticides*. Lewis, Chelsea, Michigan, USA.

Howe, C.M., et al. 2004. Toxicity of glyphosate-based pesticides to four North American frog species. *Environmental Toxicology and Chemistry* 23:1928–1938.

Howe, G.E., et al. 1998. Effect of chemical synergy and larval stage on the toxicity of atrazine and alachlor to amphibian larvae. *Environmental Toxicology and Chemistry* 17:519–525.

Howells, R.G. 2000. Reproductive seasonality of freshwater mussels (Unionidae) in Texas. Pages 35–48 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Howells, R.G. 2001. Status of freshwater mussels of the Rio Grande, with comments on other bivalves. Pages 59–73 *in* G.P. Garrett and N.L. Allan, editors. *Aquatic fauna of the northern Chihuahuan Desert*. Special Publication 46. Museum of Texas Technical University, Lubbock, USA.

Howells, R.G., et al. 1996. *Freshwater mussels of Texas*. Texas Parks and Wildlife Press, Austin, USA.

Howells, R.G., et al. 1997. Conservation status of selected freshwater mussels in Texas. Pages 117–128 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Howerth, E.W., and A.E. Keller. 2006. Experimentally induced glochidiosis in smallmouth bass (*Micropterus dolomieu*). *Veterinary Pathology* 43:1004–1007.

Hubbard, H. 1977. *Shantyboat*. University Press of Kentucky, Lexington, USA.

Hubbard, P.J. 1961. *Origins of TVA: The Muscle Shoals controversy, 1920–1932*. W.W. Norton, New York, USA.

Hubbs, D. 2000. Augmentation of natural reproduction by freshwater mussels to sustain shell harvests. Pages 49–51 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Hubbs, D. 2010. 2009 statewide commercial mussel report. Report 10-04. Tennessee Wildlife Resources Agency, Nashville, USA.

Hubbs, D., et al. 2011. 2010 Duck River quantitative mussel survey. Report 11-04. Tennessee Wildlife Resources Agency, Nashville, USA.

Hudson, R.G., and B.G. Isom. 1984. Rearing juveniles of the freshwater mussels in a laboratory setting. *Nautilus* 98:129–135.

Hughes, M.H., and P.W. Parmalee. 1999. Pre-Columbian and modern freshwater mussel (Mollusca:Bivalvia:Unionoidea) faunas of the Tennessee River: Alabama, Kentucky, and Tennessee. *Regulated Rivers: Research and Management* 15:25–42.

Hughes, R.M., and J.M. Omernik. 1983. An alternative for characterizing stream size. Pages 87–101 *in* T.D. Fontaine and S.M. Bartel, editors. *Dynamics of lotic ecosystems*. Ann Arbor Science, Ann Arbor, Michigan, USA.

Hurd, J.C. 1974. Systematics and zoogeography of the unionacean mollusks of the Coosa River drainage of Alabama, Georgia and Tennessee. Dissertation, Auburn University, Auburn, Alabama, USA.

Hurlbert, A.J., et al. 2007. Life and death: Metabolic rate, membrane composition, and life span of animals. *Physiological Reviews* 87:1175–1213.

Hutchinson, G.E. 1957. *A treatise on limnology. I. Geography, physics, and chemistry*. John Wiley, New York, USA.

Illinois Department of Natural Resources. 2004. EPT data matrix. Critical Trends Assessment Program, Springfield, Illinois, USA (http://ctap.inhs.uiuc.edu/data/data.asp).

Imlay, M.J. 1968. Environmental factors in activity rhythms of the freshwater clam *Elliptio complanatus catawbensis* (Lea). *American Midland Naturalist* 80:508–528.

Imlay, M.J. 1972. Greater adaptability of freshwater mussels to natural rather than to artificial displacement. *Nautilus* 86:7–79.

Imlay, M.J. 1973. Effects of potassium on survival and distribution of freshwater mussels. *Malacologia* 12:97–113.

Isely, F.B. 1911. Preliminary note on the ecology of the early juvenile life of the Unionidae. *Biological Bulletin (Woods Hole)* 20:77–80.

Isely, F.B. 1914. Experimental study of the growth and migration of fresh-water mussels. *Report of the U.S. Commissioner of Fisheries for 1913, Appendix* III [issued separately as U.S. Bureau of Fisheries Document 792].

Isely, F.B. 1924. The fresh-water mussel fauna of eastern Oklahoma. *Proceedings of the Oklahoma Academy of Science* 4:43–118.

Isely, F.B. 1931. A fifteen year growth record in fresh-water mussels. *Ecology* 12:616–619.

Ishibashi, R., et al. 2000. Sperm sphere in unionid mussels (Bivalvia:Unionidae). *Zoological Science* 17:947–950.

Isom, B.G. 1969. The mussel resource of the Tennessee River. *Malacologia* 7:397–425.

Isom, B.G. 1971. A biologist's look at the history of Muscle Shoals (Mussel Shoals). *Malacological Review* 4:203–206.

Isom, B.G., and R.G. Hudson. 1982. In vitro culture of parasitic freshwater mussel glochidia. *Nautilus* 96:147–151.

Jackson, D.C., and J.R. Jackson. 1989. A glimmer of hope for stream fisheries in Mississippi. *Fisheries* 14(3):4–9.

Jackson, J.K., et al. 2005. Atlantic coast rivers of the northeastern United States. Pages 20–71 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America*. Elsevier, Burlington, Massachusetts, USA.

Jansen, W.A. 1991. Seasonal prevalence, intensity of infestation, and distribution of glochidia of *Anodonta grandis simpsoniana* Lea on yellow perch, *Perca flavescens*. *Canadian Journal of Zoology* 69:964–972.

Jansen, W., et al. 2001. Glochidial mortality in freshwater mussels. Pages 185–211 *in* G. Bauer and K. Wächtler, editors. *Ecology and evolution of the freshwater mussels Unionoida*. Ecological Studies 145. Springer, Berlin, Germany.

Jass, J., and J. Glenn. 1999. Measuring the degree of variation in Wisconsin *Pyganodon grandis* (Say, 1829) (Mollusca:Bivalvia:Unionidae). *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 87:105–110.

Jass, J., and J. Glenn. 2004. Sexual dimorphism in *Lampsilis siliquoidea* (Barnes, 1823) (Bivalvia:Unionidae). *American Malacological Bulletin* 18:45–47.

Jenkins, R.E., and N.M. Burkhead. 1994. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda, Maryland, USA.

Jenkinson, J.J., and S.A. Ahlstedt. 1987. Mussel die-offs downstream from Pickwick Landing Dam, Tennessee River, 1985–1986. Pages 29–38 *in* R.J. Neves, editor. *Proceedings of the workshop on die-offs of freshwater mussels in the United States*. Upper Mississippi River Conservation Committee, Davenport, Iowa, USA.

Jenkinson, J.J., and S.A. Ahlstedt. 1993–1994. A search for additional populations of *Potamilus capax* in the St. Francis and Cache River watersheds, Arkansas and Missouri, USA. *Walkerana* 7:71–157.

Jiao, Y., et al. 2008. Models and model selection uncertainty in estimating growth rates of endangered freshwater mussel populations. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2389–2398.

Jirka, K.J., and R.J. Neves. 1992. Reproductive biology of four species of freshwater mussels (Mollusca:Unionidae) in the New River, Virginia and West Virginia. *Journal of Freshwater Ecology* 7:35–44.

Johnson, D.W. 1968. Pesticides and fishes – a review of selected literature. *Transactions of the American Fisheries Society* 97:398–424.

Johnson, L.B., et al. 1997. Landscape influences on water chemistry in midwestern stream ecosystems. *Freshwater Biology* 37:193–208.

Johnson, M.S., et al. 2010a. Status of the freshwater mussel fauna in the Powell River, Virginia and Tennessee. Unpublished report submitted to U.S. Fish and Wildlife Service, Blacksburg, Virginia, USA.

Johnson, M.S., et al. 2010b. Life history and status of *Quadrula sparsa* and *Quadrula intermedia* in the Powell, Virginia and Tennessee. Unpublished report submitted to U.S. Fish and Wildlife Service, Blacksburg, Virginia, USA.

Johnson, P.D., and K.M. Brown. 1998. Intraspecific life history variation in the threatened Louisiana pearlshell mussel, *Margaritifera hembeli*. *Freshwater Biology* 40:317–329.

Johnson, P.D., and K.M. Brown. 2000. The importance of microhabitat factors and habitat stability of the threatened Louisiana pearl shell, *Margaritifera hembeli* (Conrad). *Canadian Journal of Zoology* 78:271–277.

Johnson, P.M. 2001. Habitat associations and drought responses of mussels in the lower Flint River Basin, southwest Georgia. Thesis, University of Georgia, Athens, USA.

Johnson, R.I. 1946. *Anodonta implicata* Say. *Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard University* 1:109–116.

Johnson, R.I. 1947. *Lampsilis cariosa* Say and *Lampsilis ochracea* Say. *Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard University* 1:145–156.

Johnson, R.I. 1970. The systematics and zoogeography of the Unionidae (Mollusca:Bivalvia) of the southern Atlantic Slope Region. *Bulletin of the Museum of Comparative Zoology* 140:263–449.

Johnson, R.I. 1972. The Unionidae (Mollusca:Bivalvia) of peninsular Florida. *Bulletin of the Florida State Museum of Biological Science* 16:181–249.

Johnson, R.I. 1977. Arnold Edward Ortmann, a bibliography of his work on mollusks, with a catalogue of his recent molluscan taxa. *Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard University* 4:229–241.

Johnson, R.I. 1978. Systematics and zoogeography of *Plagiola* (= *Dysnomia* = *Epioblasma*), an almost extinct genus of freshwater mussels (Bivalvia: Unionidae) from Middle North America. *Bulletin of the Museum of Comparative Zoology* 148:239–321.

Johnson, R.I. 1980. Zoogeography of North American Unionacea (Mollusca: Bivalvia) north of the maximum Pleistocene glaciation. *Bulletin of the Museum of Comparative Zoology* 149:77–189.

Johnson, R.I. 1984. A new mussel, *Lampsilis* (*Lampsilis*) *fullerkati* (Bivalvia: Unionidae) from Lake Waccamaw, Columbus County, North Carolina, with a list of the other unionid species of the Waccamaw River system. *Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard University* 4:305–319.

Johnson, W.E., et al. 2010. Genetic restoration of the Florida panther. *Science* 329:1641–1645.

Johnston, M.O., et al. 1998. Negative correlation between male allocation and rate of self-fertilization in a hermaphroditic animal. *Proceedings of the National Academy of Science* 95:617–620.

Jokela, J., and P. Mutikainen. 1995a. Phenotypic plasticity and priority rules for energy allocation in a freshwater clam: A field experiment. *Oecologia (Berlin)* 104:122–132.

Jokela, J., and P. Mutikainen. 1995b. Effect of size-dependant muskrat (*Ondatra zibethica*) predation on the spatial distribution of a freshwater clam, *Anodonta piscinalis* Nilsson (Unionidae, Bivalvia). *Canadian Journal of Zoology* 73:1085–1094.

Jones, D.S. 1980. Annual cycle of growth increment formation in two continental shell bivalves and its paleoecologic significance. *Paleobiology* 6:331–340.

Jones, D.S. 1981. Repeating layers in the molluscan shell are not always periodic. *Journal of Paleontology* 55:1076–1082.

Jones, D.S., et al. 1990. Annual shell banding, age, and growth rate of hard clams (*Mercenaria* spp.) from Florida. *Journal of Shellfish Research* 9:215–225.

Jones, D.S., and I.R. Quitmyer. 1996. Marking time with bivalve shells: Oxygen isotopes and season of annual increment formation. *Palaios* 11:340–346.

Jones, J.W., and R.J. Neves. 2002. Life history and propagation of the endangered fanshell pearly mussel, *Cyprogenia stegaria* Rafinesque (Bivalvia: Unionidae). *Journal of the North American Benthological Society* 21:76–88.

Jones, J.W., and R.J. Neves. 2007. Freshwater mussel status: Upper North Fork Holston River, Virginia. *Northeastern Naturalist* 14:471–480.

Jones, J.W., and R.J. Neves. 2010. Descriptions of a new species and a new subspecies of freshwater mussels, *Epioblasma ahlstedti* and *Epioblasma florentina aureola* (Bivalvia: Unionidae), in the Tennessee River drainage, USA. *Nautilus* 124:77–92.

Jones, J.W., and R.J. Neves. 2011. Influence of life-history variation on demographic responses of three freshwater mussel species (Bivalvia: Unionidae) in the Clinch River, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21:57–73.

Jones, J.W., et al. 2004. Life history and propagation of the endangered dromedary pearlymussel (*Dromus dromas*) (Bivalvia: Unionidae). *Journal of the North American Benthological Society* 23:515–525.

Jones, J.W., et al. 2005. Factors affecting survival and growth of juvenile freshwater mussels cultured in recirculating aquaculture systems. *North American Journal of Aquaculture* 67:210–220.

Jones, J.W., et al. 2006a. A holistic approach to taxonomic evaluation of two closely related endangered freshwater mussel species, the oyster mussel *Epioblasma capsaeformis* and tan riffleshell *Epioblasma florentina walkeri* (Bivalvia: Unionidae). *Journal of Molluscan Studies* 72:267–283.

Jones, J.W., et al. 2006b. Genetic management guidelines for captive propagation of freshwater mussels (Unionoidea). *Journal of Shellfish Research* 25:527–535.

Jones, J.W., et al. 2010. Life history and demographics of the endangered birdwing pearlymussel (*Lemiox rimosus*) (Bivalvia: Unionidae). *American Midland Naturalist* 163:335–350.

Jones, P., and J. Silver. 1978. Red and blue-green bile pigments in the shell of *Astraea tuber* (Mollusca: Archaeogastropoda). *Comparative Biochemistry and Physiology* 63:185–188.

Jones, R.L., et al. 2005. The freshwater mussels (Mollusca: Bivalvia:Unionidae) of Mississippi. *Southeastern Naturalist* 4:77–92.

Jørgensen, C.B., et al. 1988. The mussel pump: Properties and modeling. *Marine Ecology Progress Series* 45:205–216.

Kaiser, B.E. 2005. The effects of glochidiosis on fish respiration. Thesis, Missouri State University, Springfield, USA.

Kareiva, P., et al. 2000. Recovery and management options for spring/summer Chinook Salmon in the Columbia River Basin. *Science* 290:977–979.

Karr, J.R., et al. 1985. Fish communities of midwestern rivers: A history of degradation. *BioScience* 35:90–95.

Kasprzak, K. 1986. Role of the Unionidae and Sphaeriidae (Mollusca, Bivalvia) in the eutrophic Lake Zbechy and its outflow. *Internationale Revue Der Gesamten Hydrobiologie* 71:315–334.

Kat, P.W. 1982a. Shell dissolution as a significant cause of mortality for *Corbicula fluminea* (Bivalvia:Corbiculidae) inhabiting acidic waters. *Malacological Review* 15:129–134.

Kat, P.W. 1982b. Effects of population density and substratum type on growth and migration of *Elliptio complanata* (Bivalvia:Unionidae). *Malacological Review* 15:119–127.

Kat, P.W. 1983. Sexual selection and simultaneous hermaphroditism among the Unionidae (Bivalvia:Mollusca). *Journal of Zoology (London)* 201:395–416.

Kat, P.W. 1984. Parasitism and the Unionacea (Bivalvia). *Biological Reviews of the Cambridge Philosophical Society* 59:189–207.

Keevin, T.M., et al. 1992. Long-distance dispersal of zebra mussels (*Dreissena polymorpha*) attached to hulls of commercial vessels. *Journal of Freshwater Ecology* 7:437.

Keller, A.E., and D.S. Ruessler. 1997. Determination or verification of host fish for nine species of unionid mussels. *American Midland Naturalist* 138:402–407.

Keller, A.E., and S.G. Zam. 1990. Simplification of in-vitro culture techniques for freshwater mussels. *Environmental Toxicology and Chemistry* 9:1291–1296.

Keller, A., et al. 2007. Unionid mussel sensitivity to environmental contaminants. Pages 151–167 *in* J.L. Farris and J.H. Van Hassel, editors. *Freshwater bivalve ecotoxicology*. CRC Press, Boca Raton, Florida, USA.

Kelly, H.M. 1899. A statistical study of the parasites of the Unionidae. *Bulletin of the Illinois State Laboratory of Natural History* 5:399–418.

Kelly, M.W., and J.M. Rhymer. 2005. Population genetic structure of a rare unionid (*Lampsilis cariosa*) in a recently glaciated landscape. *Conservation Genetics* 6:789–802.

Kelner, D.E., and B.E. Sietman. 2000. Relic populations of the ebony shell, *Fusconaia ebena* (Bivalvia:Unionidae), in the upper Mississippi River drainage. *Journal of Freshwater Ecology* 15:371–377.

Kenchington, E., et al. 2002. Genetics of mother-dependent sex ratio in blue mussels (*Mytilus* spp.) and implications for doubly uniparental inheritance of mitochondrial DNA. *Genetics* 161:1579–1588.

Kendall, N.W., et al. 2010. Climate effects on inter-annual variation in growth of the freshwater mussel (*Anodonta beringiana*) in an Alaskan lake. *Freshwater Biology* 55:2339–2346.

Kennedy, I. 1985. Hill Country pearls. *Texas Monthly*, October.

Kennedy, T.B., and W.R. Haag. 2005. Using morphometrics to identify glochidia from a diverse freshwater mussel community. *Journal of the North American Benthological Society* 24:880–889.

Kerans, B.L., and J.R. Karr. 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. *Ecological Applications* 4:768–785.

Kesler, D.H., and R.C. Bailey. 1993. Density and ecomorphology of a freshwater mussel (*Elliptio complanata*, Bivalvia:Unionidae) in a Rhode Island lake. *Journal of the North American Benthological Society* 12:259–264.

Kesler, D.H., and J.A. Downing. 1997. Internal shell annuli yield inaccurate growth estimates in *Elliptio complanata* and *Lampsilis radiata*. *Freshwater Biology* 57:325–332.

Kesler, D.H., and N. van Tol. 2000. Growth of the freshwater mussel *Pyganodon grandis* (Unionidae) in two west Tennessee borrow pits. *Journal of the Tennessee Academy of Science* 75:71–75.

Kesler, D.H., et al. 2001. Freshwater mussels (Unionidae) of the Wolf River in western Tennessee and Mississippi. *Journal of the Tennessee Academy of Science* 76:38–46.

Kesler, D.H., et al. 2007. Long-term monitoring of growth in the eastern Elliptio, *Elliptio complanata* (Bivalve: Unionidae), in Rhode Island: A transplant experiment. *Journal of the North American Benthological Society* 26:123–133.

Khym, J.R., and J.B. Layzer. 2000. Host fish suitability for glochidia of *Ligumia recta*. *American Midland Naturalist* 143:178–184.

Kidd, K.A., et al. 2007. Collapse of a fish population after exposure to a synthetic estrogen. *Proceedings of the National Academy of Sciences of the United States of America* 104:8897–8901.

King, T.L., et al. 1999. Intraspecific phylogeography of *Lasmigona subviridis* (Bivalvia: Unionidae): Conservation implications of range discontinuity. *Molecular Ecology* 8:S65–S78.

Kirk, S.G., and J.B. Layzer. 1997. Induced metamorphosis of freshwater mussel glochidia on nonhost fish. *Nautilus* 110:102–106.

Kirtland, J.P. 1834. Observations on the sexual characteristics of the animals belonging to Lamarck's family of naiades. *American Journal of Science and Arts* 26:117–120.

Kitchell, J.F., et al. 1977. Percid habitat: The river analogy. *Journal of the Fisheries Research Board of Canada* 34:1936–1940.

Klippel, W.E., et al. 1978. The Holocene naiad record at Rodgers Shelter in the western Ozark Highlands of Missouri. *Plains Anthropologist* 23:257–271.

Knopman, D.S., and R.A. Smith. 1993. 20 years of the Clean Water Act. *Environment* 35: 16–41.

Kobluk, D.R., and R.H. Mapes. 1989. The fossil record, function, and possible origins of shell color patterns in Paleozoic marine invertebrates. *Palaios* 4:63–85.

Koch, L.M. 1990. Quantitative mussel survey in Pools 22 and 24 of the Upper Mississippi River at mrm 300 and 309 during summer, 1988. Missouri Department of Conservation, Jefferson City, USA.

Kokko, H., and T. Ebenhard. 1996. Measuring the strength of demographic stochasticity. *Journal of Theoretical Biology* 183:169–178.

Konrad, C.P., et al. In press. Evaluating dam re-operation for freshwater conservation in the sustainable rivers project. *River Research and Applications.*

Koprivnikar, J., et al. 2007. Contaminant effects on host-parasite interactions: Atrazine, frogs, and trematodes. *Environmental Toxicology and Chemistry* 26:2166–2170.

Kotrla, M.B., and F.C. James. 1987. Sexual dimorphism of shell shape and growth of *Villosa villosa* (Wright) and *Elliptio icterina* (Conrad) (Bivalvia:Unionidae). *Journal of Molluscan Studies* 53:113–123.

Kraemer, L.R. 1970. The mantle flap in three species of *Lampsilis* (Pelecypoda:Unionidae). *Malacologia* 10:225–282.

Kraemer, L.R. 1984. Aspects of the functional morphology of some fresh-water bivalve nervous systems: Effects on reproductive processes and adaptation of sensory mechanisms in the Sphaeriacea and Unionacea. *Malacologia* 25:221–239.

Kroes, D.E., and C.R. Hupp. 2010. The effect of channelization on floodplain sediment deposition and subsidence along the Pocomoke River, Maryland. *Journal of the American Water Resources Association* 46:686–699.

Kunz, G.F. 1898. A brief history of the gathering of fresh-water pearls in the United States. *Bulletin of the U.S. Fish Commission* 17:321–330 [issued separately as U.S. Bureau of Fisheries Document 389].

Kunz, G.F., and C.H. Stevenson. 1908. *The book of the pearl.* Century, New York, USA.

Kurth, J., et al. 2007. PIT tags increase effectiveness of freshwater mussel recaptures. *Journal of the North American Benthological Society* 26:253–260.

Kurtz, J.J. 2003. The old pioneer: The journey of John F. Boepple, founder of the freshwater pearl button industry (http://69.49.80.78/museum/Update%20Web/ Boepple.htm).

Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19:573–592.

Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos* 83:353–358.

Lande, R., et al. 2003. *Stochastic population dynamics in ecology and conservation.* Oxford University Press, Oxford, UK.

Lane, E., and T.H. Birbeck. 2000. Species specificity of some bacterial pathogens of bivalve molluscs is correlated with their interaction with bivalve haemocytes. *Journal of Fish Diseases* 23:275–279.

Lang, N.J., and R.L. Mayden. 2007. Systematics of the subgenus *Oligocephalus* (Teleostei: Percidae:*Etheostoma*) with complete subgeneric sampling of the genus *Etheostoma*. *Molecular Phylogenetics and Evolution* 43:605–615.

Lassalle, G., et al. 2007. Parasite co-infection of two sympatric bivalves, the Manila clam (*Ruditapes philippinarum*) and the cockle (*Cerastoderma edule*) along a latitudinal gradient. *Aquatic Living Resources* 20:33–42.

Latendresse, J. 1980. A look at the upper Mississippi River shell industry and the Japanese cultured pearl industry. Pages 170–178 *in* J.L. Rasmussen, editor. *Proceedings of the Symposium on Upper Mississippi River Bivalve Mollusks*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Lauritsen, D.D. 1986. Filter-feeding in *Corbicula fluminea* and its effect on seston removal. *Journal of the North American Benthological Society* 5:165–172.

Layzer, J.B., and J.R. Khym. 2003–2004. Fish hosts for glochidia of the pheasant shell, *Actinonaias pectorosa*. *Walkerana* 14:79–85.

Layzer, J.B., and L.M. Madison. 1995. Microhabitat use by freshwater mussels and recommendations for determining their instream flow needs. *Regulated Rivers: Research and Management* 10:329–345.

Layzer, J.B., and L.M. Madison. 1997. Dry tissue weight as an indicator of mussel condition – a cautionary note. Pages 170–175 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Layzer, J.B., and E.M. Scott. 2006. Restoration and colonization of freshwater mussels and fish in a southeastern United States tailwater. *River Research and Applications* 22: 475–491.

Layzer, J.B., et al. 1993. Mussels: The forgotten fauna of regulated rivers – a case study of the Caney Fork River. *Regulated Rivers: Research and Management* 8:63–71.

Layzer, J.B., et al. 2003. Glochidial hosts and other aspects of the life history of the Cumberland pigtoe (*Pleurobema gibberum*). *Southeastern Naturalist* 2:73–84.

Lea, I. 1834. Observations on the naiades, and descriptions of new species of that and other families. *Transactions of the American Philosophical Society* 5(New Series):63–123.

Lea, I. 1870. *A synopsis of the family Unionidae*. 4th ed. Henry C. Lea, Philadelphia, Pennsylvania, USA.

Lee, D.S., et al., editors. 1980. *Atlas of North American freshwater fishes*. North Carolina State Museum of Natural History, Raleigh, USA.

Lee, W.S. 1886. How the muskrat opens the *Unio*. *Journal of the Trenton Natural History Society* 1:8.

Lefevre, G., and W.C. Curtis. 1910. Reproduction and parasitism in the Unionidae. *Journal of Experimental Zoology* 9:79–115.

Lefevre, G., and W.C. Curtis. 1911. Metamorphosis without parasitism in the Unionidae. *Science* 33:863–865.

Lefevre, G., and W.C. Curtis. 1912. Studies on the reproduction and artificial propagation of fresh-water mussels. *Bulletin of the Bureau of Fisheries* 30:105–201.

Leff, L.G., et al. 1990. Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicula fluminea* and *Elliptio complanata*, in a coastal plain stream. *Freshwater Biology* 24:409–416.

Leidy, J. 1887. Biographical notice of Issac Lea, LL.D. *Proceedings of the American Philosophical Society* 24:400–403.

Lellis, W.A., and T.L. King. 1998. Release of metamorphosed juveniles by the green floater, *Lasmigona subviridis*. *Triannual Unionid Report* 16:23 (http://ellipse.inhs.uiuc.edu/FMCS/TUR/default.html).

Levine, T.D. 2009. Consequences of life history variation in freshwater mussels: Demography and host relationships. Dissertation, Miami University, Oxford, Ohio, USA.

Levine, T.D., et al. 2009. Parasitism of mussel gills by dragonfly nymphs. *American Midland Naturalist* 162:1–6.

Lewis, J. 1868. Remarks on some of the Mollusca of the valley of the Mohawk. *American Journal of Conchology* 4:241–245.

Lewis, J.B. 1984. Comparative respiration in two species of freshwater unionid mussels (Bivalvia). *Malacological Review* 17:101–102.

Lewis, J.B., and P.N. Riebel. 1984. The effect of substrate on burrowing in freshwater mussels (Unionidae). *Canadian Journal of Zoology* 62:2023–2025.

Lillie, F.R. 1895. The embryology of the Unionidae: A study in cell lineage. *Journal of Morphology* 10:1–100.

Liu, H.-P., et al. 1996. Paternal mitochondrial DNA differentiation far exceeds maternal mitochondrial DNA and allozyme differentiation in the freshwater mussel, *Anodonta grandis grandis*. *Evolution* 50:952–957.

Long, K. 1981. Happy holidays: Decoration Day and the Fourth of July. *Bittersweet* 8:28–33 (http://thelibrary.springfield.missouri.org/lochist/periodicals/bittersweet/su81c.htm).

Lu, P., and R.L. Metcalfe. 1975. Environmental fate and biodegradability of benzene derivatives as studied in a model aquatic ecosystem. *Environmental Health Perspectives* 10:269–284.

Ludsin, S.A., et al. 2001. Life after death: Nutrient controls drive fish species richness, rehabilitation. *Ecological Applications* 11:731–746.

Luo, M. 1993. Host fish of four species of freshwater mussels and development of an immune response. Thesis, Tennessee Technological University, Cookeville, Tennessee, USA.

Luttikhuizen, P.C., and J. Drent. 2008. Inheritance of predominantly hidden shell colours in *Macoma balthica* (L.) (Bivalvia:Tellinidae). *Journal of Molluscan Studies* 74:363–371.

Lutz, R.A., and G.R. Clark. 1984. Seasonal and geographic variation in the shell microstructure of a salt-marsh bivalve (*Geukensia demissa* (Dillwyn)). *Journal of Marine Research* 42:943–956.

Lutz, R.A., and D.C. Rhoads. 1977. Anaerobiosis and a theory of growth line formation. *Science* 198:1222–1227.

Lydeard, C., and K. Roe. 1998. Phylogenetic systematics: The missing ingredient in the conservation of freshwater unionid bivalves. *Fisheries* 23:16–17.

Lyman, R.L. 1980. Freshwater bivalve molluscs and southern plateau prehistory: A discussion and description of three genera. *Northwest Science* 54:121–137.

Lyman, R.L. 1984. A model of large freshwater clam exploitation in the prehistoric southern Columbia Plateau culture area. *Northwest Anthropological Research Notes* 18:97–107.

Lynn, J.W. 1994. The ultrastructure of the sperm and motile spermatozeugmata released from the freshwater mussel *Anodonta grandis* (Mollusca, Bivlavia, Unionidae). *Canadian Journal of Zoology* 72:1452–1461.

Lyon, G.S., and E.D. Stein. 2009. How effective has the Clean Water Act been at reducing pollutant mass emissions to the Southern California Bight over the past 35 years? *Environmental Monitoring and Assessment* 154:413–426.

Mackie, G.L. 1984. Bivalves. Pages 351–418 *in* A.S. Tompa, et al., editors. *The Mollusca.* Vol. 7. *Reproduction*. Academic Press, Orlando, Florida, USA.

Mackie, G.L., and L.A. Flippance. 1983. Relationships between buffering capacity of water and the size and calcium content of freshwater mollusks. *Freshwater Invertebrate Biology* 2:48–55.

Mackie, G.L., and J.M. Topping. 1988. Historical changes in the unionid fauna of the Sydenham River watershed and downstream changes in shell morphometrics of three common species. *Canadian Field-Naturalist* 102:617–626.

Madson, J. 1985. Mississippi shell game. *Audubon* 87:46–69.

Magurran, A.E. 2004. *Measuring biological diversity*. Blackwell Science, Oxford, UK.

Mann C.C. 2005. *1491: New revelations of the Americas before Columbus*. Knopf Press, New York, USA.

Manning, D. 1989. Freshwater mussels (Unionidae) of the Hatchie River, a tributary to the Mississippi River, in west Tennessee. *Sterkiana* 72:11–18.

Margraf, F.J., and C.T. Knight. 2002. Evaluation of fish sampling using rotenone in a navigation lock. *Fisheries Research* 55:297–305.

Marking, L.L., and T.D. Bills. 1980. Acute effects of silt and sand sedimentation on freshwater mussels. Pages 204–211 *in* J.L. Rassmussen, editor. *Proceedings of the symposium on Upper Mississippi River bivalve mollusks.* Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Martel, A.L., and J.S. Lauzon-Guay. 2005. Distribution and density of glochidia of the freshwater mussel *Anodonta kennerlyi* on fish hosts in lakes of the temperate rain forest of Vancouver Island. *Canadian Journal of Zoology* 83:419–431.

Martel, A.L., et al. 2001. Decline and regional extirpation of freshwater mussels (Unionidae) in a small river system invaded by *Dreissena polymorpha*: The Rideau River, 1993–2000. *Canadian Journal of Zoology* 79:2181–2191.

Matteson, M.R. 1948. Life history of *Elliptio complanatus* (Dillwyn, 1817). *American Midland Naturalist* 40:690–723.

Matteson, M.R. 1955. Studies on the natural history of the Unionidae. *American Midland Naturalist* 53:126–145.

Matthews, W.J. 1998. *Patterns in freshwater fish ecology.* Kluwer, Boston, Massachusetts, USA.

Matthews, W.J., and H.W. Robison. 1998. Influence of drainage connectivity, drainage area and regional species richness on fishes of the Interior Highlands in Arkansas. *American Midland Naturalist* 139:1–19.

Matthews, W.J., et al. 2005. Southern Plains Rivers. Pages 282–325 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America.* Elsevier, Burlington, Massachusetts, USA.

Mattingly, R.L., et al. 1993. Channelization and levee construction in Illinois: Review and implications for management. *Environmental Management* 17:781–795.

Mayden, R.L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. *Systematic Zoology* 37:329–355.

McCorkle, S., et al. 1979. Rhythms of activity and oxygen consumption in the common pond clam, *Ligumia subrostrata* (Say). *Canadian Journal of Zoology* 57:1960–1964.

McCune, B., and J.B. Grace. 2002. *Analysis of ecological communities.* MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., and M.J. Mefford. 1999. *PC-ORD: Multivariate analysis of ecological data.* MjM Software Design, Gleneden Beach, Oregon, USA.

McDonald, A., et al. 2004. Rivers of dreams: On the gulf between theoretical and practical aspects of an upland river restoration. *Transactions of the Institute of British Geographers* 29:257–281.

McGregor, S.W. 2002. The mussels of Muscle Shoals. *Alabama Heritage Magazine* 64:16–23.

McGregor, S.W., and W.R. Haag. 2004. Freshwater mussels (Bivalvia: Unionidae) and habitat conditions in the upper Tombigbee River system, Alabama and Mississippi, 1993–2001. Geological Survey of Alabama Bulletin 176.

McGregor, S.W., and D.N. Shelton. 1995. A qualitative assessment of the unionid fauna of the headwaters of the Paint Rock and Flint rivers of north Alabama and adjacent areas of Tennessee, 1995. Geological Survey of Alabama, Tuscaloosa, USA.

McIntyre, S.C. 1993. Reservoir sedimentation rates linked to long-term changes in agricultural land use. *Journal of the American Water Resources Association* 29:487–495.

McKerall, W.R. 1925. History of Muscle Shoals with views of Wilson Dam. *Florence Herald*, Florence, Alabama, USA.

McLachlan, A., et al. 1995. Adaptations of bivalves to different beach types. *Journal of Experimental Marine Biology and Ecology* 187:147–160.

McMahon, R.F. 1982. The occurrence and spread of the introduced Asiatic freshwater clam, *Corbicula fluminea* (Müller), in North America: 1924–1982. *Nautilus* 96:134–141.

McMahon, R.F., and A.E. Bogan. 2001. Mollusca:Bivalvia. Pages 321–429 *in* J.H. Thorp and A.P. Covich, editors. *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, California, USA.

McMurray, S.E., et al. 1999. Recruitment in a freshwater unionid (Mollusca:Bivalvia) community downstream of Cave Run Lake in the Licking River, Kentucky. *American Malacological Bulletin* 15:57–63.

Meijer, M.-L., et al. 1990. Impact of cyprinids on zooplankton and algae in ten drainable ponds. *Hydrobiologia* 191:275–284.

Menge, B.A. 1974. Effect of wave action and competition on brooding and reproductive effort in the seastar, *Leptasterias hexactis*. *Ecology* 55:84–93.

Mettee, M.F., et al. 1996. *Fishes of Alabama*. Oxmoor House, Birmingham, Alabama, USA.

Meyers, T.R., et al. 1980. Glochidiosis of salmonid fishes. IV. Humoral and tissue responses of Coho and Chinook salmon to experimental infection with *Margaritifera margaritifera* (L.) (Pelecypoda: Margaritanidae). *Journal of Parasitology* 66:274–281.

Michaelson, D.L., and R.J. Neves. 1995. Life history and habitat of the endangered dwarf wedgemussel *Alasmidonta heterodon* (Bivalvia:Unionidae). *Journal of the North American Benthological Society* 14:324–340.

Michaux, F.A. 1805. Travels to the west of the Allegheny Mountains. Pages 188-195 *in* R. G. Thwaites, editor. *Early western travels 1748–1846*. Vol. 3. A.H. Clark, Cleveland, Ohio, USA.

Milam, C.D., et al. 2000. Reintroduction of native freshwater mussels using in vivo and in vitro propagation techniques. Pages 53–61 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Milam, C.D., et al. 2005. Acute toxicity of six freshwater mussel species (glochidia) to six chemicals: Implications for daphnids and *Utterbackia imbecillis* as surrogates for protection of freshwater mussels (Unionidae). *Archives of Environmental Contamination and Toxicology* 48:166–173.

Miller, A.C., and B.S. Payne. 1988. The need for quantitative sampling to characterize size demography and density of freshwater mussel communities. *American Malacological Bulletin* 6:49–54.

Miller, A.C., and B.S. Payne. 1993. Qualitative versus quantitative sampling to evaluate population and community characteristics at a large-river mussel bed. *American Midland Naturalist* 130:133–145.

Miller, A.C., and B.S. Payne. 1997. Density and size demography of newly established populations of *Dreissena polymorpha* in the U.S. inland waterway system. Pages 99–116 *in* F.M. D'Itri, editor. *Zebra mussels and aquatic nuisance species*. Lewis, Boca Raton, Florida, USA.

Miller, A.C., and B.S. Payne. 1998. Effects of disturbances on large-river mussel assemblages. *Regulated Rivers: Research and Management* 14:179–190.

Miller, A.C., and B.S. Payne. 2006. A retrospective analysis of a large-scale endangered species translocation project. *Environmental Practice* 8:115–124.

Miller, A.C., et al. 1984. Changes in the naiad fauna of the Cumberland River below Lake Cumberland in central Kentucky. *Nautilus* 98:107–110.

Miller, A.C., et al. 1986. Description of the habitat of the endangered mussel *Plethobasus cooperianus*. *Nautilus* 100:14–18.

Miller, A.C., et al. 1992a. Characterization of a dense mussel community (Unionidae) in the Big Sunflower River, Sharkey County, Mississippi. *Journal of the Mississippi Academy of Sciences* 37:8–11.

Miller, A.C., et al. 1992b. Characterization of a freshwater mussel (Unionidae) community immediately downriver of Kentucky Lock and Dam in the Tennessee River. *Transactions of the Kentucky Academy of Science* 53:154–161.

Miller, E.J., and S.T. Lynott. 2006. Increase of unionid mussel populations in the Verdigris River, Kansas, from 1991 to 2003. *Southeastern Naturalist* 5:383–392.

Miller, E.J., and T.D. Mosher. 2008. Commercial harvest and status of a freshwater mussel (Threeridge *Amblema plicata*) in Kansas. *Transactions of the Kansas Academy of Science* 111:118–124.

Minckley, W.L., et al. 1986. Geography of western North American freshwater fishes: Description and relationships to intra-continental tectonism. Pages 519–613 *in* C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley, New York, USA.

Moles, K.R., and J.B. Layzer. 2008. Reproductive ecology of *Actinonaias ligamentina* (Bivalvia: Unionidae) in a regulated river. *Journal of the North American Benthological Society* 27:212–222.

Morales, Y., et al. 2006a. Effects of substrate and hydrodynamic conditions on the formation of mussel beds in a large river. *Journal of the North American Benthological Society* 25:664–676.

Morales, Y., et al. 2006b. Mussel dynamics model: A hydroinformatics tool for analyzing the effects of different stressors on the dynamics of freshwater mussel communities. *Ecological Modelling* 197:448–460.

Morey, D.F., and G.M. Crothers. 1998. Clearing up clouded waters: Palaeoenvironmental analysis of freshwater mussel assemblages from the Green River shell middens, western Kentucky. *Journal of Archaelogical Science* 25:907–926.

Morgan, A., et al. 1997. Feasibility of reintroducing threatened and endangered mussels into Shoal Creek in Alabama and Tennessee. Pages 196–204 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Morley, N.J. 2010. Interactive effects of infectious diseases and pollution in aquatic mollusks. *Aquatic Toxicology* 96:27–36.

Morris, T.J., and L.D. Corkum. 1996. Assemblage structure of freshwater mussels (Bivalvia: Unionidae) in rivers with grassy and forested riparian zones. *Journal of the North American Benthological Society* 15:576–586.

Morris, T.J., and L.D. Corkum. 1999. Unionid growth patterns in rivers of differing riparian vegetation. *Freshwater Biology* 42:59–68.

Morrison, J.P.E. 1942. Preliminary report on mollusks found in the shell mounds of the Pickwick Landing basin in the Tennessee River valley. *Bureau of American Ethnology Bulletin* 129:337–392.

Morrison, T.W., et al. 1997. Predation on zebra mussels by freshwater drum and yellow perch in western Lake Erie. *Journal of Great Lakes Research* 23:177–189.

Moulton, C.A., et al. 1996. Effects of two cholinesterase-inhibiting pesticides on freshwater mussels. *Environmental Toxicology and Chemistry* 15:131–137.

Moulton, G. (editor). 2002. *The Journals of the Lewis and Clark Expedition*. University of Nebraska Press. Lincoln, USA. University of Nebraska Press/University of Nebraska-Lincoln Libraries-Electronic Text Center, The Journals of the Lewis and Clark Expedition web site: http://lewisandclark journals.unl.edu/.

Moyle, P.B., and B. Vondracek. 1985. Persistence and structure of the fish assemblages in a small California stream. *Ecology* 66:1–13.

Mueller, R.P., et al. 2011. Assessment of the species composition, densities, and distribution of native freshwater mussels along the Benton County shoreline of the Hanford Reach, Columbia River, 2004. Pacific Northwest National Laboratory, Richland, Washington, USA (http://www.pnl.gov/main/publications/ external/technical_reports/PNNL-19933.pdf).

Mulcrone, R.S. 2004. Incorporating habitat characteristics and fish hosts to predict freshwater mussel (Bivalvia:Unionidae) distributions in the Lake Erie drainage, Southeastern Michigan. Dissertation, University of Michigan, Ann Arbor, USA.

Mulvey, M., et al. 1997. Conservation genetics of North American freshwater mussels *Amblema* and *Megalonaias*. *Conservation Biology* 11:868–878.

Murphy, G. 1942. Relationship of the fresh-water mussel to trout in the Truckee River. *California Fish and Game* 28:89–102.

Myers-Kinzie, M., et al. 2001. Occurrence and distribution of freshwater mussels in small streams of Tippecanoe County, Indiana. *Proceedings of the Indiana Academy of Science* 110:141–150.

Naimo, T.J. 1995. A review of the effects of heavy metals on freshwater mussels. *Ecotoxicology* 4:341–362.

Nalepa, T.F., and J.M. Gauvin. 1988. Distribution, abundance, and biomass of freshwater mussels (Bivalvia:Unionidae) in Lake St. Clair. *Journal of Great Lakes Research* 14:411–419.

Nalepa, T.F., et al. 1991. Long-term decline in freshwater mussels (Bivalvia:Unionidae) of the western basin of Lake Erie. *Journal of Great Lakes Research* 17:214–219.

NatureServe. 2010. NatureServe explorer: An online encyclopedia of life. Version 7.0. NatureServe, Arlington, Virginia, USA (http://www.natureserve.org/explorer).

Nduku, W.K., and A.D. Harrison. 1976. Calcium as a limiting factor in the biology of *Biomphalaria pfeifferi* (Krauss) (Gastropoda:Planorbidae). *Hydrobiologia* 49:143–170.

Nedeau, E.J. 2008. *Freshwater mussels and the Connecticut River Watershed*. Connecticut River Watershed Council, Greenfield, Massachusetts, USA.

Nedeau, E.J., et al. 2000. *The freshwater mussels of Maine*. Maine Department of Inland Fisheries and Wildlife, Augusta, USA.

Nedeau, E.J., et al. 2005. Freshwater mussels of the Pacific Northwest. U.S. Fish and Wildlife Service, Vancouver, Washington, USA (http://www.fws.gov/pacific/columbiariver/musselwg.htm).

Nee, S., P.H. Harvey, and P. Cotgreave. 1992. Population persistence and the natural relationship between body size and abundance. Pages 124–136 in O.T. Sandlund, et al., editors. *Conservation of biodiversity for sustainable development*. Scandinavian University Press, Oslo, Norway.

Neel, J.K. 1941. A taxonomic study of *Quadrula quadrula* (Rafinesque). *Occasional Papers of the Museum of Zoology, University of Michigan* 448:1–8.

Neel, J.K., and W.R. Allen. 1964. The mussel fauna of the Upper Cumberland Basin before its impoundment. *Malacologia* 1:427–459.

Negus, C.L. 1966. A quantitative study of growth and production of unionid mussels in the River Thames at Reading. *Journal of Animal Ecology* 35:513–532.

Nelson, D. 1983. Sampling for freshwater mussels. Pages 90–93 *in* A.C. Miller, compiler. *Report of freshwater mollusks workshop*. U.S. Army Engineer Waterways Experimental Station, Vicksburg, Mississippi, USA.

Nelson, J.S., et al. 2004. *Common and scientific names of fishes from the United States, Canada, and Mexico*. Special Publication 29. American Fisheries Society, Bethesda, Maryland, USA.

Neumann, R. 2008. Blue cats, baitfish, and mussels. *In-Fisherman*, February.

Neves, R.J., editor. 1987. *Proceedings of the workshop on die-offs of freshwater mussels in the United States*. Upper Mississippi River Conservation Committee, Davenport, Iowa, USA.

Neves, R.J. 1993. A state-of-the-unionids address. Pages 1–10 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Neves, R.J. 1999. Conservation and commerce: Management of freshwater mussel (Bivalvia: Unionidea) resources in the United States. *Malacologia* 41:461–474.

Neves, R.J. 2004. Propagation of endangered freshwater mussels in North America. *Journal of Conchology Special Publication* 3:69–80.

Neves, R.J., and S.N. Moyer. 1988. Evaluation of techniques for age determination of freshwater mussels (Unionidae). *American Malacological Bulletin* 6:179–188.

Neves, R.J., and M.C. Odom. 1989. Muskrat predation on endangered freshwater mussels in Virginia. *Journal of Wildlife Management* 53:934–941.

Neves, R.J., and J.C. Widlak. 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. *American Malacological Bulletin* 5:1–7.

Neves, R.J., and J.C. Widlak. 1988. Occurrence of glochidia in stream drift and on fishes of the Upper North Fork Holston River, Virginia. *American Midland Naturalist* 119:111–120.

Neves, R.J., et al. 1985. An evaluation of host fish suitability for glochidia of *Villosa vanuxemi* and *V. nebulosa* (Pelecypoda:Unionidae). *American Midland Naturalist* 113:13–19.

Neves, R.J., et al. 1997. Status of aquatic mollusks in the southeastern United States: A downward spiral of diversity. Pages 43–85 *in* G.W. Benz and D.E. Collins, editors. *Aquatic fauna in peril: The southeastern perspective*. Lenz Design and Communications, Decatur, Georgia, USA.

Newton, T.J., et al. 2011. Population assessment and potential functional roles of native mussels in the upper Mississippi River. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21:122–131.

Nichols, S.J., and D. Garling. 2000. Food-web dynamics and trophic-level interactions in a multispecies community of freshwater unionids. *Canadian Journal of Zoology* 78:871–882.

Nichols, S.J., and D.A. Wilcox. 1997. Burrowing saves Lake Erie clams. *Nature* 389:921.

Nichols, S.J., et al. 2001. Lack of surface-associated microorganisms in a mixed species community of freshwater Unionidae. *Journal of Shellfish Research* 20:329–335.

Nichols, S.J., et al. 2005. Pathways of food uptake in native (Unionidae) and introduced (Corbiculidae and Dreissenidae) freshwater bivalves. *Journal of Great Lakes Research* 31:87–96.

Nicklin, L., and M.T. Balas. 2007. Correlation between unionid mussel density and EPA habitat-assessment parameters. *Northeastern Naturalist* 14:225–234.

Nico, L.G., et al. 2005. *Black carp: Biological synopsis and risk assessment of an introduced fish*. Special Publication 32. American Fisheries Society, Bethesda, Maryland.

Norris, R.H. et al. 2012. Analyzing cause and effect in environmental assessments: using weighted evidence from the literature. *Freshwater Science* 31:5–21.

Noss, R.F., et al. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. Biological Report 28. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.

Nowell, L.H., et al. 1999. *Pesticides in stream sediment and aquatic biota*. Lewis, Boca Raton, Florida, USA.

Nunnally, N.R., and E. Keller. 1979. Use of fluvial processes to minimize adverse effects of stream channelization. Report 144. Water Resources Research Institute, University of North Carolina, Charlotte, USA.

Nuttall, C.P. 1969. Coloration. Pages N70–N72 *in* R.C. Moore, editor. *Treatise on invertebrate paleontology,* Part N, Vol. I, *Mollusca 6, Bivalvia*. Geological Society of America and University of Kansas Press, Lawrence, USA.

O'Brien, C., and J. Brim Box. 1999. Reproductive biology and juvenile recruitment of the shinyrayed pocketbook, *Lampsilis subangulata* (Bivalvia: Unionidae) in the Gulf Coastal Plain. *American Midland Naturalist* 142:129–140.

O'Brien, C.A., and J.D. Williams. 2002. Reproductive biology of four freshwater mussels (Bivalvia: Unionidae) endemic to eastern Gulf Coastal Plain drainages of Alabama, Florida, and Georgia. *American Malacological Bulletin* 17:147–158.

O'Connell, M.T., and R.J. Neves. 1999. Evidence of immunological responses by a host fish (*Ambloplites repestris*) and two non-host fishes (*Cyprinus carpio* and *Carassius auratus*) to glochidia of a freshwater mussel (*Villosa iris*). *Journal of Freshwater Ecology* 14: 71–78.

Oesch, R.D. 1995. *Missouri Naiades*. Missouri Department of Conservation, Jefferson City, USA.

O'Foighil, D. 1989. Role of spermatozeugmata in the spawning ecology of the brooding oyster *Ostrea edulis*. *Gamete Research* 24:219–228.

Økland, J. 1983. Factors regulating the distribution of fresh-water snails (Gastropoda) in Norway. *Malacologia* 24:277–288.

Olden, J.D., and R.J. Naiman. 2010. Incorporating thermal regimes into environmental flows assessments: Modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biology* 55: 86–107.

Omonode, R.A., et al. 2010. Soil nitrous oxide emissions in corn following three decades of tillage and rotation treatments. *Soil Science Society of America Journal* 75:152–163.

Ortmann, A.E. 1909a. The breeding season of Unionidae in Pennsylvania. *Nautilus* 22:91–95.

Ortmann, A.E. 1909b. The destruction of the fresh-water fauna in western Pennsylvania. *Proceedings of the American Philosophical Society* 48:90–110.

Ortmann, A.E. 1910. The discharge of the glochidia in the Unionidae. *Nautilus* 24:94–95.

Ortmann, A.E. 1911. A monograph of the najades of Pennsylvania. Parts I and II. *Memoirs of the Carnegie Museum* 4:279–347.

Ortmann, A.E. 1912. Notes upon the families and genera of the najades. *Annals of the Carnegie Museum* 8:222–365.

Ortmann, A.E. 1913. The Alleghenian Divide, and its influence upon the freshwater fauna. *Proceedings of the American Philosophical Society* 52:287–390.

Ortmann, A.E. 1914. Studies in najades. (cont.). *Nautilus* 28:65–69.

Ortmann, A.E. 1915. Studies in najades (cont.). *Nautilus* 28:106–108.

Ortmann, A.E. 1918a. The anatomy of two African nayades, *Unio caffer* and *Spathawahlbergi*. *Nautilus* 31:75–78.

Ortmann, A.E. 1918b. The nayades (freshwater mussels) of the upper Tennessee drainage. With notes on synonymy and distribution. *Proceedings of the American Philosophical Society* 57:521–626.

Ortmann, A.E. 1919. *A monograph of the naiades of Pennsylvania*. Part III. *Systematic account of the genera and species*. Memoirs of the Carnegie Museum 8. Pittsburgh, Pennsylvania, USA.

Ortmann, A.E. 1920. Correlation of shape and station in freshwater mussels (naiades). *Proceedings of the American Philosophical Society* 59:269–312.

Ortmann, A.E. 1921. South American naiades; a contribution to the knowledge of the freshwater mussels of South America. *Memoirs of the Carnegie Museum* 8:451–670.

Ortmann, A.E. 1924a. The naiad-fauna of Duck River in Tennessee. *American Midland Naturalist* 9:18–62.

Ortmann, A.E. 1924b. Distributional features of naiades in tributaries of Lake Erie. *American Midland Naturalist* 9:101–117.

Ortmann, A.E. 1924c. Mussel Shoals. *Science* 60:565–566.

Ortmann, A.E. 1925. The naiad-fauna of the Tennessee River system below Walden Gorge. *American Midland Naturalist* 9:321–372.

Ortmann, A.E. 1926. The Naiades of the Green River drainage in Kentucky. *Annals of the Carnegie Museum* 17:167–188.

Ortmann, A.E., and B. Walker. 1922. On the nomenclature of certain North American Naiades. *Occasional Papers of the Museum of Zoology, University of Michigan* 112:1–75.

Owen, C.T., et al. 2010. Control of microbial contamination during in vitro culture of larval unionid mussels. *Invertebrate Reproduction and Development* 54:187–193.

Owen, C.T., et al. 2011. Muskrat predation on a diverse unionid mussel community: Impacts of prey species composition, size and shape. *Freshwater Biology* 56:554–564.

Page, L.M., et al. 1997. Aquatic biota. Pages 105–129, 141–142 *in* Illinois Department of Natural Resources Critical Trends Assessment Program. *Embarras River area assessment*. Vol. 3. *Living resources*. Illinois Natural History Survey, Champaign, USA.

Palmer, J.O., and E. Pallant. 2009. Preventing disaster on French Creek, one of the most biologically diverse rivers in North America. Pages 317–312 *in* J. Jones et al., editors. *Threats to global water security*. Springer, Dordrecht, Netherlands.

Pandolfo, T.J., et al. 2010. Upper thermal tolerances of early life stages of freshwater mussels. *Journal of the North American Benthological Society* 29:959–969.

Parker, R.S., et al. 1984. Ecology and reproductive strategy of a South Louisiana freshwater mussel, *Glebula rotundata* (Lamarck) (Unionidae:Lampsilini). *Freshwater Invertebrate Biology* 3:53–58.

Parkos, J.J., et al. 2003. Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 182–192.

Parmalee, P.W. 1967. The fresh-water mussels of Illinois. *Illinois State Museum Popular Science Series* 8:1–108.

Parmalee, P.W., and A.E. Bogan. 1998. *The freshwater mussels of Tennessee*. University of Tennessee Press, Knoxville, USA.

Parmalee, P.W., and W.E. Klippel. 1974. Freshwater mussels as a prehistoric food source. *American Antiquity* 39:421–434.

Parmalee, P.W., and W.E. Klippel. 1982. A relic population of *Obovaria retusa* in the middle Cumberland River, Tennessee. *Nautilus* 96:30–32.

Parmalee, P.W., et al. 1980. Notes on the prehistoric and present status of the naiad fauna of the middle Cumberland River, Smith County, Tennessee. *Nautilus* 94:93–105.

Parmalee, P.W., et al. 1982. Aboriginal and modern freshwater mussel assemblages (Pelecypoda:Unionidae) from the Chickamauga Reservoir, Tennessee. *Brimleyana* 8:75–90.

Paterson, C.G. 1985. Biomass and production of the unionid, *Elliptio complanata* (Lightfoot) in an old reservoir in New Brunswick, Canada. *Freshwater Invertebrate Biology* 4:201–207.

Paterson, C.G., and I.F. Cameron. 1985. Comparative energetics of two populations of the unionid, *Anodonta cataracta* (Say). *Freshwater Invertebrate Biology* 4:79–90.

Pauley, G.B. 1968. Disease of the freshwater mussel, *Margaritifera margaritifera*. *Journal of Invertebrate Pathology* 12:321–328.

Payne, B.S., and A.C. Miller. 1989. Growth and survival of recent recruits to a population of *Fusconaia ebena*. *American Midland Naturalist* 121:99–104.

Payne, B.S., and A.C. Miller. 2000. Recruitment of *Fusconaia ebena* (Bivalvia:Unionidae) in relation to discharge of the lower Ohio River. *American Midland Naturalist* 144: 328–341.

Peacock, E., et al. 2005. Pre-Columbian decline in freshwater mussels coincident with the advent of maize agriculture. *Conservation Biology* 19:547–551.

Pekkarinen, M. 1991. Sperm balls in testes of *Anodonta anatina* in the River Vantaanjoki (southern Finland). *Bivalve Studies in Finland* 1:1–3.

Pelley, J. 2003. Nitrate eyed as an endocrine disruptor. *Environmental Science and Technology* 37:162.

Perles, S.J., et al. 2003. Vertical migration, orientation, aggregation, and fecundity of the freshwater mussel *Lampsilis siliquoidea*. *Ohio Journal of Science* 103:73–78.

Peterson, J.T., et al. 2011. Estimation of mussel population response to hydrologic alteration in a southeastern U.S. stream. *Environmental Management* 48:109–122.

Petranka, J.W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C., USA.

Phelps, H.L. 1994. The Asiatic clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River estuary near Washington, D.C. *Estuaries* 17:614–621.

Pianka, E.R. 1970. On *r*- and *K*- selection. *American Naturalist* 104:592–597.

Pilarczyk, M.M., et al. 2006. Current and recent historical freshwater mussel assemblages in the Gulf Coastal Plain. *Southeastern Naturalist* 5:205–226.

Pilsbry, H.A. 1927. Arnold Edward Ortmann. *Nautilus* 40:100–111.

Pip, E. 2000. The decline of freshwater molluscs in southern Manitoba. *Canadian Field-Naturalist* 114:555–560.

Pipe, R.K., and J.A. Coles. 1995. Environmental contaminants influencing immune function in marine bivalve mollusks. *Fish and Shellfish Immunology* 5:581–595.

Pitzer, D.E. 1989. The original boatload of knowledge down the Ohio River: William Maclure's and Robert Owen's transfer of science and education to the midwest, 1825–1826. *Ohio Journal of Science* 89:128–142.

Poff, N.L., and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76:606–627.

Poff, N.L., and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805–1818.

Poff, N.L., et al. 1997. The natural flow regime. *Bioscience* 47:769–784.

Poff, N.L., et al. 2003. River flows and water wars: Emerging science for environmental decision making. *Frontiers in Ecology and the Environment* 1:298–306.

Poff, N.L., et al. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America* 104:5732–5737.

Poly, W.J. 1997. Habitat, diet, and population structure of the federally endangered palezone shiner, *Notropis albizonatus* Warren and Burr, in Little South Fork (Cumberland River), Kentucky. Thesis, Southern Illinois University, Carbondale, USA.

Poole, K.E., and J.A. Downing. 2004. Relationship of declining mussel biodiversity to stream-reach and watershed characteristics in an agricultural landscape. *Journal of the North American Benthological Society*, 23:114–125.

Porter, C.M. 1986. *The eagle's nest: Natural history and America ideas, 1812–1842*. University of Alabama Press, Tuscaloosa, USA.

Posey, W.R. 1997. Location, species composition and community estimates for mussel beds in the St. Francis and Ouachita Rivers in Arkansas. Thesis, Arkansas State University, Little Rock, USA.

Post, R.H. 1938. The subsistence quest. Pages 9–34 *in* L. Spier, editor. *The Sinkaietk or Southern Okanogan of Washington*. General Series in Anthropology 6. George Banta, Menasha, Wisconsin, USA.

Pou-Rovira, Q., et al. 2009. Presence of the alien Chinese pond mussel *Anodonta woodiana* (Lea, 1834) (Bivalvia, Unionidae) in the Iberian Peninsula. *Graellsia* 65: 67–70.

Power, M.E., et al. 1988. Biotic and abiotic controls in river and stream communities. *Journal of the North American Benthological Society* 7:456–479.

Powers, S.L., et al. 2004. Conservation genetics of the ashy darter, *Etheostoma cinereum* (Percidae:subgenus *Allohistium*), in the Cumberland and Tennessee Rivers of the southeastern United States. *Copeia* 2004:632–637.

Prezant, R.S., and K. Chalermwat. 1984. Flotation of the bivalve *Corbicula fluminea* as a means of dispersal. *Science* 225:1491–1493.

Price, J.E., and C.B. Eads. 2011. Brooding patterns in three freshwater mussels of the genus *Elliptio* in the Broad River in South Carolina. *American Malacological Bulletin* 29:121–126.

Pritchard, J. 2001. An historical analysis of mussel propagation and culture: Research performed at the Fairport Biological Station. Report to US Army Corp of Engineers, Rock Island District, Rock Island, Illinois, USA (http://www.fws.gov/ midwest/mussel/documents.html).

Pynnönen, K.S., and J. Huebner. 1995. Effects of periodic low pH exposure on the valve movements of the freshwater bivalve *Anodonta cygnea* L. *Water Research* 9:2579–2582.

Raab, L.M. 1992. An optimal foraging analysis of pre-Columbian shellfish collecting on San Clemente Island, California. *Journal of Ethnobiology* 12:63–80.

Rafinesque, C.S. 1818. Discoveries in natural history, made during a journey through the Western region of the United States. *American Monthly Magazine and Critical Review* 3:354–355 [reprinted in Binney, W.G., and G.W. Tryon. 1864. *The complete writings of Constantine Smaltz Rafinesque on recent and fossil conchology*. H. Bailliere, New York, USA].

Rafinesque, C.S. 1820. Monographie des coquilles bivalves fluviatiles de la Riviere Ohio, contenant douze genres et soixante-huit especes. *Annales Générales des SciencesPhysiques, Bruxelles* 5:287–322 [translated by Poulson, C.A. 1832. *A monograph of the fluviatile bivalve shells of the River Ohio containing twelve genera and sixty-eight species*. J. Dobson, Philadelphia, Pennsylvania, USA].

Rafinesque, C.S. 1831. *Continuation of a monograph of the bivalve shells of the river Ohio and other rivers of the western states*. Published privately in Philadelphia, Pennsylvania, USA [reprinted in Binney, W.G., and G.W. Tryon. 1864. *The complete writings of Constantine Smaltz Rafinesque on recent and fossil conchology*. H. Bailliere, New York, USA].

Raikow, D.F., and S.K. Hamilton. 2001. Bivalve diets in Midwestern U.S. stream: A stable isotope enrichment study. *Limnology and Oceanography* 46:514–522.

Randklev, C.R., et al. In press. False spike, *Quadrula Mitchelli* (Bivalvia: Unionoidea), is not extinct: first account of a live population in over 30 years. *American Malacological Bulletin*.

Rashleigh, B. 2008. Nestedness in riverine mussel communities: Patterns across sites and fish hosts. *Ecography* 31:612–619.

Rashleigh, B., and D.L. DeAngelis. 2007. Conditions for coexistence of freshwater mussel species via partitioning of fish host resources. *Ecological Modelling* 201:171–178.

Raulerson, C.L. 1960. The ecology of a small Georgia mountain stream, with special emphasis on the mussel, *Elliptio hopetonensis Lea*. Thesis, Emory University, Atlanta, Georgia, USA.

Ray, R.A. 1999. Abundance, diversity, and habitat preference of freshwater mussels (Bivalvia: Unionoidea) in Sulphur Fork Creek and lower Red River, Tennessee and Kentucky. Thesis, Austin Peay State University, Clarksville, Tennessee, USA.

Relyea, R.A. 2005. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. *Ecological Applications* 15:618–627.

Remington, P.S., Jr., and W.J. Clench. 1925. Vagabonding for shells. *Nautilus* 38:127–143.

Renwick, W.H., et al. 2005. Trends in recent reservoir sedimentation rates in southwestern Ohio. *Journal of Soil and Water Conservation* 60:72–79.

Resh, V.H., et al. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433–455.

Reuling, F.H. 1919. Acquired immunity to an animal parasite. *Journal of Infectious Diseases* 24:337–346.

Rhoads, D.C., and G. Pannella. 1970. The use of molluscan shell growth patterns in ecology and paleoecology. *Lethaia* 3:143–161.

Rhoads, S.N. 1899. On a recent collection of Pennsylvanian mollusks from the Ohio River system below Pittsburg. *Nautilus* 12:133–138.

Ricciardi, A., and H.J. MacIsaac. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology and Evolution* 15:62–65.

Ricciardi, A., and J.B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. *Conservation Biology* 13:1220–1222.

Ricciardi, A., and D. Simberloff. 2009. Assisted colonization is not a viable conservation strategy. *Trends in Ecology and Evolution* 24:248–253.

Ricciardi, A., et al. 1995. Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1449–1461.

Ricciardi, A., et al. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* 67:613–619.

Richard, P.E., et al. 1991. Structure of the gill during reproduction in the unionids *Anodonta grandis, Ligumia subrostrata*, and *Carunculina parva texasensis*. *Canadian Journal of Zoology* 69:1744–1754.

Richardson, C.A. 1989. An analysis of the microgrowth bands in the shell of the common mussel *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom* 69:477–491.

Richter, B.D., et al. 2003. Ecologically sustainable water management: Managing river flows for ecological integrity. *Ecological Applications* 13:206–224.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Rickleffs, R.E., and G.L. Miller. 2000. *Ecology*. 4th ed. W.H. Freeman, New York, USA.

Riusech, F.A., and M.C. Barnhart. 2000. Host suitability and utilization in *Venustaconcha ellipsiformis* and *Venustaconcha pleasii* (Bivalvia:Unionidae) from the Ozark Plateaus. Pages 83–91 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Roberts, A.D., and M.C. Barnhart. 1999. Effects of temperature, pH, and CO_2 on transformation of the glochidia of *Anodonta suborbiculata* on fish hosts in vitro. *Journal of the North American Benthological Society* 18:477–487.

Roberts, A.D., et al. 2009. An assessment of freshwater mussel (Bivalvia: Margaritiferidae and Unionidae) populations and heavy metal sediment contamination in the Big River, Missouri. Final Report to U.S. Fish and Wildlife Service, Columbia, Missouri (http://www.fws.gov/midwest/semonrda/).

Roberts, J., et al. 1995. Effect of carp, *Cyprinus carpio*, an exotic benthivorous fish, on aquatic plants and water quality in experimental ponds. *Marine and Freshwater Research* 46:1171–1180.

Robinson, J.V., and G.A. Wellborn. 1988. Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea*: Fish predation effects. *Oecologia* 77:445–452.

Robison, H.W. 1986. Zoogeographic implications of the Mississippi River basin. Pages 267–285 *in* C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley, New York, USA.

Robison, H.W., and T.M. Buchanan. 1988. *Fishes of Arkansas*. University of Arkansas Press, Fayetteville, USA.

Rodland, D.L., et al. 2009. Changes in gape frequency, siphon activity, and thermal response in the freshwater bivalves *Anodonta cygnea* and *Margaritifera falcata*. *Journal of Molluscan Studies* 75:51–57.

Roe, K.J., and P.D. Hartfield. 2005. *Hamiota*, a new genus of freshwater mussel (Bivalvia: Unionidae) from the Gulf of Mexico drainages of the southeastern United States. *Nautilus* 119:1–10.

Roe, K.J., and W.R. Hoeh. 2003. Systematics of freshwater mussels (Bivalvia: Unionoida). Pages 91–122 *in* C. Lydeard and D.R. Lindberg, editors. *Molecular systematics and phylogeography of mollusks*. Smithsonian Books, Washington, D.C., USA.

Roe, K.J., and C. Lydeard. 1998a. Species delineation and the identification of evolutionary significant units: Lessons from the freshwater mussel genus *Potamilus* (Bivalvia:Unionidae). *Journal of Shellfish Research* 17:1359–1363.

Roe, K.J., and C. Lydeard. 1998b. Molecular systematics of the freshwater mussel genus *Potamilus* (Bivalvia:Unionidae). *Malacologia* 39:195–205.

Roe, K.J., et al. 1997. Identification of a fish host of the inflated heelsplitter *Potamilus inflatus* (Bivalvia:Unionidae) with a description of its glochidium. *American Midland Naturalist* 138:48–54.

Roe, K.L., et al. 2001. Phylogeographic analysis of the threatened and endangered superconglutinate-producing mussels of the genus *Lampsilis* (Bivalvia:Unionidae). *Molecular Ecology* 10:2225–2234.

Rogers, C.L., and R.V. Dimock. 2003. Acquired resistance of bluegill sunfish *Lepomis Macrochirus* to glochidia larvae of the freshwater mussel *Utterbackia imbecillis* (Bivalvia:Unionidae) after multiple infections. *Journal of Parasitology* 89:51–56.

Rogers, S.O., et al. 2001. Life history and population biology of the endangered tan riffleshell (*Epioblasma florentina walkeri*) (Bivalvia:Unionidae). *Journal of the North American Benthological Society* 20:582–594.

Rogers-Lowery, C.L., and R.V. Dimock. 2006. Encapsulation of attached ectoparasitic glochidia larvae of freshwater mussels by epithelial tissue on fins of naïve and resistant host fish. *Biological Bulletin* 210:51–63.

Rohlf, F.J., and R.R. Sokal. 1969. *Statistical tables*. W.H. Freeman, San Francisco, California, USA.

Rooke, J.G., and G.L. Mackie. 1984. Mollusca of six low-alkalinity lakes in Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 41:777–782.

Rosenberg, D.M., et al. 2005. Nelson and Churchill River basins. Pages 852–901 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America*. Elsevier, Burlington, Massachusetts, USA.

Rosenberg, G.D., and M.T. Henschen. 1986. Sediment particles as a cause of nacre staining in the freshwater mussel, *Amblema plicata* (Say) (Bivalvia:Unionidae). *Hydrobiologia* 135:167–178.

Rosenzweig, J.A. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.

Rosewater, J. 1959. Calvin Goodrich; a bibliography and catalogue of his species. *Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard* 2:189–208.

Ross, S.T. 2001. *The inland fishes of Mississippi*. University Press of Mississippi, Oxford, Mississippi, USA.

Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population size. *Conservation Biology* 5:325–329.

Rypel, A.L., and J.B. Mitchell. 2007. Summer nocturnal patterns in freshwater drum (*Aplodinotus grunniens*). *American Midland Naturalist* 157:230–234.

Rypel, A.L., et al. 2008. Validation of annual growth rings in freshwater mussel shells using cross dating. *Canadian Journal of Fisheries and Aquatic Sciences* 65:2224–2232.

Rypel, A.L., et al. 2009. Pervasive hydrologic effects on freshwater mussels and riparian trees in southeastern floodplain ecosystems. *Wetlands* 29:497–504.

Salbenblatt, J.A., and A.L. Edgar. 1964. Valve activity in fresh-water pelecypods. *Papers of the Michigan Academy of Science, Arts, and Letters* 49:177–186.

Saunders, D.L., et al. 2002. Freshwater protected areas: Strategies for conservation. *Conservation Biology* 16:30–41.

Savazzi, E., and Y. Peiyi. 1992. Some morphological adaptations in freshwater bivalves. *Lethaia* 25:195–209.

Savidge, T.W. 2006. Freshwater mussel surveys of the Pee Dee River basin in South Carolina. Report by the Nature Conservancy, Columbia, South Carolina, USA (http://www.nature.org/wherewework/northamerica/states/southcarolina/science/).

Say, T. 1830–1838. *American conchology, or descriptions of the shells of North America. Illustrated by coloured figures from original drawings executed from nature, Parts 1–7*. New Harmony, Indiana, USA [reprinted in W.G. Binney, editor. 1858. *The complete writings of Thomas Say on the conchology of the United States*. H. Bailliere, New York, USA].

Scarpino, P.V. 1985. *Great River: An environmental history of the upper Mississippi, 1890-1950*. University of Missouri Press, Columbia, USA.

Schanzle, R.W., and K.S. Cummings. 1991. A survey of the freshwater mussels (Bivalvia: Unionidae) of the Sangamon River basin, Illinois. *Illinois Natural History Survey Biological Notes* 137:1–25.

Schanzle, R.W., et al. 2004. The freshwater mussels (Bivalvia:Unionidae) of the Fox River basin, Illinois and Wisconsin. *Illinois Natural History Survey Biological Notes* 141:1–35.

Schlosser, I.J. 1982a. Fish community structure and function along two habitat gradients in a headwater stream. *Ecological Monographs* 52:395–414.

Schlosser, I.J. 1982b. Trophic structure, reproductive success, and growth rate of fishes in a natural and modified headwater stream. *Canadian Journal of Fisheries and Aquatic Sciences* 39:968–978.

Schlosser, I.J. 1990. Environmental variation, life history attributes, and community structure instream fishes: Implications for environmental management and assessment. *Environmental Management* 14:621–628.

Schmerfeld, J. 2006. Reversing a textbook tragedy. *Endangered Species Bulletin* 31:12–13.

Schmidt, R.E. 1986. Zoogeography of the northern Appalachians. Pages 137–159 *in* C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley, New York, USA.

Schoener, T.W. 1989. The ecological niche. Pages 79–113 *in* J.M. Cherret, editor. *Ecological concepts*. Blackwell Science, Oxford, UK.

Scholla, M.H., et al. 1987. Evaluation of a mussel die-off in the Tennessee River. Pages 144–151 *in* R.J. Neves, editor. *Proceedings of the workshop on die-offs of freshwater mussels in the United States*. Upper Mississippi River Conservation Committee, Davenport, Iowa, USA.

Schöne, B.R., et al. 2004. A 217-year record of summer air temperature reconstructed from freshwater pearl mussels (*M. margaritifera*, Sweden). *Quaternary Science Reviews* 23:1803–1816.

Schöne, B.R., et al. 2005a. Mutvei's solution: An ideal agent for resolving microgrowth structures in biogenic carbonates. *Palaeogeography, Palaeoclimatology, Palaeoecology* 228:149–166.

Schöne, B.R., et al. 2005b. Daily growth rates in shells of *Arctica islandica*: Assessing subseasonal environmental controls on a long-lived bivalve mollusk. *Palaios* 20:78–92.

Schöne, B.R., et al. 2005c. Climate records from a bivalved Methusaleh (*Arctica islandica*, Mollusca; Iceland). *Palaeogeography, Palaeoclimatology, Palaeoecology* 228:130–148.

Schoof, R. 1980. Environmental impact of channel modification. *Water Resources Bulletin* 16:697–701.

Schwalb, A.N., and M.T. Pusch. 2007. Horizontal and vertical movements of unionid mussels in a lowland river. *Journal of the North American Benthological Society* 26:261–272.

Schwartz, J.S., et al. 2011. Use of fish functional traits to associate instream suspended sediment transport metrics with biological impairment. *Environmental Monitoring and Assessment* 179:347–369.

Schwartz, M.L., and R.V. Dimock. 2001. Ultrastructural evidence for nutritional exchange between brooding unionid mussels and their glochidia larvae. *Invertebrate Biology* 120:227–236.

Scruggs, G.D. 1960. Status of fresh-water mussel stocks in the Tennessee River. *U.S. Fish and Wildlife Sevice Special Scientific Report* 370:1–41.

Seager, R., et al. 2009. Drought in the southeastern United States: Causes, variability over the last millennium, and the potential for future hydroclimate change. *Journal of Climate* 22:5021–5045.

Seilacher, A. 1972. Divaricate patterns in pelecypod shells. *Lethaia* 5:325–343.

Seilacher, A. 1990. Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology* 3:289–311.

Sepkoski, J.J., and M.A. Rex. 1974. Distribution of freshwater mussels: Coastal rivers as biogeographic islands. *Systematic Zoology* 23:165–188.

Serb, J.M. 2006. Discovery of genetically distinct sympatric lineages in the freshwater mussel *Cyprogenia aberti* (Bivalvia:Unionidae). *Journal of Molluscan Studies* 72:425–434.

Serb, J.M., et al. 2003. Molecular systematics of the North American freshwater bivalve genus *Quadrula* (Unionidae: Ambleminae) based on mitochondrial ND1 sequences. *Molecular Phylogenetics and Evolution* 28:1–11.

Sethi, S.A., et al. 2004. Response of unionid mussels to dam removal in Koshkonong Creek, Wisconsin. *Hydrobiologia* 525:157–165.

Shadoan, M.K., and R.V. Dimock. 2000. Differential sensitivity of hooked (*Utterbackia imbecillis*) and hookless (*Megalonaias nervosa*) glochidia to chemical and mechanical stimuli (Bivalvia: Unionidae). Pages 93–102 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.

Shaler, N.S. 1887. Notes on the *Taxodium distichium*, or bald cypress. *Memoirs of the Museum of Comparative Zoology* 16:1–15.

Sharpe, A.J., and E.G. Nichols. 2007. Use of stable nitrogen isotopes and permeable membrane devices to study what factors influence freshwater mollusk survival in the Conasauaga River. *Environmental Monitoring and Assessment* 132:275–295.

Sheehan, R.J., et al. 1989. Fate of freshwater mussels transplanted to formerly polluted reaches of the Clinch and North Fork Holston rivers, Virginia. *Journal of Freshwater Ecology* 5:139–149.

Sheldon, A.L. 1987. Rarity: Patterns and consequences for stream fishes. Pages 203–209 *in* W.J. Matthews and D.C. Heins, editors. *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman, USA.

Shelton, D.N. 1997. Observations on the life history of the Alabama pearl shell, *Margaritifera marrianae* R.I. Johnson, 1983. Pages 26–29 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Shelton, D.N. 2006. A survey of the freshwater mussels (Bivalvia: Unionacea) of the Mobile River Delta. Report to the Nature Conservancy of Alabama, Birmingham, USA.

Shields, F.D., et al. 2000. Cyclic perturbation of lowland river channels and ecological response. *Regulated Rivers: Research and Management* 16:307–325.

Shields, F.D., et al. 2007. Can warmwater streams be rehabilitated using watershed-scale standard erosion control measures alone? *Environmental Management* 40:62–79.

Shira, A.F. 1913. The mussel fisheries of Caddo Lake and the Cypress and Sulphur rivers of Texas and Louisiana. *U.S. Bureau of Fisheries Economic Circular* 6:1–10.

Shira, A.F. 1919. The necessity of state legislation in the conservation of fresh-water mussels. *Transactions of the American Fisheries Society* 49:38–41.

Shirey, P.D., and G.A. Lamberti. 2010. Assisted colonization under the U.S. Endangered Species Act. *Conservation Letters* 3:45–52.

Shuman, J.R. 1995. Environmental considerations for assessing dam removal alternatives for river restoration. *Regulated Rivers: Research and Management* 11:249–261.

Sickel, J.B. 1980. Correlation of unionid mussels with bottom sediment composition in the Altamaha River, Georgia. *Bulletin of the American Malacological Union* 1980:10–13.

Sickel, J.B., and C.C. Chandler. 1982. Commercial mussel and Asiatic clam fishery evaluation. Report for project 2-367-R to Kentucky Department of Fish and Wildlife Resources, Frankfort, USA.

Sickel, J.B., and C.C. Chandler. 1996. Unionid fauna of the lower Cumberland River from Barkley Dam to the Ohio River, Kentucky (Mollusca: Bivalvia: Unionidae). *Transactions of the Kentucky Academy of Science* 57:33–46.

Sietman, B.E., et al. 1999. Colonization of bedrock by freshwater mussels (Bivalvia: Unionidae). *American Midland Naturalist* 141:209–211.

Sietman, B.E., et al. 2012. Mantle display and glochidia release behaviors of five quadruline freshwater mussel species (Bivalvia: Unionidae). *American Malacological Bulletin* 30:39–46.

Silverman, H., et al. 1987. Maternal calcium contribution to glochidial shells in freshwater mussels (Eulamellibranchia:Unionidae). *Journal of Experimental Zoology* 242:137–146.

Silverman, H., et al. 1997. Clearance of laboratory cultured bacteria by freshwater bivalves: Differences between lentic and lotic unionids. *Canadian Journal of Zoology* 75:1857–1866.

Simberloff, D. 1996. Impacts of introduced species in the United States. *Consequences* 2:13–22.

Simmons, M. 2011. Rare mussels found in Emory River. *News-Sentinel* (Knoxville), May 26.

Simon, A. 1989. The discharge of sediment in channelized alluvial streams. *Journal of the American Water Resources Association* 25:1177–1188.

Simon, A., and S.E. Darby. 2002. Effectiveness of grade-control structures in reducing erosion along incised river channels: The case of Hotophia Creek, Mississippi. *Geomorphology* 42:229–254.

Simpson, C.T. 1899. The pearly fresh-water mussels of the United States; their habits, enemies, and diseases, with suggestions for their protection. *Bulletin of the U.S. Fish Commission* 18:279–288 [issued separately as U.S. Bureau of Fisheries Document 413].

Simpson, C.T. 1900a. Synopsis of the naiades, or pearly fresh-water mussels. *Proceedings of the United States National Museum* 22:501–1044.

Simpson, C.T. 1900b. On the evidence of the Unionidae regarding the former courses of the Tennessee and other southern rivers. *Science* 12:133–136.

Simpson, G.B. 1884. Anatomy and physiology of *Anodonta fluviatilis*. *New York State Museum of Natural History Annual Report* 35:169–191.

Singer, E.E. 2010. Mill dam effects on freshwater mussel growth in an Alabama stream. Thesis, Appalachian State University, Boone, North Carolina, USA.

Smathers, K.L. 1990. An analysis of a bivalve (Mollusca:Bivalvia) community in the Licking River, at Moores Ferry, Kentucky. Thesis, Eastern Kentucky University, Richmond, USA.

Smith, D.G. 1979. Sexual characteristics of *Margaritifera margaritifera* (Linnaeus) populations in central New England. *Veliger* 21:381–383.

Smith, D.G. 1985. Recent range expansion of the freshwater mussel *Anodonta implicata* and its relationship to clupeid fish restoration in the Connecticut River System. *Freshwater Invertebrate Biology* 4:105–108.

Smith, D.G. 2000. Investigations of the byssal gland in juvenile unionids. Pages 103–107 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Smith, D.G. 2001. Systematics and distribution of the Recent Margaritiferidae. Pages 33–49 *in* G. Bauer and K. Wächtler, editors. *Ecology and evolution of the freshwater mussels Unionoida. Ecological Studies* 145. Springer, Heidelberg, Germany.

Smith, D.G., et al. 2003. Gametogenetic cycle, reproductive anatomy, and larval morphology of *Popenaias popeii* (Unionoida) from the Black River, *New Mexico. Southwestern Naturalist* 48:333–340.

Smith, D.R., et al. 2000. How much excavation is needed to monitor freshwater mussels? Pages 203–218 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Smith, D.R., et al. 2001. Survey protocol for assessment of endangered freshwater mussels in the Allegheny River, Pennsylvania. *Journal of the North American Benthological Society* 20:118–132.

Smith, H.M. 1899. The mussel fishery and pearl-button industry of the Mississippi River. *Bulletin of the U.S. Fish Commission* 18:289–314.

Smith, H.M. 1919. Fresh water mussels: A valuable national resource without sufficient protection. *U.S. Bureau of Fisheries Economic Circular* 43:1–5.

Smith, M.G. 2006. Dam removal: A taxonomy with implications for economic analysis. *Journal of Contemporary Water Research and Education* 134:34–38.

Smith, T.A., and D.L. Crabtree. 2010. Freshwater mussel (Unionidae:Bivalvia) distributions and densities in French Creek, Pennsylvania. *Northeastern Naturalist* 17:387–414.

Smock, L.A., et al. 2005. Atlantic coast rivers of the southeastern United States. Pages 72–122 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America*. Elsevier, Burlington, Massachusetts, USA.

Southall, J.B. 1925. Mussel survey of Lake Pepin in 1924. With a discussion of the effects of the system of the alternate closure of sections of the lake to the taking of mussels. *U.S. Bureau of Fisheries Economic Circular* 57:1–3.

Sparks, B.L., and D.L. Strayer. 1998. Effects of low dissolved oxygen on juvenile *Elliptio complanata* (Bivalvia:Unionidae). *Journal of the North American Benthological Society* 17:129–134.

Sparks, R.E., and K.D. Blodgett. 1983. Effects of three commercial harvesting methods on mussel beds. Aquatic Biology Technical Series 1983 (10). Illinois Natural History Survey, Champaign, USA.

Spidle, A.P., et al. 1994. Identification of the Great Lakes quagga mussel as *Dreissena bugensis* from the Dnieper River, Ukraine, on the basis of allozyme variation. *Canadian Journal of Fisheries and Aquatic Sciences* 51:1485–1489.

Spinden, H.J. 1908. The Nez Perce Indians. *Memoirs of the American Anthropological Association* 2:167–274.

Spooner, D.E., and C.C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. *Freshwater Biology* 51:1016–1024.

Spooner, D.E., and C.C. Vaughn. 2008. A trait-based approach to species' roles in stream ecosystems: Climate change, community structure, and material cycling. *Oecologia* 158:307–317.

Spooner, D.E., and C.C. Vaughn. 2009. Species richness and temperature influence mussel biomass: A partitioning approach applied to natural communities. *Ecology* 90:781–790.

Spooner, D.E., and C.C. Vaughn. 2012. Species traits and environmental gradients interact to govern primary production in freshwater mussel communities. *Oikos* 121: 403–416,

Spooner, D.E., et al. 2012. Species traits and environmental conditions govern the relationship between biodiversity effects across trophic levels. *Oecologia* 168:533–548.

Stalnaker, C.B., et al. 1995. *The instream flow incremental methodology: A primer for IFIM*. Biological Report 29. National Biological Service, U.S. Fish and Wildlife Service, Washington, D.C., USA.

Stanley, S.M. 1977. Trends, rates, and patterns of evolution in the Bivalvia. Pages 209–250 *in* A. Hallam, editor. *Patterns of evolution*. Elsevier, Amsterdam, Netherlands.

Stanley, S.M. 1981. Infaunal survival: Alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology* 7:384–393.

Stanley, S.M. 1988. Adaptive morphology of the shell in bivalves and gastropods. Pages 105–141 *in* E.R. Trueman and M.R. Clarke, editors. *The Mollusca*. Vol. 11. *Form and function*. Academic Press, San Diego, California, USA.

Stansbery, D.H. 1964. The Mussel (Muscle) Shoals of the Tennessee River revisited. *American Malacological Union Annual Reports* 1964:25–28.

Stansbery, D.H. 1965. The naiad fauna of the Green River at Munfordville, Kentucky. *American Malacological Union Annual Reports* 1965:13–14.

Stansbery, D.H. 1966. Observations on the habitat distribution of the naiad *Cumberlandia monodonta* (Say, 1829). *American Malacological Union Annual Reports* 1966:29–30.

Stansbery, D.H. 1967. Growth and longevity of naiades from Fishery Bay in Western Lake Erie. *American Malacological Union Annual Reports* 34:10–11.

Stansbery, D.H. 1970. 2. Eastern freshwater mollusks. (I.) The Mississippi and St. Lawrence river systems. *Malacologia* 10:9–22.

Stansbery, D.H. 1971. Rare and endangered freshwater mollusks in eastern United States. Pages 5–18 *in* S.E. Jorgenson and R.W. Sharp, editors. *Proceedings of a symposium on rare and endangered mollusks (naiads) of the US*. U.S. Fish and Wildlife Service, Twin Cities, Minnesota, USA.

Stansbery, D.H. 1976. The status of endangered fluviatile mollusks in central North America. *Epioblasma turgidula* (Lea, 1858). Unpublished report to U.S. Fish and Wildlife Service, Washington, D.C., USA.

Stansbery, D.H. 1983. Some sources of nomenclatorial and systematic problems in unionid mollusks. Pages 46–62 *in* A.C. Miller, compiler. *Report of freshwater mollusks workshop*. U.S. Army Engineer Waterways Experimental Station, Vicksburg, Mississippi, USA.

Stansbery, D.H., and C.B. Stein. 1983. Mollusk collections at the Ohio State University Museum of Zoology. Pages 94–113 *in* A.C. Miller, compiler. *Report of freshwater mollusks workshop*. U.S. Army Engineer Waterways Experimental Station, Vicksburg, Mississippi, USA.

Starliper, C.E., et al. 2008. A survey of the indigenous microbiota (bacteria) in three species of mussels from the Clinch and Holston rivers, Virginia. *Journal of Shellfish Research* 27:1311–1317.

Starnes, L.B., and W.C. Starnes. 1985. Ecology and life history of the Mountain Madtom, *Noturus eluetherus* (Pisces:Ictaluridae). *American Midland Naturalist* 114:331–341.

Starrett, W.C. 1971. A survey of the mussels (Unionacea) of the Illinois River: A polluted stream. *Illinois Natural History Survey Bulletin* 30:267–403.

Stearns, S.C. 1983. The influence of size and phylogeny on patterns of covariation among life-history traits in the mammals. *Oikos* 41:173–187.

Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.

Stein, R.A., and J.F. Kitchell. 1975. Selective predation by carp (*Cyprinus carpio* L.) on benthic molluscs in Skadar Lake, Yugoslavia. *Journal of Fish Biology* 1975:391–399.

Steingraeber, M.T., et al. Thermal criteria for early life stage development of the winged mapleleaf mussel (*Quadrula fragosa*). *American Midland Naturalist* 157:297–311.

Stephens, P.A., et al. 1999. What is the Allee Effect? *Oikos* 87:185–190.

Steponaitis, V.P. 1986. Prehistoric archaeology in the southeastern United States, 1970–1985. *Annual Review of Anthropology* 15:363–404.

Sterki, V. 1898. Some observations on the genital organs of Unionidae, with reference to classification. *Nautilus* 12:18–21, 28–32.

Stern, E.M., and D.L. Felder. 1978. Identification of host fishes for four species of freshwater mussels (Bivalvia:Unionidae). *American Midland Naturalist* 100:233–236.

Stewart, D.T., et al. 1996. Degree of selective constraint as an explanation of the different rates of evolution of the gender-specific mitochondrial DNA lineages in the mussel *Mytilus*. *Genetics* 143:1349–1357.

Stewart, P.M., and T.O. Swinford. 1995. Identification of sediment and nutrient sources impacting a critically endangered mussel species' habitat in a small agricultural stream. Pages 45–64 *in* J.R. Pratt, et al., editors. *Making environmental science: A Festschrift in honor of John Cairns, Jr.* Ecoprint, Portland, Oregon, USA.

Stine, J.K. 1993. *Mixing the waters: Environment, politics, and the building of the Tennessee-Tombigbee Waterway*. University of Akron Press, Akron, Ohio, USA.

Stockard, S.W. 1904. History of pearls and pearling in Arkansas. Pages 166–171 *in The history of Lawrence, Jackson, Independence and Stone counties in the third judicial district of Arkansas*. Arkansas Democrat, Little Rock, USA.

Strange, R.M., and B.M. Burr. 1997. Intraspecific phylogeography of North American highland fishes: A test of the Pleistocene vicariance hypothesis. *Evolution* 51:885–897.

Strayer, D.L. 1981. Notes on the microhabitats of unionid mussels in some Michigan streams. *American Midland Naturalist* 106:411–415.

Strayer, D.L. 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia:Unionidae) distribution in southeastern Michigan, USA. *Freshwater Biology* 13:253–264.

Strayer, D.L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1389–1395.

Strayer, D.L. 1993. Macrohabitats of freshwater mussels (Bivalvia:Unionacea) in streams of the northern Atlantic Slope. *Journal of the North American Benthological Society* 12:236–246.

Strayer, D.L. 1999a. Use of flow refuges by unionid mussels in rivers. *Journal of the North American Benthological Society* 18:468–476.

Strayer, D.L. 1999b. Effects of alien species on freshwater mollusks in North America. *Journal of the North American Benthological Society* 18:74–98.

Strayer, D.L. 2006. Challenges for freshwater invertebrate conservation. *Journal of the North American Benthological Society* 25:271–287.

Strayer, D.L. 2008. *Freshwater mussel ecology: A multifactor approach to distribution and abundance*. University of California Press, Berkeley, USA.

Strayer, D.L. 2010. Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* 55 (Supplement 1):152–174.

Strayer, D.L., and A.R. Fetterman. 1999. Changes in the distribution of freshwater mussels (Unionidae) in the Upper Susquehanna River Basin, 1955–65 to 1996–97. *American Midland Naturalist* 142:328–339.

Strayer, D.L., and K.J. Jirka. 1997. *The pearly mussels of New York State*. New York State Museum Memoir 26. Albany, New York, USA.

Strayer, D.L., and J. Ralley. 1993. Microhabitat use by an assemblages of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *Journal of the North American Benthological Society* 12:247–258.

Strayer, D.L., and L.C. Smith. 1996. Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River. *Freshwater Biology* 36:771–779.

Strayer, D.L., et al. 1981. Biomass and annual production of the freshwater mussel *Elliptio complanata* in an oligotrophic softwater lake. *Freshwater Biology* 11:435–440.

Strayer, D.L., et al. 1994. Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. *Freshwater Biology* 31:239–248.

Strayer, D.L., et al. 1996a. A range-wide assessment of populations of *Alasmidonta heterodon*, an endangered freshwater mussel (Bivalvia: Unionidae). *Journal of the North American Benthological Society* 15:308–317.

Strayer, D.L., et al. 1996b. Arrival, spread, and early dynamics of a zebra mussel (*Dreissena polymorpha*) population in the Hudson River estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1143–1149.

Strayer, D.L., et al. 2004. Changing perspectives on pearly mussels, North America's most imperiled animals. *BioScience* 54:429–439.

Stroud, P.T. 1995. Forerunner of American conservation: Naturalist Thomas Say. *Forest and Conservation History* 39:184–190.

Stuart, S.N., et al. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.

Suloway, L. 1981. The unionid (Mollusca: Bivalvia) fauna of the Kankakee River in Illinois. *American Midland Naturalist* 105:233–239.

Surber, T. 1913. Notes on the natural hosts of fresh-water mussels. *Bulletin of the U.S. Bureau of Fisheries* 32:103–116 [issued separately as U.S. Bureau of Fisheries Document 778].

Surber, T. 1915. Identification of the glochidia of fresh-water mussels. Report of the US Commissioner of Fisheries for 1914 Appendix 5:1–9 [issued separately as U.S. Bureau of Fisheries Document 813].

Swift, C.R., et al. 1986. Zoogeography of the freshwater fishes of the southeastern United States: Savannah River to Lake Pontchartrain. Pages 213–265 *in* C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley, New York, USA.

Szafoni, R.E., et al. 2000. Freshwater mussels (Mollusca: Unionidae) of the Middle Branch, North Fork Vermilion River, Illinois/Indiana. *Transactions of the Illinois State Academy of Science* 93:229–237.

Tankersley, R.A. 1996. Multipurpose gills: Effect of larval brooding on the feeding physiology of freshwater unionid mussels. *Invertebrate Biology* 115:243–255.

Tankersley, R.A. 2000. Florescence techniques for evaluating the lipid content of larval and juvenile freshwater mussels. Pages 115–125 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Tankersley, R.A., and R.V. Dimock Jr. 1992. Quantitative analysis of the structure and function of the marsupial gills of the freshwater mussel *Anodonta cataracta*. *Biological Bulletin (Woods Hole)* 182:145–154.

Tankersley, R.A., and R.V. Dimock. 1993. Endoscopic visualization of the functional morphology of the ctenidia of the unionid mussel *Pyganodon cataracta*. *Canadian Journal of Zoology* 71:811–819.

Taskinen, J. 1998. Influence of trematode parasitism on the growth of a bivalve host in the field. *International Journal for Parasitology* 28:599–602.

Taskinen, J., and E.T. Valtonen. 1995. Age-, size-, and sex-specific infection of *Anodonta piscinalis* (Bivalvia:Unionidae) with *Rhipidocotyle fennica* (Digenea: Bucephalidae) and its influence on host reproduction. *Canadian Journal of Zoology* 73:887–897.

Taylor, C.A., et al. 2007. A reassessment of the conservation status of crayfishes of the United States and Canada after 10+ years of increased awareness. *Fisheries* 32:372–389.

Taylor, C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: Local processes and regional patterns. *Freshwater Biology* 36:385–396.

Tedla, S., and C.H. Fernando. 1969. Observations on the glochidia of *Lampsilis radiata* (Gmelin) infesting yellow perch, *Perca flavescens* (Mitchill) in the Bay of Quinte, Lake Ontario. *Canadian Journal of Zoology* 47:705–712.

Tennessee-Tombigbee Waterway Development Authority. 2007. About the Tenn-Tom Waterway: Waterway construction. Columbus, Mississippi, USA (http://www.tenntom.org/about/ttwconstruction.htm).

Tepe, W.C. 1943. Hermaphroditism in *Carunculina parva*, a fresh water mussel. *American Midland Naturalist* 29:621–623.

Tevesz, M.J.S., and J.G. Carter. 1980. Environmental relationships of shell form and structure in Unioncean bivalves. Pages 295–322 *in* D.C. Rhoads and R.A. Lutz, editors. *Skeletal growth of aquatic organisms*. Plenum Press, New York, USA.

Tevesz, M.J.S., et al. 1985. Life habits and distribution of riverine *Lampsilis radiata luteola* (Mollusca:Bivalvia). *Kirtlandia* 41:27–34.

Theler, J.L. 1987. Pre-Columbian freshwater mussel assemblages of the Mississippi River in southwestern Wisconsin. *Nautilus* 101:143–150.

Theler, J.L. 1990. A possible Oneota freshwater mussel cache intended for ceramic tempering material. *Journal of the Iowa Archeological Society* 37:1–3.

Theler, J.L. 1991. Aboriginal utilization of freshwater mussels at the Azatlan site, Wisconsin. Pages 315–332 *in* J.R. Purdue, et al., editors. *Beamers, bobwhites, and blue-points:*

Tributes to the career of Paul W. Parmalee. Scientific Papers 23. Illinois State Museum, Springfield, USA.

Thiel, P.A. 1987. Recent events in the mussel mortality problem on the Upper Mississippi River. Pages 66–75 *in* R.J. Neves, editor. *Proceedings of the workshop on die-offs of freshwater mussels in the United States*. Upper Mississippi River Conservation Committee, Davenport, Iowa, USA.

Thiel, P.A., and A.W. Fritz. 1993. Mussel harvest and regulations in the Upper Mississipi River system. Pages 11–18 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Thompson, D. 1973. Feeding ecology of diving ducks on Keokuk Pool, Mississippi River. *Journal of Wildlife Management* 37:367–381.

Thorp, J.H., et al. 1998. Responses of Ohio River and Lake Erie dreissenid molluscs to changes in temperature and turbidity. *Canadian Journal of Fisheries and Aquatic Sciences* 55:220–229.

Threlfall, W. 1986. Seasonal occurrence of *Anodonta cataracta* Say, 1817, glochidia on three-spined sticklebacks, *Gasterosteus aculeatus* Linneaus. *Veliger* 29:231–234.

Tiemann, J.S., et al. 2011. A review of the interactions between catfishes and freshwater mollusks in North America. Pages 733–743 *in* P.H. Michaletz and V.H. Travnichek, editors. *Conservation, ecology, and management of catfish: the second international symposium*. American Fisheries Society, Symposium 77, Bethesda, Maryland.

Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.

Time. 1930. Animals: Buttons to be. December 8.

Time. 1969. America's sewage system and the price of optimism. August 1.

Tippit, R.N., et al. 1997. Modifying Cumberland River system reservoir operations to improve mussel habitat. Pages 229–235 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Todd, R.M. 1993. Tennessee's commercial musseling regulations. Pages 32–37 *in* K.S. Cummings, et al., editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Traill, L.W., et al. 2010. Pragmatic population viability targets in a rapidly changing world. *Biological Conservation* 143:28–34.

Trautman, M.B. 1981. *The fishes of Ohio*. Ohio State University Press, Columbus, USA.

Trdan, R.J. 1981. Reproductive biology of *Lampsilis radiata siliquoidea* (Pelecypoda: Unionidae). *American Midland Naturalist* 106:243–248.

Trdan, R.J., and W.R. Hoeh. 1982. Eurytopic host use by two congeneric species of freshwater mussel (Pelecypoda:Unionidae:Anodonta). *American Midland Naturalist* 108:381–388.

Trdan, R.J., and W.R. Hoeh. 1993. Relocation of two state-listed freshwater mussel species (*Epioblasma torulosa rangiana* and *Epioblasma triquetra*) in Michigan. Pages 100–105 *in* K.S. Cummings, et al, editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Trimble, S.W., and P. Crosson. 2000. US soil erosion rates: Myth and reality. *Science* 289:248–250.

Tucker, J.K. 1996. Post-flooding strandings of unionid mussels. *Journal of Freshwater Ecology* 11:433–438.

Tucker, M.E. 1927. Morphology of the glochidium and juvenile of the mussel *Anodonta imbecillis*. *Transactions of the American Microscopical Society* 46:286–293.

Tucker, M.E. 1928. Studies on the life cycles of two species of fresh-water mussels belonging to the genus *Anodonta*. *Biological Bulletin* 54:117–127.

Tudorancea, C. 1972. Studies on Unionidae populations from the Crapina-Jijila complex of pools (Danube zone liable to inundation). *Hydrobiologia* 39:527–561.

Tuomi, J., et al. 1983. Alternative concepts of reproductive effort, costs of reproduction, and selection in life history evolution. *American Zoologist* 23:25–34.

Turgeon, D.D., et al. 1998. *Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks*. 2nd ed. Special Publication 26. American Fisheries Society, Bethesda, Maryland, USA.

Turner, R.D. 1946. John Gould Anthony with a bibliography and catalogue of his species. *Occasional Papers on Mollusks, Museum of Comparative Zoology, Harvard University* 1:81–108.

Turner, T.F., et al. 2000. Nested cladistic analysis indicates population fragmentation shapes genetic diversity in a freshwater mussel. *Genetics* 154:777–785.

Tyrrell, M., and D.J. Hornbach. 1998. Selective predation by muskrats on freshwater mussels in 2 Minnesota rivers. *Journal of the North American Benthological Society* 17:301–310.

Underwood, A.J., and R.G. Creese. 1976. Observations on the biology of the trochid gastropod *Austrocochlea constricta* (Lamarck) (Prosobranchia). II. The effects of available food on shell-banding pattern. *Journal of Experimental Marine Biology and Ecology* 23:229–240.

USACOE (US Army Corps of Engineers). 2011. The Wolf Creek dam seepage problem (http://www.lrn.usace.army.mil/wolfcreek/seepage.htm).

USEPA (U.S. Environmental Protection Agency). 1990. The quality of our nation's water: A summary of the 1988 National Water Quality Inventory. EPA report 440/4-90-005. U.S. Environmental Protection Agency, Washington, D.C., USA.

USEPA (U.S. Environmental Protection Agency). 2005. Stream channelization. Fact sheet number 1, EPA Region 7, Kansas City, Kansas (http://www.epa.gov/region7/wetlands/pdf/ChannelizationFS04-Final.pdf).

USEPA (U.S. Environmental Protection Agency). 2009. Draft 2009 update. Aquatic life ambient water quality criteria for ammonia – freshwater. EPA-822-D-09-001, USEPA, Washington, DC .

USEPA (U.S. Environmental Protection Agency). 2011. Atrazine background. Pesticides: topical and chemical fact sheets (http://www.epa.gov/pesticides/factsheets/index.htm).

USFWS (U.S. Fish and Wildlife Service). 1983. Green blossom pearly mussel recovery plan. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

USFWS (U.S. Fish and Wildlife Service). 1991. Speckled pocketbook mussel (*Lampsilis streckeri*) recovery plan. U.S. Fish and Wildlife Service, Jackson, Mississippi, USA.

USFWS (U.S. Fish and Wildlife Service). 1998. Japanese-owned Tennessee Shell Company pays $1 million in restitution for illegally buying and transporting overseas thousands of pounds of freshwater mussels. Press release (http://www.fws.gov/southeast/news/1998/r98-063.html).

USFWS (U.S. Fish and Wildlife Service). 2000. Recovery plan for Mobile River basin aquatic ecosystem. U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

USFWS (U.S. Fish and Wildlife Service). 2009a. Tennessee man pleads guilty to Lacey Act violations. Press release (http://www.fws.gov/southeast/news/2009/r09-021.html).

USFWS (U.S. Fish and Wildlife Service). 2009b. Fanshell mussel recovery action plan. USFWS Ecological Services Field Office, Frankfort, Kentucky (http://www.fws. gov/ecos/ajax/docs/action_plans/doc3064.pdf).

USFWS (U.S. Fish and Wildlife Service). 2011. Freshwater mussels of the upper Mississippi River system. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota, USA (http://www.fws.gov/midwest/mussel/documents/upper_mississippi_illinois_river_mussels_2003.pdf).

USFWS and NMFS (U.S. Fish and Wildlife Service and National Marine Fisheries Service). 2000. Policy regarding controlled propagation of species listed under the Endangered Species Act. *Federal Register* 65:56916–56922.

USGS (U.S. Geological Survey). 2011. Progression of zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. rostriformis bugensis*) distributions in North America (http://fl.biology.usgs.gov/Nonindigenous_Species/ZM_Progression/zm_progression.html).

Utter, F. 2003. Genetic impacts of fish introductions. Pages 357–378 *in* E.M. Hallerman, editor. *Population genetics: Principles and applications for fisheries scientists*. American Fisheries Society, Bethesda, Maryland, USA.

Utterback, W.I. 1916a. The naiades of Missouri. V. *American Midland Naturalist* 4:311–327.

Utterback, W.I. 1916b. Parasitism among Missouri naiades. *American Midland Naturalist* 4:518–521.

Utterback, W.I. 1931. Sex behavior among naiades. *Proceedings of the West Virginia Academy of Science* 5:43–45.

Valdovinos, C., and P. Pedreros. 2007. Geographic variations in shell growth rates of the mussel *Diplodon chilensis* from temperate lakes of Chile: Implications for biodiversity conservation. *Limnologica* 37:63–75.

Valentine, B.D., and D.H. Stansbery. 1971. An introduction to the naiads of the Lake Texoma region, Oklahoma, with notes on the Red River fauna. *Sterkiana* 42:1–40.

van Arsdale, R.B., and R.T. Cox. 2007. The Mississippi's curious origins. *Scientific American* January 2007:76–82B.

van der Schalie, H. 1938a. The naiad fauna of the Huron River, in southeastern Michigan. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 40:1–83.

van der Schalie, H. 1938b. Contributing factors in the depletion of naiades in the eastern United States. *Basteria* 3:51–57.

van der Schalie, H. 1939a. Distributional studies of the naiads as related to geomorphology. *Journal of Geomorphology* 2:251–257.

van der Schalie, H. 1939b. Additional notes on the naiades (fresh-water mussels) of the lower Tennessee River. *American Midland Naturalist* 22:452–457.

van der Schalie, H. 1940a. The naiad fauna of the Chipola River, in northwestern Florida. *Lloydia* 3:191–208.

van der Schalie, H. 1940b. Aestivation of fresh-water mussels. *Nautilus* 53:137–138.

van der Schalie, H. 1963. Mussel distribution in relation to former stream confluence in northern Michigan, U.S.A. *Malacologia* 1:227–236.

van der Schalie, H. 1969. Two unusual unionid hermaphrodites. *Science* 163:1333–1334.

van der Schalie, H. 1970. Hermaphroditism among North American freshwater mussels. *Malacologia* 10:93–112.

van der Schalie, H. 1981. Perspectives on North American malacology. I. Mollusks in the Alabama River drainage: Past and present. *Sterkiana* 71:24–40.

van der Schalie, H., and F. Locke. 1941. Hermaphroditism in *Anodonta grandis*, a fresh-water mussel. *Occasional Papers of the Museum of Zoology, University of Michigan Number* 432:1–7.

van der Schalie, H., and A. van der Schalie. 1950. The mussels of the Mississippi River. *American Midland Naturalist* 44:449–466.

van der Schalie, H., and A. van der Schalie. 1963. The distribution, ecology, and life history of the mussel, *Actinonaias ellipsiformis* (Conrad), in Michigan. *Occasional Papers of the Museum of Zoology, University of Michigan* 633:1–17.

Van Dyke, A.P., et al. 1980. Archaeological recovery at 11-RI-337, an early middle woodland shell midden in East Moline, Illinois. *Wisconsin Archeologist* 61:125–256.

van snik Gray, E., et al. 2002. Host identification for *Strophitus undulatus* (Bivalvia: Unionidae), the creeper, in the Upper Susquehanna River basin, Pennsylvania. *American Midland Naturalist* 147:153–161.

Vannote, R.L., and G.W. Minshall. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proceedings of the National Academy of Sciences of the United States of America* 79:4103–4107.

Vaughn, C.C. 1993. Can biogeographic models be used to predict the persistence of mussel populations in rivers? Pages 117–122 *in* K.S. Cummings, et al, editors. *Conservation and management of freshwater mussels*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Vaughn, C.C. 1997a. Regional patterns of mussel species distributions in North American rivers. *Ecography* 20:107–115.

Vaughn, C.C. 1997b. Catastrophic decline of the mussel fauna of the Blue River, Oklahoma. *Southwestern Naturalist* 42:333–336.

Vaughn, C.C., and C.C. Hakenkamp. 2001. The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology* 46:1431–1446.

Vaughn, C.C., and D.E. Spooner. 2006a. Unionid mussels influence macroinvertebrate assemblage structure in streams. *Journal of the North American Benthological Society* 25:691–700.

Vaughn, C.C., and D.E. Spooner. 2006b. Scale-dependent associations between native freshwater mussels and invasive *Corbicula*. *Hydrobiologia* 568:331–339.

Vaughn, C.C., and C.M. Taylor. 2000. Macroecology of a host-parasite relationship. *Ecography* 23:11–20.

Vaughn, C.C., et al. 1996. The current and historical mussel fauna of the Kiamichi River, Oklahoma. *Southwestern Naturalist* 41:325–328.

Vaughn, C.C., et al. 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: Species roles and effects of abundance. *Hydrobiologia* 527:35–47.

Vaughn, C.C., et al. 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. *Ecology* 88:1654–1662.

Vaughn, C.C., et al. 2008. Community foodweb ecology of freshwater mussels. *Journal of the North American Benthological Society* 27:409–423.

Vermeij, G.J. 1980. Drilling predation in a population of the edible bivalve *Andara granosa* (Arcidae). *Nautilus* 94:123–125.

Vermeij, G.J. 1993. *A natural history of shells*. Princeton University Press, Princeton, New Jersey, USA.

Vermeij, G.J., and E.C. Dudley. 1985. Distribution of adaptations: A comparison between the functional shell morphology of freshwater and marine pelecypods. Pages 461–478 *in* E.R. Trueman and M.R. Clarke, editors. *The Mollusca*. Vol. 10. *Evolution*. Academic Press, Harcourt Brace Jovanovich, New York, USA.

Vertrees, H.H. 1913. *Pearls and pearling*. Fur News Publishing, New York, USA.

Vidrine, M.F. 1993. *The historical distributions of freshwater mussels in Louisiana*. Gail Q. Vidrine Collectables, Eunice, Louisiana, USA.

Villella, R.F., et al. 2004. Estimating survival and recruitment in a freshwater mussels population using mark-recapture techniques. *American Midland Naturalist* 151:114–133.

Virginia Department of Game and Inland Fisheries. 2010. Aquatic Wildlife Conservation Center 2010 propagation summary (http://www.dgif.virginia.gov/awcc/ freshwater-mussel-restoration/awcc-release-summary-2010.pdf).

Vitousek, P.M., et al. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7:737–750.

Voelz, N.J., et al. 1998. Upstream mobility of the Asiatic clam *Corbicula fluminea*: Identifying potential dispersal agents. *Journal of Freshwater Ecology* 13:39–45.

Voightlander, C.W., and W.L. Poppe. 1989. The Tennessee River. Pages 372–384 *in Proceedings of the International Large River Symposium*. Canadian Special Publication of Fisheries and Aquatic Sciences 106. Department of Fisheries and Oceans, Ottawa, Canada.

Wächtler, K., et al. 2001. Larval types and early postlarval biology in naiads (Unionoida). Pages 93–125 *in* G. Bauer and K. Wächtler, editors. *Ecology and evolution of the freshwater mussels Unionoida*. *Ecological Studies* 145. Springer, Berlin, Germany.

Wadhwani, A. 2010. Mussels take a dive in West Tennessee river towns. *The Tennessean*, October 17.

Walker, B. 1900. The origin and distribution of the land and freshwater Mollusca of North America. *Michigan Academy of Science* 1:43–61.

Waller, D.L., and L.E. Holland-Bartels. 1988. Fish hosts for glochidia of the endangered freshwater mussel *Lampsilis higginsi* Lea (Bivalvia:Unionidae). *Malacological Review* 21:119–122.

Waller, D.L., and B.A. Lasee. 1997. External morphology of spermatozoa and spermatozeugmata of the freshwater mussel *Truncilla truncata* (Mollusca: Bivalvia: Unionidae). *American Midland Naturalist* 138:220–223.

Waller, D.L., and L.G. Mitchell. 1989. Gill tissue reactions in walleye *Stizostedion vitreum vitreum* and common carp *Cyprinus carpio* to glochidia of the freshwater mussel *Lampsilis radiata siliquoidea*. *Diseases of Aquatic Organisms* 6:81–87.

Waller, D.L., et al. 1985. Artificial infestation of largemouth bass and walleye with glochidia of *Lampsilis ventricosa* (Pelecypoda:Unionidae). *Freshwater Invertebrate Biology* 4:152–153.

Waller, D.L., et al. 1999. Behavioral responses to disturbance in freshwater mussels with implications for conservation and management. *Journal of the North American Benthological Society* 18:381–390.

Walling, D.E., and B.W. Webb. 1992. Water quality I. Physical characteristics. Pages 48–72 *in* P. Calow and G.E. Petts, editors. *The rivers handbook.* Vol. I. Blackwell, Oxford, UK.

Walter, R.C., and D.J. Merritts. 2008. Natural streams and the legacy of water-powered mills. *Science* 319:299–304.

Wanamaker, A.D., et al. 2008. Very long-lived mollusks confirm 17th century AD tephra-based radiocarbon reservoir ages for north Icelandic shelf waters. *Radiocarbon* 50:399–412.

Wang, N., et al. 2007. Acute toxicity of copper, ammonia, and chlorine to glochidia and juveniles of freshwater mussels (Unionidae). *Environmental Toxicology and Chemistry* 26:2036–2047.

Wang, N., et al. 2008. Influence of pH on the acute toxicity of ammonia to juvenile freshwater mussels (Fatmucket, *Lampsilis siliquoidea*) *Environmental Toxicology and Chemistry* 27: 1141–1146.

Wang, Y., et al. 1994. Accumulation of 2,4-D and glyphosate in fish and water hyacinth. *Water, Air, and Soil Pollution* 74:397–403.

Ward, G.M., et al. 2005. Gulf coast rivers of the southeastern United States. Pages 124–178 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America*. Elsevier, Burlington, Massachusetts. USA.

Warren, M.L., and S.M. Call. 1983. First records of *Ligumia subrostrata*, *Toxolasma texasensis*, and *Uniomerus tetralasmus* for Kentucky. *Transactions of the Kentucky Academy of Science* 44:164–165.

Warren, M.L., and W.R. Haag. 2005. Spatio-temporal patterns of the decline of freshwater mussels in the Little South Fork Cumberland River, USA. *Biodiversity and Conservation* 14:1383–1400.

Warren, R.E. 1991. Ozarkian fresh-water mussels (Unionoidea) in the upper Eleven Point River, Missouri. *American Malacological Bulletin* 8:131–137.

Watabe, N. 1988. Shell structure. Pages 69–104 *in* E.R. Trueman and M.R. Clarke, editors. *The Mollusca*. Vol. 11. *Form and function*. Academic Press, San Diego, California, USA.

Waters, T.F. 1995. *Sediment in streams: Sources, biological effects and control.* American Fisheries Society Monograph 7. American Fisheries Society, Bethesda, Maryland, USA.

Watters, G.T. 1992. Unionids, fishes, and the species-area curve. *Journal of Biogeography* 19:481–490.

Watters, G.T. 1994a. An annotated bibliography of the reproduction and propagation of the Unionoidea (primarily of North America). Miscellaneous Contributions 1. Ohio Biological Survey, Columbus, USA.

Watters, G.T. 1994b. Form and function of unionoidean shell sculpture and shape (Bivalvia). *American Malacological Bulletin* 11:1–20.

Watters, G.T. 1995. Sampling freshwater mussel populations: The bias of muskrat middens. *Walkerana* 7:63–69.

Watters, G.T. 1996. Small dams as barriers to freshwater mussels (Bivalvia, Unionoida) and their hosts. *Biological Conservation* 75:79–85.

Watters, G.T. 1997. Individual-based models of mussel-fish interactions: A cautionary study. Pages 45–62 *in* K.S. Cummings et al., editors. *Conservation and management of freshwater mussels II: Initiatives for the future*. Upper Mississippi River Conservation Committee, Rock Island, Illinois, USA.

Watters, G.T. 1999. Morphology of the conglutinate of the kidney shell freshwater mussel, *Pychobranchus fasciolaris*. *Invertebrate Biology* 118:289–295.

Watters, G.T. 2000. Freshwater mussels and water quality: A review of the effects of hydrologic and instream habitat alterations. Pages 261–274 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Watters, G.T. 2001. The evolution of the Unionacea in North America, and its implications for the worldwide fauna. Pages 281–307 *in* G. Bauer and K. Wätchler, editors. *Ecology and evolution of the freshwater mussels Unionoida*. Ecological Studies 145. Springer, Berlin, Germany.

Watters, G.T. 2002. The kinetic conglutinate of the creeper freshwater mussel, *Strophitus undulates* (Say, 1817). *Journal of Molluscan Studies* 68:155–158.

Watters, G.T. 2008a. Electric elliptio land in North America. Ohio State University, Museum of Biological Diversity, Columbus, USA (http://www.biosci.ohio-state.edu/~molluscs/Elliptio/index.htm).

Watters, G.T. 2008b. The morphology of conglutinates and conglutinate-like structures in North American freshwater mussels: A scanning electron microscopy study. *Novapex Société* 9:1–20.

Watters, G.T., and C.J. Myers Flaute. 2010. Dams, zebras, and settlements: The historical loss of freshwater mussels in the Ohio River mainstem. *American Malacological Bulletin* 28:1–12.

Watters, G.T., and S.H. O'Dee. 1996. Shedding of untransformed glochidia by fishes parasitized by *Lampsilis fasciola* Rafinesque, 1820 (Mollusca:Bivalvia: Unionidae): Evidence of acquired immunity in the field? *Journal of Freshwater Ecology* 11:383–388.

Watters, G.T., and S.H. O'Dee. 1998. Metamorphosis of freshwater mussel glochidia (Bivalvia:Unionidae) on amphibians and exotic fishes. *American Midland Naturalist* 139:49–57.

Watters, G.T., and S.H. O'Dee 1999. Glochidia of the freshwater mussel *Lampsilis* overwintering on fish hosts. *Journal of Molluscan Studies* 65:453–459.

Watters, G.T., and S.H. O'Dee. 2000. Glochidial release as a function of water temperature: Beyond bradyticity and tachyticity. Pages 135–140 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Watters, G.T., et al. 2001. Patterns of vertical migration in freshwater mussels (Bivalvia: Unionoida). *Journal of Freshwater Ecology* 16:541–549.

Watters, G.T., et al. 2009. *The freshwater mussels of Ohio*. Ohio State University Press, Columbus, USA.

Way, C.M. 1989. Dynamics of filter-feeding in *Musculium transervsum* (Bivalvia: Sphaeriidae). *Journal of the North American Benthological Society* 8:243–249.

Weaver, L.R., et al. 1991. Reproductive biology and fish hosts of the Tennessee clubshell *Pleurobema oviforme* (Mollusca:Unionidae) in Virginia. *American Midland Naturalist* 126:82–89.

Webb, B.W., and D.E. Walling. 1992. Water quality II. Chemical characteristics. Pages 73–100 *in* P. Calow and G.E. Petts, editors. *The rivers handbook. Vol. I*. Blackwell, Oxford, UK.

Webb, W.S., and D.L. DeJarnette. 1942. An archeological survey in Pickwick Basin in adjacent portions of the states of Alabama, Mississippi, and Tennessee. Bulletin 129. Bureau of American Ethnology, Washington, D.C., USA.

Weinstein, R.A., and A.A. Dumas. 2008. The spread of shell-tempered ceramics along the northern coast of the Gulf of Mexico. *Southeastern Archaeology* 27:202–221.

Weisensee, H. 1916. Die Geschlechtsverhaltnisse und der Geschlechtsapparat bei *Anodonta. Zeitschrift für Wissenschaftliche Zoologie* 115:262–335.

Weiss, J.L., and J.B. Layzer. 1995. Infestations of glochidia on fishes in the Barren River, Kentucky. *American Malacological Bulletin* 11:153–159.

Whalen, P.J., et al. 2002. Kissimmee River restoration: A case study. *Water Science and Technology* 45:55–62.

Wheeler, H.E. 1935. Timothy Abbott Conrad, with particular reference to his work in Alabama one hundred years ago. *Bulletin of American Paleontology* 23:1–157.

White, C.A. 1907. The ancestral origin of the North American Unionidae or freshwater mussels. *Smithsonian Miscellaneous Collections* 48:75–88.

White, D., et al. 2005. Ohio River basin. Pages 374–424 *in* A.C. Benke and C.E. Cushing, editors. *Rivers of North America*. Elsevier, Burlington, Massachusetts, USA.

White, D.S. 1979. The effect of lake-level fluctuations on *Corbicula* and other pelecypods in Lake Texoma, Texas and Oklahoma. Pages 81–88 *in Proceedings of the First International Corbicula Symposium*. Texas Christian University Research Foundation, Ft. Worth, USA.

White, M.P., et al. 2008. Life history and host fish identification for *Fusconaia burkei* and *Pleurobema strodeanum* (Bivalvia: Unionidae). *American Malacological Bulletin* 24:121–125.

Whitman, R.L., and W.J. Clark. 1982. Availability of dissolved oxygen in interstitial waters of a sandy creek. *Hydrobiologia* 92:651–658.

Whittier, T.R., et al. 2008. A calcium-based invasion risk assessment of zebra and quagga mussels (*Dreissena* spp). *Frontiers in Ecology and the Environment* 6:180–184.

Wilcox Progressive Era. 2007. Wife charged in 2006 death of mussel diving husband found shot in the head. Camden, Alabama, USA.

Wiley, E.O., and R.L. Mayden. 1985. Species and speciation in phylogenetic systematics, with examples from the North American fish fauna. *Annals of the Missouri Botanical Garden* 72:596–635.

Williams, G.C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. *American Naturalist* 100:687–690.

Williams, J.C. 1969. Mussel fishery investigation: Tennessee, Ohio and Green rivers. Project 4-19-R. Kentucky Department of Fish and Wildlife Resources and Murray State University Biological Station, Murray, USA.

Williams, J.C., and G.A. Schuster. 1989. Freshwater mussel investigations of the Ohio River, mile 317.0 to mile 981.0. Kentucky Department of Fish and Wildlife Resources, Division of Fisheries, Frankfort, USA.

Williams, J.D., and A. Fradkin. 1999. *Fusconaia apalachicola*, a new species of freshwater mussel (Bivalvia:Unionidae) from precolumbian archeological sites in the Apalachicola Basin of Alabama, Florida, and Georgia. *Tulane Studies in Zoology and Botany* 31:51–62.

Williams, J.D., and D.H. Stansbery. 1972. A preliminary report on the naiad mollusks (Bivalvia: Naiadoida) of the Tombigbee River in the vicinity of Columbus, Mississippi (Abstract). *ASB Bulletin* 19:110.

Williams, J.D., et al. 1992. Effects of impoundments on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee rivers in western Alabama. *Bulletin of the Alabama Museum of Natural History* 13:1–10.

Williams, J.D., et al. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18:6–22.

Williams, J.D., et al. 2008. *Freshwater mussels of Alabama and the Mobile Basin in Georgia, Mississippi, and Tennessee*. University of Alabama Press, Tuscaloosa, USA.

Williams, J.D., et al. 2011. Annotated synonymy of the recent freshwater mussel taxa of the families Margaritiferidae and Unionidae described from Florida and drainages contiguous with Alabama and Georgia. *Bulletin of the Florida Museum of Natural History* 51:1–84.

Williamson, E.B. 1905. Odonata, Astacidae, and Unionidae collected along the Rockcastle River at Livingston, Kentucky. *Ohio Naturalist* 5:309–312.

Willoughby, L. 1999. *Flowing through time: A history of the lower Chattahoochee River*. University of Alabama Press, Tuscaloosa, USA.

Wilson, C.B., and H.W. Clark. 1912. The mussel fauna of the Kankakee basin. *Report and Special Papers of the US Fish Commission* 1911:1–52 [issued separately as U.S. Bureau of Fisheries Document 758].

Wilson, C.B., and H.W. Clark. 1914. The mussels of the Cumberland River and its tributaries. *U.S. Bureau of Fisheries Document* 781:1–63.

Wilson, C.B., and E. Danglade. 1912. The mussel fauna of central and northern Minnesota. *U.S. Bureau of Fisheries Economic Circular* 3:1–6.

Winemiller, K.O., and K.A. Rose. 1992. Patterns of life history diversification in North American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Science* 49:2196–2218.

Winkler, F.M., et al. 2001. Inheritance of the general shell color in the scallop *Argopecten purpuratus* (Bivalvia:Pectinidae). *Journal of Heredity* 92:521–525.

Winn, J.N. 1978. *Muscle Shoals canal . . . life with the canalers*. Strode, Huntsville, Alabama, USA.

Wood, E.M. 1974. Development and morphology of the glochidium larvae of *Anodonta cygnea* (Mollusca: Bivalvia). *Journal of Zoology* (London) 173:1–13.

Wood, R.M., and R.L. Mayden. 1993. Systematics of the *Etheostoma jordani* species group (Teleostei:Percidae), with descriptions of three new species. *Bulletin of the Alabama Museum of Natural History* 16:31–46.

Woody, C.A., and L. Holland-Bartels. 1993. Reproductive characteristics of a population of the washboard mussel *Megalonaias nervosa* (Rafinesque 1820) in the Upper Mississippi River. *Journal of Freshwater Ecology* 8:57–66.

Wright, S.J. 1980. Density compensation in island avifaunas. *Oecologia* 45:385–389.

Wright, W.G. 1988. Sex change in the Mollusca. *Trends in Ecology and Evolution* 3:137–140.

Wu, M., et al. 2010. Still poisoning the well: Atrazine continues to contaminate surface water and drinking water in the United States. Natural Resources Defense Council, Washington, D.C., USA.

Yeager, B.L., and R.J. Neves. 1986. Reproductive cycle and fish hosts of the rabbit's foot mussel, *Quadrula cylindrica strigillata* (Mollusca:Unionidae) in the Upper Tennessee River drainage. *American Midland Naturalist* 116:329–340.

Yeager, B.L., and C.F. Saylor. 1995. Fish hosts for four species of freshwater mussels (Pelecypoda:Unionidae) in the Upper Tennessee River drainage. *American Midland Naturalist* 133:1–6.

Yeager, M.M., et al. 1994. Feeding and burrowing behaviors of juvenile rainbow mussels, *Villosa iris* (Bivalvia:Unionidae). *Journal of the North American Benthological Society* 13:217–222.

Yeager, M.M., et al. 2000. Competitive interactions between early life stages of *Villosa iris* (Bivalvia:Unionidae) and adult Asian clams (*Corbicula fluminea*). Pages 253–259 *in* R.A. Tankersley et al., editors. *Freshwater Mollusk Symposia proceedings*. Ohio Biological Survey, Columbus, USA.

Yokley, P. 1972. Life history of *Pleurobema cordatum* (Rafinesque, 1820) (Bivalvia: Unionacea). *Malacologia* 11:351–364.

Young, D. 1911. The implantation of the glochidium on the fish. *University of Missouri Bulletin Science Series* 2:1–16.

Young, M., and J. Williams. 1984a. The reproductive biology of the freshwater pearl mussel *Margaritifera margaritifera* in Scotland. I. Field studies. *Archiv für Hydrobiologie* 99:405–422.

Young, M., and J. Williams. 1984b. The reproductive biology of the freshwater pearl mussel *Margaritifera margaritifera* in Scotland. II. Laboratory studies. *Archiv für Hydrobiologie* 100:29–44.

Yusa, Y. 2007. Causes of variation in sex ratio and modes of sex determination in the Mollusca – an overview. *American Malacological Bulletin* 23:89–98.

Zahner-Meike, E., and J.M. Hanson. 2001. Effect of muskrat predation on naiads. Pages 163–184 in G. Bauer and K. Wächtler, editors. *Ecology and evolution of the freshwater mussels Unionoida*. Ecological Studies 145. Springer, Berlin, Germany.

Zale, A.V., and R.J. Neves. 1982a. Reproductive biology of four freshwater mussel species (Mollusca:Unionidae) in Virginia. *Freshwater Invertebrate Biology* 1:17–28.

Zale, A.V., and R.J. Neves. 1982b. Fish hosts of four species of lampsiline mussels (Mollusca:Unionidae) in Big Moccasin Creek, Virginia. *Canadian Journal of Zoology* 60: 2535–2542.

Zale, A.V., and R.J. Neves. 1982c. Identification of a fish host for *Alasmidonta minor* (Mollusca: Unionidae). *American Midland Naturalist* 107:386–388.

Zambrano, L., and D. Hinojosa. 1999. Direct and indirect effects of carp (*Cyprinus carpio* L.) on macrophyte and benthic communities in experimental shallow ponds in central Mexico. *Hydrobiologia* 408–409:131–138.

Zanatta, D.T., and R.W. Murphy. 2006. Evolution of active host-attraction strategies in the freshwater mussel tribe Lampsilini (Bivalvia:Unionidae). *Molecular Phylogenetics and Evolution* 41:195–208.

Zanatta, D.T., and R.W. Murphy. 2008. The phylogeographical and management implications of genetic population structure in the imperiled snuffbox mussel, *Epioblasma triquetra* (Bivalvia:Unionidae). *Biological Journal of the Linnean Society* 93:371–384.

Zanatta, D.T., et al. 2007a. Reassessment of the phylogenetic relationships among *Anodonta, Pyganodon*, and *Utterbackia* (Bivalvia: Unionoida) using mutation coding of allozyme data. *Proceedings of the Academy of Natural Sciences of Philadelphia* 156: 211–216.

Zanatta, D.T., et al. 2007b. Population structure and mantle display polymorphisms in the wavy-rayed lampmussel, *Lampsilis fasciola* (Bivalvia:Unionidae). *Canadian Journal of Zoology* 85:1169–1181.

Zieritz, A., and D.C. Aldridge. 2011. Sexual, habitat-constrained and parasite-induced dimorphism in the shell of a freshwater mussel (*Anodonta anatina*, Unionidae). *Journal of Morphology* 272:1365–1375.

Zigler, S.J., et al. 2008. Importance of physical and hydraulic characteristics to unionid mussels: A retrospective analysis in a reach of large river. *Hydrobiologia* 598:343–360.

Zimmerman, G.F., and F.A. de Szalay. 2007. Influence of unionid mussels (Mollusca: Unionidae) on sediment stability: An artificial stream study. *Fundamental and Applied Limnology* 168:299–306.

Zimmerman, L.L., and R.J. Neves. 2002. Effects of temperature on duration of viability for glochidia of freshwater mussels (Bivalvia:Unionidae). *American Malacological Bulletin* 17:31–35.

Zimmerman, L.L., et al. 2003. Control of predacious flatworms *Macrostomum* sp. in culturing juvenile freshwater mussels. *North American Journal of Aquaculture* 65:28–32.

Ziuganov, V.V., et al. 2000. Life span variation of the freshwater pearl shell: A model species for testing longevity mechanisms in animals. *Ambio* 29:102–105.

Ziuganov, V.V., et al. 2001. The pearl mussel-salmon community in the Varzuga River, northwest Russia: Problems of environmental impacts. Pages 359–366 in G. Bauer and K. Wächtler, editors. *Ecology and evolution of the freshwater mussels Unionoida*. Ecological Studies 145. Springer, Berlin, Germany.

Zouros, E., et al. 1994. An unusual type of mitochondrial DNA inheritance in the blue mussel *Mytilus*. *Proceedings of the National Academy of Sciences of the United States of America* 91:7463–7467.

Index