

CHAPTER 4

Life Histories of Potamodromous Fishes

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Definitions of potamodromy, potamodromous migrations and movements

Potamodromous fishes move and complete their life cycle entirely within freshwater. Myers (1949) proposed the term potamodromous to distinguish freshwater migratory fishes from diadromous fishes, which migrate between the sea and freshwater and oceanodromous fishes that migrate wholly within the sea. Diadromous fishes include anadromous, catadromous and amphidromous fishes (see Chapter 2, Morais and Daverat 2016). Despite its historical precedence, potamodromous has not been broadly accepted. Three other terms, 'non-anadromous', 'resident', and 'inland' are more commonly substituted in the fisheries literature. Unfortunately, these three terms have multiple definitions, as well as regional connotations which may confound their application to a broad geographic area (Gresswell et al. 1997). Consequently, potamodromous provides a more precise and more broadly applicable definition of fishes that remain wholly within freshwater.

Although potamodromous fishes are widespread among freshwater fish assemblages, the significance of potamodromy has received far less attention than diadromy (Northcote 1998). Unlike diadromy, no global analysis of potamodromous species has been undertaken, and it is limited by the difficulties in amassing information for inconspicuous and little-studied species, especially in the tropics (Flecker et al. 2010). Potamodromous fishes were included in a group-by-group review by Lucas and Baras (2001) of the migration and life cycle characteristics of species representative of families of fishes exhibiting migration in fresh and brackish water environments. Lucas and Baras (2001) explained that information was limited for some groups of freshwater fishes mostly found in tropical freshwater regions. This was partly because

of a paucity of information concerning spatial ecology at the species level; some of these groups (Cichlidae, Characiformes and Siluriformes) are very speciose, totaling over 5,000 species and representing nearly 50% of all fish species in freshwater (Lucas and Baras 2001). Flecker et al. (2010) reported that in both the tropics and temperate zone, potamodromy is likely the most common form of migration in stream fishes. Similarly, Lucas and Baras (2001) observed that in many large tropical rivers, more than 95% of the migratory fishes are potamodromous.

Migration and movements between biomes on a daily, seasonal, or annual basis, represents a fundamental aspect of the ecology of populations and individuals (Hobson 1999). Despite residing only in freshwater, for a variety of reasons, potamodromous fishes move and migrate various distances throughout their life cycle. As Dingle and Drake (2007) observed, our understanding of the movements of organisms has been hindered by imprecise and ambiguous terminology. As a result, it may be useful to begin by defining the terms movement and migration.

Movement may be defined as the act of changing locations or positions. In potamodromous fishes, these movements are most commonly associated with seeking essential resources (i.e., food) and they may be in response to other organisms (i.e., seeking cover from predators). For example, a potamodromous sculpin *Cottus* spp. residing in a pool may suddenly move and change 'position' to consume an aquatic insect larvae on the stream substrate. This same sculpin may change its 'location' in the same pool by moving beneath a boulder to escape an avian predator. Dingle (1996) observed that most movements occur within a relatively well defined area or home range. An organism travels or moves within its home range to acquire the resources it needs to survive. The size of the home range will tend to vary depending on the habitat and the size and movement abilities of the organism (Dingle 1996). Consequently, the sculpin in our example above, will have a much smaller home range compared to the average home range size (mean home range of 146 ha) for a 70–100 cm long muskellunge *Esox masquinongy* (Miller and Menzel 1986).

Movements and associated behaviors within a home range have also been termed 'station keeping' and perhaps the most prominent example is foraging (Kennedy 1985; Dingle 1996). Foraging is a repetitive and meandering movement that focuses on locating resources (food, cover, or mates). Foraging characteristically occurs on short timescales and small spatial scales within the home range (Dingle and Drake 2007). In our examples above, depending in part on food availability, the much larger and faster swimming muskellunge will potentially forage within a much larger area compared to the sculpin. A specialized form of foraging, that includes to-and-fro movements, is the diel vertical movement of fishes such as alewife *Alosa pseudoharengus* to consume zooplankton (Janssen and Brandt 1980). Another example of a 'station keeping' behavior is the territorial behavior that results in agonistic encounters between individuals. McNicol et al. (1985) reported frequent agonistic interactions between young-of-the-year brook trout *Salvelinus fontinalis*, in a second-order woodland stream.

Migration differs substantially from the often repetitive movements within home ranges described above. Home range movements are primarily in response to local resources. Migration is considered a more specialized type of movement, often,

but not necessarily occurring at larger temporal and spatial scales. Dingle (1996) emphasized that migration differs from other types of movements both qualitatively and quantitatively. Unlike the sculpin, muskellunge, and alewife movements described above, Dingle (1996) observed that migration is not a proximate response to resources nor does it serve to keep an organism in its habitat. Rather, migration results in fishes moving from one habitat and relocating to another habitat outside their home range. Dingle (1996) observed that the most distinctive feature of migration is that migrants do not respond to sensory cues from resources (e.g., food or shelter) that would typically elicit responses. For example, during their annual migration to spawning sites, adult walleye *Stizostedion vitreum vitreum* may feed or temporarily seek shelter. However, unlike the above referenced foraging movement of a muskellunge within its home range, the presence of an abundant food source or suitable cover will not cause migrating walleye to stop. Their upstream migration ceases only when adult walleye arrive at their spawning location (i.e., Crowe 1962).

Migration involves two levels, the behavioral level that applies to individuals and the ecological level that applies to populations (Dingle and Drake 2007). Therefore, a broad conceptual understanding of migration encompasses both its mechanism and its function. Northcote (1978) distinguished migration from other types of fish movements and suggested four main features: (1) resulting in an alternation between two or more well-separated habitats; (2) occurring with regular periodicity (often seasonal) within the individual lifespan; (3) involving a large fraction of the population; and (4) being directed rather than a random wandering or passive drift. Decades later, Dingle and Drake (2007) suggested that migration represents four different but overlapping concepts which are very similar to those of Northcote (1978). The concepts of Dingle and Drake (2007) are also applicable to potamodromous fishes: (1) a type of locomotory activity that is notably persistent, undistracted, and straightened out (i.e., fall downstream migrations of adult westslope cutthroat trout *Salmo clarkia lewisii* to overwintering areas in large pools) (Bjornn and Mallet 1964); (2) a relocation of the animal that is on a much greater scale, and involves movement of much longer duration, than those arising in its normal daily activities (i.e., spring upstream migrations of mature walleye to spawning areas) (Crowe 1962); (3) a seasonal to-and-fro movement of populations between regions where conditions are alternately favorable or unfavorable (i.e., summer upstream migrations of brook trout seeking cold water refugia (Petty et al. 2012) followed by fall downstream migrations to more suitable overwintering habitats) (Chisholm et al. 1987); and (4) movements leading to redistribution or dispersal within a spatially extended population (i.e., downstream drift of newly hatched white sucker *Catostomus commersoni* larvae to areas with higher zooplankton production) (Corbett and Powles 1986). Dingle and Drake (2007) explained that migration of types 1 and 2 relate to individual organisms, while types 3 and 4 explicitly concern populations. Further, type 1 migration describes a process, whereas the other three migrations describe the outcomes (for individuals or populations) of migration by individuals.

Baker (1978) proposed that the sum of all migrations and movements during an organism's lifetime be termed a 'lifetime track'. An organism's lifetime track is essentially the time series of its successive locations throughout its lifetime

(Dingle and Drake 2007). Technological advances in tracking devices now allow biologists to more explicitly monitor a fishes' lifetime track. Hanson et al. (2007), for example, applied a whole-lake acoustic telemetry array to closely monitor the three-dimensional position of largemouth bass *Micropterus salmoides* across multiple temporal and spatial scales. Between November 2003 and April 2004, the authors simultaneously monitored 20 largemouth bass with transmitters (equipped with pressure and temperature sensors) at 15 second intervals with sub-meter accuracy. A fishes' lifetime track is influenced by its size, life history traits, ability to migrate, geographic range, and habitat. Dingle (1996) emphasized an important concept when he observed that the composite of movements, migrations, and stationary elements that form the lifetime track is determined by natural selection. The dynamics of fish populations are in turn influenced by the migrations and movements of the individual fishes it contains (Dingle 1996).

A strategy can be defined as a genetically determined life history type or behavior which has evolved because it maximizes fitness of individuals and populations (Gross 1987). Fitness can be defined as lifetime reproductive success. As Gross et al. (1988) summarized, the importance of food intake for growth, decreased mortality, increased fecundity, and improved breeding success is well documented. Gross et al. (1988) compared the distribution of diadromous fishes to global patterns in aquatic productivity and concluded that food availability is an important factor determining both where migratory fishes occur and their direction of movement.

Migration and movements are very widespread strategies in potamodromous fishes (Northcote 1978) and ultimately result in fish switching habitats. Salmonids, for example, change habitats many times during their growth and development, and each change within and across life stages involves migration (Thorpe 1988). Early studies of fish migration relied on external marks to track individuals between habitats in an effort to characterize timing and duration. As Lucas and Baras (2001) observed, the relative inadequacy of early techniques used to investigate the migration of freshwater fishes contributed to the idea that many freshwater fishes exhibit very little movement, which is now viewed as a misplaced paradigm (Gowan et al. 1994). Fisheries biology is moving from descriptive studies to more mechanistic approaches that strive to understand the ecological and evolutionary importance of migration. Cooke et al. (2008), for example, advanced understanding of sockeye salmon *Oncorhynchus nerka* migration through the integration of disciplines including physiology, behavior, functional genomics, and experimental biology.

Understanding habitat connectivity and the characteristics of essential habitats utilized by potamodromous species, throughout their often complex life histories, is essential to their effective conservation. Such knowledge can effectively be directed to conserve the habitats that are critical for various species life stages (e.g., Myers et al. 1987). In this chapter, we include a broad spatial and temporal spectrum of migrations and movements by potamodromous fishes; ranging from short-distance (~ 1–2 meter) diel movements of juvenile bull trout *Salvelinus confluentus* seeking winter concealment in interstitial areas of stream substrates (Thurow 1997), to very long distance (> 650 km) spawning migrations of adult Colorado pikeminnow *Ptychocheilus lucius* over several months (Irving and Modde 2000).

Taxonomic and biogeographic distribution of potamodromous fishes

Taxonomists currently list 33,592 identified fish species worldwide with 217 new species added in 2015 as of August 3, 2015 (Eschmeyer and Fong 2015). In 2006, 27,977 species of fish were identified and about 43% (11,952) were considered strictly freshwater species (Nelson 2006). If 40% of currently known fish species worldwide reside strictly in freshwater, then it is likely that more than 13,000 fish species meet our definition as potamodromous fishes. Flecker et al. (2010) observed that, collectively, potamodromous species can represent a substantial proportion of fish biomass even in the largest freshwater ecosystems. In South America, for example, potamodromous fishes are dominated by large pimelodid catfish and characins, many of commercial importance. In Africa, potamodromous species include characins, siluroids, cyprinids, and mormyrids that move from lakes to tributaries and upstream swamps to spawn. In Asia, among the best known potamodromous fishes are pangasiid catfish and cyprinids, such as some barbs, as well as members of the genus *Tor* that are known to ascend Himalayan streams (Welcomme 1985).

Ross (2013) reported that the freshwater fish fauna of North America is the most diverse and thoroughly researched temperate fish fauna in the world. As a result of the abundance of literature describing North American freshwater fishes, this chapter will focus on well-studied potamodromous fishes within North America.

Worldwide, potamodromous fishes represent at least 31 orders of fishes. Thirteen of those orders are not native to North America. These include: Atheriniformes, Ceratodontiformes, Characiformes, Gonorynchiformes, Gymnotiformes, Mugiliformes, Osteoglossiformes, Pleuronectiformes, Rajiformes, Scorpaeniformes, Synbranchiformes, Syngnathiformes, and Tetraodontiformes. North American potamodromous species are extremely diverse and represent 18 distinct orders: Lepisosteiformes (gars), Amiiformes (bowfin), Hiodontiformes (mooneye), Clupeiformes (alewife), Osmeriformes (smelt), Percopsiformes (trout-perch, cave fishes, and pirate perch), Acipenseriformes (sturgeons, and paddlefishes), Cypriniformes (minnows, carp, and suckers), Siluriformes (catfishes), Esociformes (pikes and pickerels), Salmoniformes (whitefish, trout, and salmon), Scorpaeniformes (sculpin), Perciformes (bass, sunfish, perch, cichlids, and drums), Gadiformes (burbot), Atheriniformes (silversides), Cyprinodontiformes (top minnows, killifish, and pupfish), Gasterosteiformes (sticklebacks), and Petromyzontiformes (lamprey) (Eschmeyer 2013).

Within North America, these 18 orders represent 29 families of fish that reside wholly within freshwater. An additional two families (Clupeidae and Osmeridae) were formerly anadromous, but have been introduced, as alewife and rainbow smelt *Osmerus esperlantis*, respectively, and are now landlocked within the freshwaters of the Great Lakes and other North American waters (Scott and Crossman 1973). Adding to this diverse list of potamodromous species is the potential for several anadromous species to develop potamodromous populations. Northcote (1997), for example, described four North American species of Pacific salmon that now have permanent freshwater residence. Three species, pink salmon *Oncorhynchus gorbuscha*, coho salmon *Oncorhynchus kisutch*, and Chinook salmon *Oncorhynchus tshawytscha* developed potamodromous populations after introductions to the Great Lakes (Scott and Crossman

1973). Sea lamprey *Petromyzon marinus* also established potamodromous forms after introductions to the Great Lakes (Clemens et al. 2010). Potamodromous populations develop naturally in landlocked sockeye or kokanee *Oncorhynchus nerka*, as well as in landlocked salmon or Ouananiche; the freshwater form of Atlantic salmon *Salmo salar*. Boucher (2004) reported that prior to 1868 landlocked salmon occurred naturally in four Maine River Basins. After extensive stocking, Maine supported one of the largest sport fisheries for landlocked salmon in the world with fisheries in 176 lakes and about 464 km of rivers and streams (Boucher 2004). Outside North America, other anadromous salmonid forms of *Oncorhynchus* including masu salmon *Oncorhynchus masou*, and Biwa trout *Oncorhynchus rhodurus* also develop potamodromous populations (Northcote 1997). Other formerly anadromous species such as white sturgeon *Acipenser transmontanus* have similarly developed potamodromous forms after becoming landlocked above dams and impoundments in the Columbia and Kootenai Rivers (Jager et al. 2001). Some landlocked fish populations may reacquire former life history strategies after being 'unlocked' (see Chapter 2).

Key characteristics of potamodromous fishes

The 18 orders of North American potamodromous fishes represent thousands of diverse fish species that exhibit a variety of life stages, life history strategies, and associated movements. Despite this diversity, all of the North American potamodromous fishes persisting in riverine or lacustrine environments share some common life stages and life history strategies.

Life stages

Schlosser's (1991) provided a useful synthesis of freshwater fish life stages. Fish vary dramatically in size and behavior, from embryo to larvae, then to juvenile and subsequently to sub-adult and to adult (Fig. 4.1). For more detailed descriptions of the life stages of a variety of North American fishes, see Scott and Crossman (1973). Life begins when fertilized eggs are either buried within substrates, broadcast over the surface of substrates, broadcast into the water column, or attached to plant material. Eggs mature after an incubation period lasting anywhere from a few days (i.e., Cypriniformes) to several months (i.e., Salmoniformes) when they hatch to produce a free embryo phase (Schlosser 1991). During the brief free embryo phase, potamodromous fishes rely on energy sources provided entirely by an egg yolk sac. For a thorough review of yolk sac absorption, see Heming and Buddington (1988). In some groups (i.e., Salmoniformes, Petromyzontiformes) the yolk-sac embryos remain hidden in the substrate and do not emerge until the yolk sac is completely absorbed (Schlosser 1991). In others (i.e., walleye) hatched embryos begin feeding before the yolk sac is absorbed, after which fry disperse into open water (Scott and Crossman 1973). As soon as the free embryo phase is complete, the fish begin feeding on external energy sources, and at this point they are termed larvae. The larval phase is variable in length and ends after completion of the axial skeleton and development of a fully formed organ system and fins (Schlosser 1991). When fully formed the

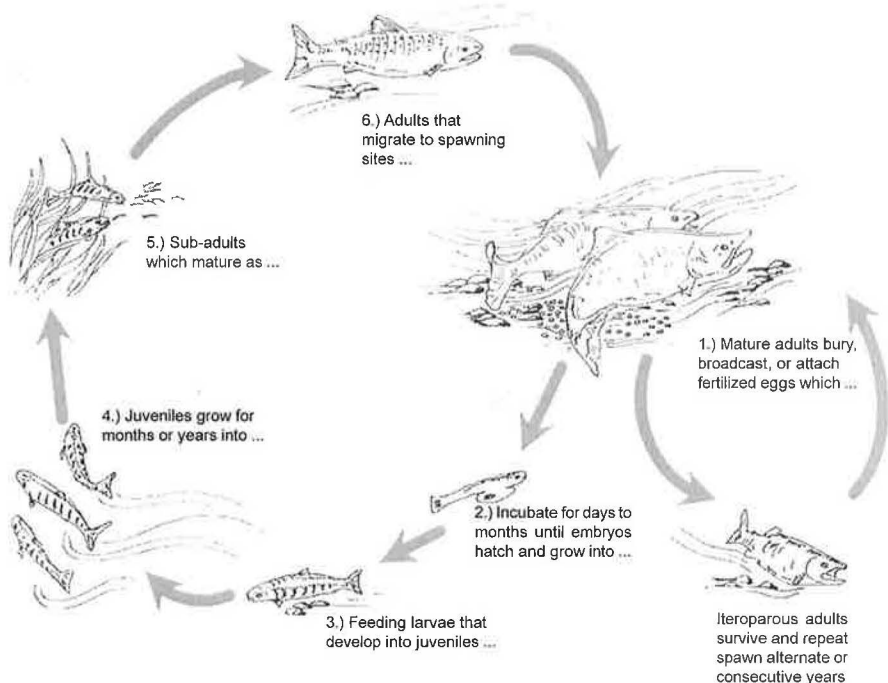


Figure 4.1. Common life stages of North American potamodromous fishes in riverine and lacustrine environments (revised from Thurow 1982).

larvae become juveniles (Schlosser 1991). During the juvenile stage, fish undergo a number of seasonally favorable periods with rapid growth, followed by seasonally unfavorable periods with reduced growth until sexual maturity is reached (Schlosser 1991). In North American temperate streams, these favorable and unfavorable periods frequently involve migration between summer and winter habitats. Depending on the species, the juvenile life stage may encompass months or years (Schlosser 1991). Juveniles ultimately develop into sub-adults, the life stage immediately prior to sexually mature adults. After sexual maturity is attained, adults complete spawning migrations to locate appropriate sites for egg deposition and re-initiation of the life cycle (Schlosser 1991). In iteroparous species, surviving adults return to repeat spawn in alternate or consecutive years (Schlosser 1991).

Life-history strategies

Within these general life stages, tremendous diversity occurs in the specific life-history characteristics of the different fish species. For example, substantial variation occurs in spawning migrations; seasonal occurrence of eggs, young, and adults; and feeding habitats. Consequently, no single life history definition is all inclusive and, as Northcote (1997) observed, one may wish to further define the life history forms of potamodromous fishes. Riverine reproductive migrations of salmonids have been

applied to partition them into four main life history forms: fluvial (spawn and rear in large rivers and streams), fluvial-adfluvial (spawn in tributaries and rear in streams, rivers, and tributaries), lacustrine-adfluvial (spawn in lake tributaries and rear primarily in lakes), and allacustrine (spawn in lake outlets and rear primarily in lakes) (Varley and Gresswell 1988) (Fig. 4.2). These various life stages and life history types may be applied to begin describing the diverse types of migrations; including reasons for migrations, migration timing, and the ways fish migrate.

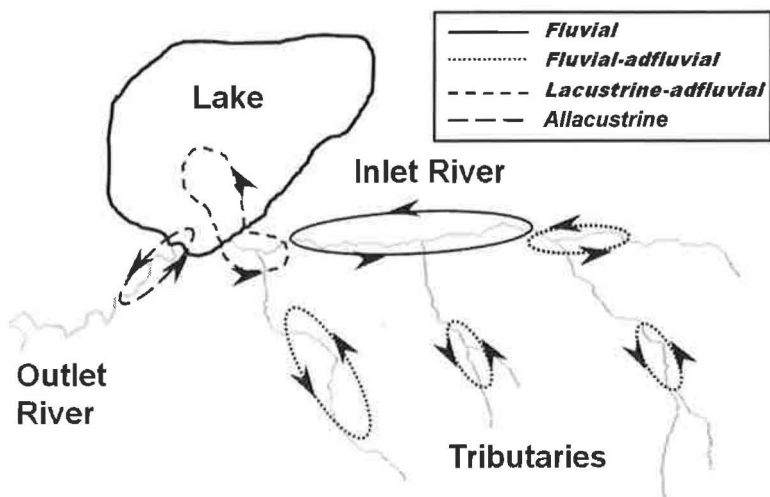


Figure 4.2. Potamodromous salmonid life history forms (adapted from Varley and Gresswell 1988). Ovals and arrows represent migration paths between spawning and rearing areas in rivers, tributaries, and lakes.

Types of migration

Potamodromous fishes exhibit complex life cycles and habitat-use patterns that are integrated with the diversity of their various life stages and associated body sizes (Northcote 1984; Schlosser 1991). Northcote (1984) explained that migratory behavior arises from spatial, seasonal, and ontogenetic separation of optimal habitats for growth, survival, and reproduction. Schlosser (1991) described the basic migrations of stream fishes among three types of habitat (feeding, overwintering, and spawning). Northcote (1997) examined riverine populations of 34 species of salmonids in detail, and he summarized potamodromy as a cyclic sequence of three types of migrations (trophic, refuge, and reproductive) between three respective habitats (feeding, overwintering, and spawning) (Fig. 4.3).

Migration is known to be an important tactic for thermoregulation of coldwater species (Petty et al. 2012). Consequently, refuge migrations by potamodromous fishes may be of two primary types; migrations by fish seeking overwinter refuge habitat and refuge migrations by fishes seeking cover or thermoregulation during non-winter periods. The three types of migration outlined by Schlosser (1991) and Northcote (1997) were adopted by me and I revised destination habitat types to include both

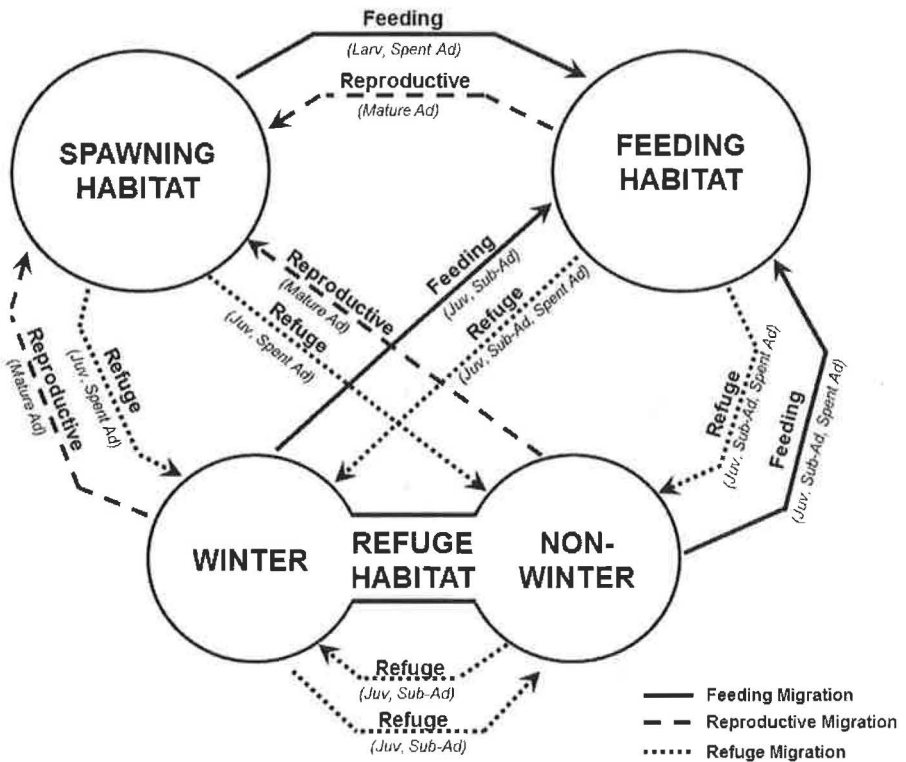


Figure 4.3. Generalized movements (Feeding, Reproductive, and Refuge Migrations) by North American potamodromous fishes with emphasis on patterns of migration between essential feeding, spawning, and refuge habitats (revised from Schlosser 1991 and Northcote 1997). Legend: Larvae-Larv, Juvenile-Juv, Sub-Adults-Sub-Ad, Adults-Ad.

overwintering refuge and non-winter refuge habitats. One can therefore summarize potamodromy as a cyclic sequence of migrations (feeding, refuge and reproduction) among four types of habitat (feeding, winter refuge, non-winter refuge and spawning) (Fig. 4.3).

After hatching, most potamodromous fishes migrate during each of the four subsequent mobile life stages (larvae, juvenile, sub-adult, and adult) (Figs. 4.1, 4.3). The diversity of destination habitats and movement patterns by potamodromous fishes in riverine and lacustrine systems reflect seasonal habitat preferences, as well as shifts in preferred habitats as fishes develop among life stages (Northcote 1984; Schlosser 1991). This broad temporal and spatial scale of movement can be illustrated by a series of examples from each of the four major life stages summarized in Table 4.1. After larval fish emerge, some may drift passively with stream or lake currents (Brown and Armstrong 1985). Others may begin feeding, even before their yolk sac is absorbed (i.e., walleye noted above).

After fish attain the juvenile stage, the diversity of movements may further increase. If there is an abundant food supply, if cover is adequate (i.e., water depth,

Table 4.1. Generalized migrations and movements by North American potamodromous fishes in riverine and lacustrine environments. These movements reflect seasonal habitat preferences as well as life stage related shifts in preferred habitats as fishes develop to maturity.

Life Stage	Type	Movement	Destination Habitat	References
I. Adult	Maturing adults (Pre-Spawning)	Feeding migration	Feeding/rearing	Crowe 1962
		Refuge migration	Thermal refugia/staging	Bjornn and Mallet 1964
		Refuge migration	Overwintering	Swanberg 1997
		Diel summer movements	Feeding to resting and back	Janssen and Brandt 1980
		Diel winter movements	Concealment out and back	Wang et al. 2007
	Gravid adults (Spawning)	Reproductive migration	Spawning	Irving and Modde 2000
	Spent adults (Post-Spawning) Iteroparous	Feeding migration	Feeding/rearing	Swanberg 1997
		Refuge migration	Thermal refugia/staging	Stevens and DuPont 2011
		Refuge migration	Overwintering	
		Diel summer movements	Feeding to resting and back	
		Diel winter movements	Concealment out and back	
	Kelts (Post-spawning)	Passive dispersal and death	Downstream in riverine or drift in lacustrine	Brown and Mackay 1995
II. Embryos	Emerged with yolk sac	Diel movements Passive dispersal	Feeding/rearing Downstream in riverine or drift in lacustrine	Scott and Crossman 1973
III. Larvae	Free swimming larvae	Passive dispersal Feeding migration Refuge migration Refuge migration Diel summer movements Diel winter movements	Downstream in riverine or drift in lacustrine Feeding/rearing Thermal refugia/cover Overwintering Feeding to resting and back Concealment out and back	Tyus and McAda 1984 Corbett and Powles 1986

IV. Juvenile	Diverse juvenile ages and sizes	Feeding migration Refuge migration Refuge migration Diel summer movements Diel winter movements	Feeding/rearing Thermal refugia/cover Overwintering Feeding to resting and back Concealment out and back	Wolfert 1963 McNicol et al. 1985 Chisholm et al. 1987 Thurrow 1997
V. Sub-adult	Sexually immature	Feeding migration Refuge migration Refuge migration Diel summer movements Diel winter movements Pied Piper migrations	Feeding/rearing Thermal refugia/staging Overwintering Feeding to resting and back Concealment out and back Unknown	Janssen and Brandt 1980 Schill et al. 1994 Petty 2012

overhead cover) and if other rearing conditions are favorable (i.e., suitable water temperatures), juveniles may establish a home range and move within that range until winter when they will complete a refuge migration to overwintering refuge habitat (Schlosser 1991). However, juveniles may migrate to feeding and or non-winter refuge habitats outside a home range if food or cover is lacking, or if water temperatures increase above the suitable range (Petty et al. 2012). The scale and number of movements are also influenced by the longevity of the life stages. Female lake sturgeon *Acipenser fulvescens*, for example, may not attain sexual maturity until an age of approximately 20 years (Threader and Broussau 1986). Consequently, juvenile lake sturgeon may complete numerous migrations to a series of feeding, non-winter refuge, and winter refuge habitats (Threader and Broussau 1986). As Northcote (1997) observed, preferred habitats are not necessarily the same ones occupied during the previous year migrations. The locations of preferred habitats may change as the fish grow, age, and have different habitat requirements (Schlosser 1991). In their final life stages, both sub-adult and adult fishes also complete annual migrations to a series of feeding and winter refuge habitats (Schlosser 1991), as well as non-winter refuge habitats (Petty et al. 2012).

Gerking (1959) defined homing as "the return to a place formerly occupied instead of going to other equally probable places". The effects of homing or fidelity to the same habitats are addressed below. Longer lived species, such as the lake sturgeon (maximum age of 154 years) (Scott and Crossman 1973), have the potential to complete hundreds of annual feeding and refuge migrations. To add to this complexity of movements, adults of all species also complete reproductive migrations to appropriate spawning habitats (Schlosser 1991). Since many potamodromous species, such as Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri*, are iteroparous, surviving adults complete spawning migrations over multiple years which further increases the complexity of migrations (Thurrow et al. 1988). If repeat spawning adults return to the same spawning site, this 'homing' behavior will reduce the number of different spawning habitats an individual fish migrates to. If fish do not have high fidelity to the same spawning site, this will add further spatial complexity to spawning migrations.

As Northcote (1997) observed, the apparent simplicity of a table or figure used to summarize movements of potamodromous fishes is deceiving. Within each of the four mobile life stages, many types of movements are repeated and a large diversity of habitats may be utilized over very large temporal and spatial scales. Examples of feeding, refuge, and spawning migrations are provided below. Temporal and spatial scales of migration between these habitats are directly influenced by the species life histories and habitat requirements. Flathead catfish *Pylodictis olivaris*, for example, may not require expansive stretches of river in order to complete critical life stages, so they tend to have relatively smaller home ranges and exhibit more localized movements (Daugherty and Sutton 2005). Alternatively, alligator gars *Atractosteus spatula* and other long-lived, large-bodied, and highly mobile species, as sturgeon *Acipenser* spp. and paddlefish *Polydon* spp., tend to have large home ranges (Minns 1995) and complete extensive migrations because habitats used for reproduction, refuge, and feeding are dispersed. Diel movements or other movements within home ranges, which are of more restricted spatial and temporal scale, are addressed later.

Feeding migrations

Migrations to preferred feeding habitats, with either more abundant or more suitable prey, may be completed by all four mobile life stages (larvae, juveniles, sub-adults, and adults). Larval Colorado pikeminnow drifted from spawning areas in the lower Yampa River downstream to shallow, productive nursery habitats in the Green River (Tyus and McCada 1984). The authors observed that this larval life history strategy, which likely benefited the Colorado pikeminnow formerly, could be implicated in its decline in the lower Colorado River, where dams may have blocked migration routes and degraded nursery habitats. Similarly, newly hatched white sucker larvae drifted downstream on a feeding migration to areas with higher zooplankton production (Corbett and Powles 1986).

Juveniles of many species migrate to preferred feeding areas. In Lake Erie, yearling walleye migrated from a known nursery area and traveled primarily north toward the Western Basin during their first year, and in succeeding years moved progressively toward the extreme western end of the lake. Marked juvenile walleye migrated an average of 40 km from the nursery area and one juvenile migrated more than 320 km (Wolfert 1963).

Wang et al. (2007) monitored movements of adult walleye across Lake Erie and suggested these migrations may be a response to spatial patterns in prey abundance (soft-rayed prey preferred cooler temperatures). Knight et al. (1984) and Knight and Vondracek (1993) observed shifts in walleye diets according to the availability of prey, and confirmed that adult walleyes prefer to feed on soft-rayed fish (i.e., spottail shiner *Notropis hudsonius*, and clupeids (i.e., alewife) rather than on spiny-rayed fish (i.e., yellow perch *Perca flavescens*). Clupeids and spiny-rayed fish are fast-growing forage fish that become invulnerable to walleye predation after one growing season, whereas smaller soft-rayed fish of all ages are easily caught and digested by walleyes (Knight and Vondracek 1993).

Surviving adults also migrate to feeding or refuge habitats after spawning. The distance that iteroparous forms migrate, their post-spawning condition, and the quality of the habitats they migrate to, likely influence their ability to survive and repeat spawn (Brown and Mackay 1995). Brown and Mackay (1995) reported cutthroat trout post-spawning mortality of less than 14%, but noted that other researchers have observed much higher (60%) post-spawning mortality rates. This relatively low spawning mortality may have been a result of shorter migrations to spawning areas in their watershed, compared with cutthroat trout migrations in the other studied basins (Brown and Mackay 1995).

Refuge migrations

Refuge migrations occur for a variety of purposes, including seasonal refuge from severe conditions, such as extreme low temperatures during winter or low water and dissolved oxygen deficit in floodplains during the dry season (Flecker et al. 2010). Refuge migrations may be of two primary types: (1) migrations by fish seeking overwinter refuge habitat; (2) migrations by fish seeking refuge habitats during non-winter periods.

Non-winter refuge migrations: As water temperature increase in spring, mature bull trout begin migrating from overwintering refuge habitats, at lower elevations, toward spawning areas, at higher elevations (Swanberg 1997). Spawning does not commence for several months, and between spring and late summer, adult bull trout migrate to and stage in thermally suitable refuge habitats for varying periods of time (Swanberg 1997). As water temperatures increased in mid-June, adult bull trout sometimes exhibited rapid upstream migrations to higher elevation habitats (Schill et al. 1994). Movements related to the seeking of thermal refugia have also been reported for other potamodromous species. Brook trout migrated upstream in summer while seeking cold water refugia (Petty et al. 2012). Stevens and Dupont (2011) observed westslope cutthroat trout, rainbow trout *Oncorhynchus mykiss*, and mountain whitefish *Prosopium williamsoni* moving into cooler Coeur d'Alene River side channels as main-river water temperatures increased. Movements and aggregations of salmonids seeking coldwater refugia in streams have also been documented for brook trout (Baird and Krueger 2003) and rainbow trout (Kaya et al. 1977; Ebersole et al. 2001; Sutton et al. 2007). Lake dwelling brook trout (Biro 1998) and lake trout *Salvelinus namaycush* (Snucins and Gunn 1995) have been similarly observed moving into cooler water areas as water temperatures rose in lakes.

Potamodromous fishes may also exhibit high fidelity to suitable summer refuge habitats. Individual smallmouth bass *Micropterus dolomieu* returned to the same 5 km reach of summer habitat (Langhurst and Schoenike 1990). Daugherty and Sutton (2005) similarly observed flathead catfish homing to summer habitats.

Winter refuge migrations: Overwinter ecology of stream-dwelling fishes is perhaps the least understood aspect of their life history. Many fishes occupy different habitats in winter than in summer. As water temperatures decline, fish move from summer habitat into suitable overwintering areas, often at much lower elevations (Bjornn and Mallet 1964). These lower elevation overwintering habitats may provide more benign conditions such as warmer water temperatures, less anchor ice, and more opportunities to escape predators. The distances fish move also seem to be influenced by the proximity of suitable overwintering habitat (Chapman and McLeod 1987). For example, at the onset of winter, stream-dwelling salmonids in the Intermountain West (northwestern USA) typically adopt two overwintering strategies, migration to more suitable overwinter habitats or concealment within their home range if the local habitat is suitable (Thurow 1997). Chapman and McLeod (1987) suggested juvenile salmonids seek overwintering areas in the most upstream locations near summer rearing areas. After locating suitable overwinter habitat, juvenile salmonids typically select areas of low water velocity and enter concealment cover (Edmundson et al. 1968; Cunjak 1988; Thurow 1997). In contrast, adult fishes often overwinter in deep water habitats. For example, adult westslope cutthroat trout migrated more than 100 km downstream to overwinter in large, deep pools (Bjornn and Mallet 1964). Similarly, as water temperatures declined below 16°C in autumn, smallmouth bass migrated long distances downstream (69–87 km) from summer habitats to overwintering habitats in deep pools (Langhurst and Schoenike 1990). Munther (1970) and Paragamian (1981) similarly observed adult smallmouth bass moving into deep pools as temperatures cooled, but neither described long-range movements. Langhurst and Schoenike (1990) suggest the paucity

of deep pools near summer habitat may have been the reason for the long migration of smallmouth bass they documented. Fall migrations of bull trout to lower elevation overwintering habitats are also well documented. Many adult bull trout migrate, more than 100 km, to overwinter in deep pools in the lower portions of watersheds (Schill et al. 1994; Swanberg 1997; Hogan and Scarnecchia 2006). Brook trout (Chisholm et al. 1987) and channel catfish *Ictalurus punctatus* have also been observed migrating downstream in fall to more suitable overwintering habitats (Pellet et al. 1998).

Homing behavior in fishes is believed to facilitate development of population-specific adaptations to the habitat occupied (Leggett 1977). For example, alligator gar exhibited high fidelity to overwintering sites (Kluender 2011). This fidelity to high quality overwintering areas may optimize survival.

Spawning migrations

Seasonal migrations to spawning sites are very common in potamodromous fishes. Mature walleye complete upstream migrations to spring spawning areas (Crowe 1962), while fall spawning species, such as bull trout, also migrate to spawning areas (Swanberg 1997). Natal homing or natal philopatry is well documented in several potamodromous species, most commonly in salmonids (Hasler and Scholz 1983; Northcote 1984). Homing may also result in reproductive isolation producing fish stocks unique in behavior, energetics, and reproductive characteristics (Leggett 1977).

High levels of natal homing have been reported for coregonines, thymallines, and salmonines (Northcote 1997). Although non-salmonids are less studied, homing to a previous spawning location has been reported in Colorado pikeminnow (Tyus 1985), walleye (Crowe 1962), longnose suckers *Catostomus catostomus* and white suckers (Geen et al. 1966), northern pike *Esox lucius* (Miller et al. 2001), muskellunge (Crossman 1990), channel catfish (Pellet et al. 1998), paddlefish *Polyodon spathula* (Firehammer and Scarnecchia 2007), razorback suckers *Xyrauchen texanus* (Tyus and Karp 1990), white bass *Morone chrysops* (Horral 1981), and alligator gar (Kluender 2011).

There are advantages to maintaining high levels of reproductive homing: eggs are deposited in suitable habitat and homing tends to balance the number of spawners with the reproductive capacity of the area (Northcote 1997). Despite the benefits of homing, some straying may also have a long term selective advantage; enabling species to invade new areas and repopulate old ones in the wake of stochastic events (Lindsey et al. 1959). Following the 1980 eruption of Mount St. Helens in Washington (USA), native cutthroat trout and sculpin, that found refugia in ice covered lakes or less-impacted tributaries, were able to recolonize streams where fish populations had been extirpated (Bisson et al. 2005).

In some potamodromous species, sub-adults complete a unique type of migration that may be associated with adult fish movements. These migrations could be termed 'Pied Piper' migrations, since immature, sub-adult fish appear to follow mature adults as they are migrating to spawning sites. Schill et al. (1994) reported sub-adult bull trout migrating upstream in Rapid River along with mature bull trout from April–July. In August, the sub-adult bull trout stopped migrating before reaching spawning

sites and subsequently reversed their migration back downstream to other habitats (Schill et al. 1994). The authors reported that the likelihood of this behavior increased in bull trout smaller than 45 cm in length, suggesting the downstream movements may be associated with the seeking of summer thermal refugia or feeding habitats.

Diel and lesser scale movements

As described previously, movements within home ranges are primarily in response to local resources and typically consist of station-keeping behaviors such as foraging or agonistic behavior. Such movements also differ from migrations because of their more restricted spatial and temporal scales. Smaller and shorter-lived species, such as *Cottus* spp., tend to require smaller home ranges if all critical habitats are available locally in contrast to the species described above (i.e., gar and sturgeon) with much large home ranges and extensive migrations.

Diel movements represent a specialized type of movement within home ranges and may be associated with feeding or refuge movements. The extent and timing of diel vertical movements of adult alewives in Lake Michigan, for example, coincided with diel movements of mysis zooplankton (*Mysis relicta*). Both mysis and adult alewife concentrated at the bottom during the day and migrated upwards to the base of the thermocline at night, with their stomach contents indicating the alewife vertical movements were mechanistically linked to feeding behavior (Janssen and Brandt 1980). In winter, at water temperatures less than 2°C, juvenile bull trout exhibited diel behavioral movements. During the day, all bull trout were concealed in the substrate, while at night, some bull trout moved out of daytime concealment cover into the water column (Thurow 1997). At night, Thurow (1997) observed feeding and resting, primarily in pool and run habitats.

Benefits of potamodromy

Fish migration has been described as a life history syndrome involving energetic trade-offs between movements and energetic output (Schaffer and Elson 1975; Leggett 1977). Movements between habitats create both costs and benefits; costs include energy and physiological demands for osmoregulation, the energetic demands of swimming, and exposure to predators and disease (Gross 1987). The benefits of potamodromy could be organized into three categories: survival benefits to potamodromous fishes, benefits to humans, and lastly, benefits to the functioning of the entire ecosystem.

The benefits of potamodromous migratory behavior to individual fishes and populations were described by Northcote (1984) as arising from spatial, seasonal, and ontogenetic separation of optimal habitats for growth, survival, and reproduction. As described above in the section 'Types of Migration' and Table 4.1, published research suggests that migratory behavior allows potamodromous fishes to: (1) optimize growth by accessing more productive areas; (2) improve survival: perhaps via improved growth; increased overwinter survival; access to refugia from severe conditions such as drought, unsuitable temperatures or low oxygen concentration; and predator avoidance; (3) enhance reproductive fitness: perhaps via improved adult condition,

increased fecundity, and access to optimal spawning habitat. Northcote (1997) additionally observed that North American potamodromous fishes have probably recolonized rivers and streams repeatedly over the past million years or more in the face of several glaciations, ice recessions, and interglacial periods. To do so, they may have evolved migratory behavioral patterns adapted to life in highly changeable and unpredictable systems (Northcote 1997). Consequently, migratory behavior also allows potamodromous fishes to: (4) recolonize previously extirpated habitats; (5) disperse to vacant habitats; and (6) maintain beneficial aspects of source/sink dynamics (Hanski and Gilpin 1991), even in very dynamic landscapes.

The importance of freshwater migratory species to humans has long been realized. Humans have exploited migratory freshwater fishes for thousands of years (Lucas and Baras 2001). Potamodromous fishes continue to support essential commercial and recreational fisheries across their world wide range. Revenga et al. (2000) reported that in 1997, inland fisheries landings accounted for 7.7 million metric tons. Taking into account the inland capture, fisheries are estimated to be underreported by two or three times, so the contribution to direct human consumption is likely to be at least twice as high (Revenga et al. 2000). The authors reported that at the global level, inland fisheries landings have been increasing since 1984 with most of this increase in Asia, Africa, and more moderately in Latin America. In North America, Europe, and the former Soviet Union, landings have declined, whereas in Oceania they have remained stable (Revenga et al. 2000).

Over the past two decades, there is increasing recognition that migratory species can also be major ecological drivers shaping both the structure and function of freshwater ecosystems (Flecker et al. 2010). Potamodromous fishes provide benefits to the entire ecosystem via a host of direct and indirect mechanisms as consumers, ecosystem engineers, modulators of biogeochemical processes, and transport vectors (Flecker et al. 2010). Consequently, the loss of key species can have widespread consequences in ecosystems (e.g., Hooper et al. 2005) and this has also led to growing interest in the roles species have in ecosystem function.

Flecker et al. (2010) provided a thorough description of the different processes by which potamodromous fishes subsidize streams and how these subsidies are linked to migration type. The authors described different types of fish migrations and considered their importance from the perspective of ecosystem subsidies. Material subsidies are the transfer of energy, nutrients, and other resources resulting in direct changes in resource pools within ecosystems. In contrast, process subsidies arise from feeding, spawning, or other activities of migratory species that directly affect process rates within recipient ecosystems. Although the presence of migratory individuals can modulate ecosystem functioning under both types of subsidy; the key difference is that material subsidies involve direct delivery of new material (e.g., fish carcasses, gametes), whereas process subsidies affect the dynamics and cycling of existing material (e.g., movement of substrate during spawning, parasitic hosts) (Flecker et al. 2010). For example, the physical and chemical effects of removing algae and periphyton by grazing and sediment-feeding fishes, such as prochilodontids, as well as seed dispersal by large-bodied frugivorous characins, represent potentially key process subsidies by migratory fishes in some large South American rivers (Flecker et al. 2010). Flecker et al. (2010) speculated that process subsidies are more

widespread than material subsidies from migratory stream fishes, because they are independent of the type of migration patterns, life history, and distance traveled.

The potential for migratory fish to represent major material subsidies is largest when: (1) the biomass of migrants is high relative to ecosystem size; (2) the availability of nutrients and energy is low in the recipient ecosystem (i.e., oligotrophic); and (3) there is an effective mechanism for liberating nutrients and energy from migratory fishes and retaining those materials within the food web of the recipient ecosystem (Flecker et al. 2010). The authors note that the most efficient mechanisms for liberating nutrients generally involve: (1) local mortality of migrants in the recipient ecosystem due to programmed senescence in semelparous species; (2) local migrant mortality due to predation, parasitism, and disease in iteroparous species; or (3) excretion and gamete deposition by spawning fishes. Regardless of whether nutrients are re-released via decomposition of carcasses, excretion, or gamete release, a mechanism for the liberation and retention of nutrients and energy originating elsewhere is crucial for material subsidies to be significant. Although some of the best examples of material subsidies derived from migratory fishes have emerged from research on Pacific salmon, potamodromous fishes also have considerable potential to represent major material subsidies, especially when they display the requisite features of large migrant biomass and high local mortality or nutrient release in streams of comparatively low nutrient status (Flecker et al. 2010). The authors noted that perhaps the most likely potamodromous candidates for significant nutrient inputs to North American streams are the large, abundant, and widely distributed suckers and redhorses (Catostomidae). The authors cite research by Linderman et al. (2004) documenting that runs of longnose suckers *Catostomus catostomus* exceeded those of Pacific salmon in Alaska's George River. Although most catostomids are long-lived and iteroparous, Flecker et al. (2010) summarized research to illustrate high breeding mortality, as well as results in oligotrophic tributaries of Lake Michigan which indicate that spring migrations of white sucker and longnose sucker are closely associated with a time-lagged increase in dissolved phosphorus concentrations. Though they have not been studied in the context of material subsidies, substantial inputs of energy and nutrients to streams might also be provided by many other potamodromous North American fishes, including percids, salmonids, esocids, moronids, and osmerids (Flecker et al. 2010).

In addition to conveying material subsidies, migratory fishes can strongly affect stream ecosystem processes through their feeding and other activities (Flecker et al. 2010). The authors posit that in addition to migrant biomass, the potential for migratory fish to represent strong process subsidies is influenced by 'migrant interaction strength' and the degree to which a migratory species is functionally unique in a particular ecological setting. Flecker et al. (2010) noted that, by definition, strong interactors would be keystone species; their impacts on ecosystem structure and function would be substantial and disproportionately greater than would be predicted based on their biomass alone. For example, migratory fishes that are hosts of parasitic stages of mussel larvae are functionally unique, and even small numbers of fishes as hosts could be crucial to the dispersal and demography of mussel populations (Flecker et al. 2010).

Migratory fishes can influence important process subsidies in stream ecosystems through a diversity of mechanisms including functioning as: physical ecosystem engineers, chemical ecosystem engineers or modulators of nutrient cycles, seed

dispersers, directly and indirectly as consumers, and vectors of contaminants and pathogens (Flecker et al. 2010). Two examples of process subsidies in North American potamodromous fishes are described below, for more information on other types of process subsidies, please see Flecker et al. (2010). Yellowstone cutthroat trout, for example, act as ecosystem engineers during spawning by constructing redds and altering the morphology of the stream bed, removing fine sediments, dislodging aquatic insects and potentially increasing drift, and coarsening the substrate (Thurrow and King 1994). Fishes can modify their chemical environment by altering element cycles directly (e.g., Percidae excretion and egestion) or indirectly (e.g., reduced algal demand caused by Catostomidae feeding) (Flecker et al. 2010). A large migration of fish that stay and feed within the recipient local stream can therefore constitute both material (addition of carcasses and gametes) and process subsidies from an excretion standpoint (Flecker et al. 2010).

Morphological adaptations for migration

It is beyond the scope of this chapter to address the highly variable morphological adaptations of potamodromous fishes. These adaptations may influence their swimming performance during migration and movements. Readers are urged to review Videler (1993): Chapter 2 describes the structure of the muscles as swimming apparatus; Chapter 3 describes the body axis and fins; and Chapter 4 describes how body shape, skin, and other special adaptations affect swimming performance. On an interesting note, Portz and Tyus (2004) emphasized the importance of experimental observation for examining potential morphological adaptations for swimming. The authors reported that native Colorado River Basin humpback chub *Gila cypha* and razorback sucker possess a large nuchal hump. Portz and Tyus (2004) noted that although several authors have suggested the hump confers a hydrodynamic advantage to life in fast flow, this premise has not been confirmed with experimental work. Instead, Portz and Tyus (2004) argue that the large humps represent convergent evolution prompted by predation from sympatric Colorado pikeminnow, the top piscivore in the Colorado River system. Lack of jaw teeth and a relatively small jaw gape limit the maximum prey size that Colorado pikeminnow can consume and the large nuchal hump provides a deep body that is difficult or impossible to ingest (Portz and Tyus 2004).

Research needs

Our ability to conserve and restore potamodromous fishes will be enhanced by increased knowledge in several key research areas. Despite the rich history of excellent work that has been accomplished to date, additional research is needed to improve our future understanding of: metapopulation dynamics, detailed migratory behaviors, overwintering behaviors and habitats, and the effects of a changing climate.

Metapopulation-scale information is critical for understanding factors that influence fish population persistence. Hanski and Gilpin (1991) defined a metapopulation as a group of spatially disjunct populations linked by immigration and emigration. Consequently, some populations and their migrations may be

disproportionately important for the survival of the species. Distinguishing between source and sink populations is fundamental to identifying populations essential for species persistence. As highlighted by Rosenfeld and Hatfield (2006), failing to distinguish source and sink populations may result in protection of sinks instead of sources, inappropriate identification of critical habitat, and underestimation of the probability of extinction. These authors listed three key information needs at the metapopulation scale: (1) determining the status of discrete populations as sources or sinks; (2) identifying corridors for dispersal and evaluating the probability of exchange between populations; and (3) assessing the probability of subpopulation persistence based on risk of extinction from combined natural and anthropogenic impacts.

Despite many decades of work, our understanding of the migratory behavior of many potamodromous species remains incomplete. Lee et al. (1997) focused a major portion of their comprehensive assessment of the distribution and status of fishes in the interior Columbia River Basin, on seven 'key' salmonids, in part, because these species were widely distributed and well understood. However, despite the rich history and many decades of excellent salmonid research, Northcote (1997) reported that our understanding of the migratory behavior of many salmonids remained incomplete. As Cooke et al. (2008) observed, given the complexity of migration and its role in a myriad of management and conservation situations, in addition to understanding migration timing and extent, we also need to understand the fundamental processes that enable some fish to migrate vast distances, the causes of mortality during migrations, and the factors that cause some fish to migrate and others not to. With few exceptions, the migratory behavior of most non-salmonid potamodromous fishes is even less well understood, especially in remote areas. As Flecker et al. (2010) observed, in the temperate zone, the ecological significance of material subsidies by potamodromous fishes is a ripe area for research. Migration studies would also benefit from being more broadly based; there is a need to focus on migration as a behavioral, ecological, and evolutionary phenomenon (Dingle and Drake 2007). Dingle and Drake (2007) also observed that since movements to exploit separated and ephemeral habitats transcend species and taxonomic groups, research should do likewise. New technologies and interdisciplinary approaches that integrate positional telemetry with other disciplines (e.g., stress physiology, functional genomics, oceanography, experimental biology) hold promise to enhance future research on fish migration and ultimately provide fisheries managers with the knowledge to better manage and conserve migratory fishes globally (Cooke et al. 2008).

Overwinter ecology of fishes is perhaps the least understood aspect of their life history, and the need for winter investigations has long been recognized (Hubbs and Trautman 1935). We have an incomplete understanding of winter habitat, the extent of winter movements, or how winter conditions regulate fish populations. For example, Chisholm et al. (1987) observed that, despite the array of winter habitat research on brook trout, no studies had focused on the extent of winter movement or the specific habitat features selected. Similarly, although several studies suggest that the abundance and quality of overwinter habitat may limit fish abundance (Bustard and Narver 1975; Campbell and Neuner 1985; McMahon and Hartman 1989), the role of winter conditions in regulating fish populations remains poorly understood. Identifying and describing overwinter habitat is an important step in maintaining critical habitats

(Thurow 1997) and conserving native fishes. Additional research is necessary to improve our understanding of the extent of winter movements, fish behaviors during winter, and the role of overwinter habitat in regulating potamodromous fish populations.

Potamodromous fishes are dependent on an abundant supply of water of a suitable temperature. Consequently, studies dedicated to estimate the impacts of climate change on potamodromous fishes will improve the management of habitats and species. Wenger et al. (2010), for example, observed that hydrologic regimes in the western United States have undergone substantial changes over the last half century, including trends toward earlier snowmelt runoff (Mote et al. 2005), reduced water yields and lower summer flows (Luce and Holden 2009), and increased or altered flood risk. Consequently, Isaac and Rieman (2013) observed that the question is not whether, but how fast, stream biotas are shifting or being extirpated by temperature increases associated with climate change. Although empirical evidence exists for shifts in the timing of migrations and spawning (Crozier et al. 2011), as well as poleward and upstream range expansions (Milner et al. 2011), little evidence exists of broadscale range contractions, despite the extensive changes predicted by numerous bioclimatic models. Better approaches are needed to document the response of stream biotas to climate change. Such information is fundamental to understanding if species responses are accurate predictions of the rate at which isotherms near thermally mediated species boundaries are shifting to higher elevations or latitudes (Isaac and Rieman 2013).

Conservation and restoration of potamodromous fishes

Potamodromous fishes are imperiled world-wide and more than 20% of the world's freshwater fish are extinct or have become threatened or endangered in recent decades (Revenga et al. 2000). Revenga et al. (2000) observed that globally, the greatest overall threat for the long-term sustainability of inland fishery resources is the loss of fishery habitat and the degradation of the terrestrial and aquatic environment; historical trends in commercial fisheries data for well-studied rivers show dramatic declines over the 20th century, mainly from habitat degradation, invasive species, and overharvesting. Liermann et al. (2012) assessed implications of dams for global freshwater fish diversity and reported that nearly 50% of the 397 freshwater ecoregions evaluated were obstructed by large- and medium-size dams, and approximately 27% faced additional obstruction. Threatened ecoregions were found on all continents (Liermann et al. 2012). In North America's interior Columbia River basin, Lee et al. (1997) reported that 45 of 88 native fish taxa were identified as threatened, sensitive, or of special concern by state or federal agencies or the American Fisheries Society. Eight of those species are anadromous which results in 37 of 80 potamodromous fish taxa identified as threatened, sensitive, or of special concern within the interior Columbia River Basin.

Identification and protection of critical habitat is central to the management of species at risk (Rosenfeld and Hatfield 2006). The rationale for protecting critical habitat is rooted in the observation that particular habitats are often disproportionately important to population limitation (Fausch et al. 2002), and therefore habitat protection can be prioritized. A general consensus of strategies, designed to conserve species and

aquatic biological diversity, is that conservation and rehabilitation should focus first on the best remaining examples of aquatic biological integrity and diversity (Thurow et al. 1997). However, protection of critical habitats and population stronghold will not be sufficient; such reserves never will be large or well distributed enough to maintain biological diversity (Franklin 1993). Watershed rehabilitation and the development of more ecologically compatible land-use policies are also required (Thurow et al. 1997). As Rosenfeld and Hatfield (2006) observed, a key component of potamodromous fish species persistence is the management of habitat and human activities outside of critical habitat. Ultimately, conservation of potamodromous fishes will require a more integrated, broad-scale view of management than has been practiced historically. An assumed goal of ecosystem management is to maintain, or rehabilitate, the integrity of aquatic ecosystems and to provide for the long-term persistence of native (and in some cases desirable nonnative) fishes and other species (Grumbine 1994). Note that non-native species might be desirable if they fill an open niche such as some Pacific salmon species in the Great Lakes (Kohler and Courtenay 1986) or if they provide fisheries values in cases where habitats have been so severely degraded as to be unsuitable for native species restoration. As Thurow et al. (1997) observed, achieving the goal of ecosystem management will require the maintenance, or rehabilitation, of a network of well-connected, high-quality habitats that support a diverse assemblage of native species, the full expression of potential life histories and their movements, and the genetic diversity necessary for long-term persistence and adaptation in a variable environment. Ecosystem management, then, also implies using active management to reestablish more complete or natural structure, function, and processes whenever possible (Thurow et al. 1997). Lastly, effective conservation and restoration efforts for potamodromous fishes will also require an improved understanding of the effects of a changing climate (Isaac and Rieman 2013) as well as increasing knowledge of metapopulation dynamics, detailed migratory behaviors, and overwintering behaviors and habitats.

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