Chapter 13

Centrarchid identification and natural history

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13.1 Introduction

The family Centrarchidae (Order: Perciformes) is one of the most diverse, widespread, and conspicuous fish families native to freshwater habitats of North America. Among endemic fish families of North America, only the North American catfish family (Ictaluridae) has more species. The family name, Centrarchidae, refers to the anal fin spines of species in the family, and the common name, sunfishes, to the bright breeding colors displayed by males of some species in the family. Because of their diversity, wide distribution, and economic value, some of the earliest taxonomic descriptions and natural history observations on North American freshwater fishes focused on the centrarchids (e.g., Linnaeus 1758; Lacépède 1801; Rafinesque 1820; Abbott 1870).

The family contains 34 extant species classified in eight genera, but morphological and genetic evidence suggests that additional, but currently unrecognized, diversity exists within most of tbe genera. The most diverse genus, *Lepomis*, the bream (or panfish) of anglers, is comprised of 13 extant species, but at least 8 of these show evidence of polytypy (e.g., Bermingham and Avise 1986; Fox 1997; Harris 2005). The genus *Micropterus*, referred to collectively as black basses (Philipp and Ridgway 2002), contains eight extant species, but again, at least three species are polytypic (e.g., Stark and Echelle 1998; Kassler 2002; Miller 2005). The genera *Ambloplites* (rock basses), *Enneacanthus* (banded sunfishes), and *Pomoxis* (crappies) contain four, three, and two extant species, respectively, and at least one species each of *Ambloplites* and *Enneacanthus* is polytypic (Koppelman 2000; T. Darden, South Carolina Department of Natural Resources, personal communication). The genera *Acantharchus, Archoplites*, and *Centrarchus* are monotypic, but populations of both *Acantharchus pomotis* and *Archoplites interruptus* show geographical patterns of morphological divergence (Cashner *et al.* 1989; Moyle 2002).

The natural range of extant centrarchids is confined primarily to warm, freshwater habitats in North America east of the western continental divide except for the Sacramento perch (*A. interruptus*), whose native range is west of the divide in the Central Valley of California (San Joaquin-Sacramento, Pajaro, Salinas river drainages, Moyle 2002). The northern natural continental limit of the family is occupied by members of *Lepomis, Ambloplites, Pomoxis*, and *Micropterus* in the St. Lawrence River, northern Great Lakes, and southwestern Hudson Bay drainages in eastern Canada (Scott and Crossman 1973). The Rio Conchos (Rio Grande drainage) (*Lepomis*) and Rio Soto la Marina (*Micropterus*, Miller and Smith 1986; Miller 2005) of northern Mexico delimit the southern continental limits of the native range of extant centrarchids. The Mississippi River Basin and, to a lesser extent, the Gulf and Atlantic Slope drainages harbor the most diverse assemblages of native centrarchids (Warren *et al.* 2000). The native ranges of *Pomoxis* and *Lepomis* largely coincide with that of *Micropterus*, but both extend farther northwest into the northern plains drainages, and the native range of *Lepomis* extends farther northeast into southern New Brunswick (Scott and Crossman 1973). Members of *Acantharchus* and *Enneacanthus* are confined to drainages of the Atlantic Coastal Plain, peninsular Florida, and eastern Gulf Coastal Plain (Page and Burr 1991). The native range of *Centrarchus* overlaps *Acantharchus* and *Enneacanthus* but extends into drainages of the western Gulf Coastal Plain of eastern Texas and north to southern Illinois and Indiana in the lower Mississippi River Basin. Centrarchids, particularly the genera *Ambloplites, Lepomis, Micropterus*, and *Pomoxis* are among the most widely introduced groups of fishes in the world. Nonnative populations are established across much of temperate North America and intercontinentally (e.g., South America, Europe, Africa, Asia, Oceania) and are often associated with adverse ecological consequences for the native fauna (e.g., Robbins and MacCrimmon 1974; De Moor and Bruton 1988; FAO 1998; Fuller *et al.* 1999; Rahel 2000; Jackson 2002; Jang *et al.* 2002; Moyle 2002).

The most distinctive characteristic of centrarchids is their reproductive behavior. Males in the family construct and defend a well-defined, depressional, oval- to circular-shaped nest. Downward-directed thrusts of the caudal fin are a primary and conspicuous nest-building activity in most centrarchids (caudal sweeping, Miller 1963), but a variety of other actions may also be used as the male clears the nesting area (e.g., sweeping of the pectoral fins, pushing stones, or transporting debris by mouth) (Dickson 1949; Hunter 1963; Miller 1963; Gross and Nowell 1980; Noltie and Keenleyside 1987b). Centrarchids may nest solitarily or colonially. Solitary nesters (nests >1 m apart) tend to nest near simple cover (e.g., bases of logs, rocks, or macrophytes) and defend a territory exceeding the nest perimeter (>2.5 m, Colgan and Ealey 1973; Avila 1976; Winemiller and Taylor 1982; Colgan and Brown 1988; Ridgway 1988; Jennings and Philipp 1992b; Scott 1996). Colonies of nests, consisting of several to hundreds of abutting nests, tend to occur in shallow open water, and in dense colonies nest defense is constrained primarily to the nest perimeter (Hunter 1963; Colgan *et al.* 1981; Gross and MacMillan 1981; Gross 1982). Spawning can occur immediately after nest construction or be delayed for several days, during which the male defends the nest and surrounding territory and waits for spawning-ready females (Carr 1946; Kramer and Smith 1962; Boyer and Vogele 1971; Miller and Kramer 1971; Avila 1976; Vogele 1975a; Colgan and Gross 1977; Gross and Nowell 1980; Cooke *et al.* 2001b).

Male aggression intensifies during the courtship and spawning period. Males over nests display to nearby or approaching males and females using combinations of many behaviors (e.g., caudal sweeping, nest hovering, fin spreading, mouth gapes, jaw snaps, lateral displays, substrate biting, and opercular spreads). Male to male aggressive interactions, including combat, are not uncommon, particularly among colonial-nesting species. Males most frequently rush toward an interloper with a quick retreat to the nest (thrust, Miller 1963), but if the intruder does not retreat, males laterally display, spread opercles, or actually ram, push, bite, or jaw grasp the other male. Much of male aggression is directed at or near the head and opercular area, but frayed fins and body abrasions of males attest to the vigorousness of male aggression in defense of the nesting territory (Hunter 1963; Keenleyside 1967, 1971; Colgan and Gross 1977; Gross and Nowell 1980).

Male courtship of females may be preceded by attempts to repulse females near the nest, behaviors that coax or guide the female to the nest, or both. Repeated repulsion of approaching females by males is documented in *Archoplites* (Mathews 1965), *Ambloplites* (Gross and Nowell 1980; Petrimoulx 1984; Noltie and Keenleyside 1987b), *Lepomis* (e.g., Hunter 1963; Huck and Gunning 1967; Keenleyside 1967; Ballantyne and Colgan 1978a,b,c), and *Pomoxis* (Siefert 1968). If ready to spawn, a female, assuming a subordinate demeanor, continues to slowly approach the nest despite repeated attacks by the male. Male-leading or -guiding courtship behaviors are known in *Lepomis, Micropterus*, and *Centrarchus*, although *Lepomis* females often enter nests with little or no overt courtship (Carr 1942; Dickson 1949; Hunter 1963; Keenleyside 1967; Chew 1974; Coble 1975; Vogele 1975a; Avila 1976; Gross 1982; Ridgway *et al.* 1989; Lukas and Orth 1993; Cooke *et al.* 2001b). Repulsing or guiding male behaviors directed at females may be species or context specific, are difficult to separate cleanly into courtship or aggression, and often co-occur (Keenleyside 1967; Ballantyne and Colgan 1978a,b,c).

Once a pair is situated over the nest, they orient broadside and head to head and swim in slow, tight circles over the nest. The pair settles to the substrate, and egg deposition occurs as the female tilts away from the male and presses her vent near the substrate; the male presses his vent to the female's while remaining upright or rolling toward the female. Egg and sperm release is accompanied by shuddering in both sexes; the demersal, adhesive eggs adhere to the nest substrate and to one another in clumps. Typically the pair rests, then repeats the sequence multiple times, until the male chases the female out of the nest. Rests between spawning bouts tend to shorten as the spawning event continues. These sequences may be in quick succession if the pair is not interrupted by intruders, but completion of spawning with a single female may occur over extended periods (15 minutes to 3.5 hours), even without interruption (Siefert 1968; Neves 1975; Vogele 1975a; Gross 1982, 1991; Isaac *et al.* 1998; Cooke *et al.* 2001b). After spawning, males aggressively guard the eggs and larvae, but the length of male parental care after the eggs hatch differs among genera and species within genera.

Today, centrarchids are the primary focus of the recreational fishing industry in the United States and much of southeastern Canada. The relatively large size of many centrarchids, vulnerability to natural baits or artificial lures, and the excellent taste of the flesh combine to create a popular sport fishery worth billions of dollars a year. The black basses (*Micropterus*), particularly the Florida bass and largemouth bass, the bream or panfishes (*Lepomis*), especially the bluegill, and the crappies (*Pomoxis*) are sought by anglers more than any fresh or saltwater sport fishes in the United States. Angler numbers and days spent fishing for centrarchids dwarf those reported for salmonids, walleye, or saltwater fishes (USFWS 2002).

A prodigious body of information is available on centrarchid natural history. Most research, however, has focused on a relatively few but important sport fish species, and there is no single-source recent summary of natural history information for all species in family. The objective here is to provide synopses of the characteristics and the natural history of the

8 genera and 34 species of centrarchid fishes and to provide a dichotomous key to the family. A secondary objective of this chapter is to highlight species for which information on their natural history is lacking, fragmentary or anecdotal.

13.2 Generic and species accounts

The bulk of the chapter consists of a separate account for each genus and each species within a genus, with the exception of monotypic genera. Only species accounts are given for monotypic genera. Within the characteristics sections of generic and species accounts, the definition of counts, standard length (SL), total length (TL), and other measurements follow standard ichthyological methods (see Page and Burr 1991; Jenkins and Burkhead 1994; Boschung and Mayden 2004) or are given in the citations associated with that section. Counts are presented as a total range, that is, 19 to 25; a modal (usual) count followed by a range, that is, usually 22, 19 to 25; or the most frequently encountered range of counts (ca. $\geq$90%) and the extremes, that is, (19)21 to 23(25). Only published sources were used to designate a confirmed freshwater mussel host (e.g., mussel larvae successfully infected and transformed on a centrarchid host). A putative host is similarly defined, except that the data are from unpublished sources and need verification. Published or unpublished accounts of mussel larvae infection on a centrarchid species without observation of transformation to the juvenile stage are not included.

13.3 *Acantharchus pomotis* (Baird)

13.3.0.1 Mud sunfish

Characteristics: Moderately oblong and robust body, depth <0.4 of SL. Large, terminal mouth, lower jaw projecting slightly, supramaxilla large ($\leq$2 times into length of maxilla), upper jaw extending beyond middle of eye. Eye large, diameter greater than snout length. Three to four parallel, brown to olive-black stripes across face (above eye, through eye, along upper jaw) and four to five dark brown stripes along side, often broken into mottling. Opercle with two flat extensions; opercular tab short and deep, spot prominent, dark brown to black, with orange (in large individuals) or light ventral and dorsal edges. Rounded caudal fin. Long dorsal fin, 10 to 12 spines, 9 to 13 rays, 20 to 24 total; and moderate length anal fin, 4 to 6 spines, 9 to 11 rays, 14 to 16 total. Dorsal fin continuous with shallow gap between spines and rays. Dorsal fin base about 1.7 to 1.9 times longer than anal fin base. Stout, moderate length gill rakers (5–7). Cycloid scales on head and body. Lateral line scales, 32 to 45; cheek scale rows, (5)6 to 8(9); breast scale rows, (10)12 to 14(16); branchiostegal rays, 7; pectoral rays, 14 to 15; vertebrae, 29 or 30. Teeth on endopterygoid, ectopterygoid, palatine (villiform), and glossohyal (tongue, one elongate patch) bones; vertebrae, 30 (13 + 17) (Bailey 1938; Cashner 1974; Cashner *et al.* 1989; Page and Burr 1991; Mabee 1993).

Size and age: Typically 25 to 91 mm TL at age 1. Large individuals measure 150 mm TL and reach age 4+ to 8+ (maximum 206 mm TL, 190 g) (Breder and Redmond 1929; Mansueti and Elser 1953; Cashner *et al.* 1989; Page and Burr 1991; Pardue 1993; Jenkins and Burkhead 1994). North Carolina populations grew more rapidly in length and were shorter lived (4 vs 7–8 years) than populations in Maryland and New York (Mansueti and Elser 1953; Pardue 1993).

Coloration: Dorsum and background of sides light olive or greenish gold to dark green or brown; olive to chocolate brown longitudinal stripes or mottling on sides. Ventral head and breast yellowish tan, mottled posteriorly on belly to flanks. Median fins olivaceous to dark brown, may be mottled in small individuals. Tips of anal spines and rays often darkened to produce marginal band. Caudal with broad, dark band at base; median rays may be darkened from base to tip, creating a striped effect. Dull red or brown iris. Little sexual dimorphism evident and no perceptible color changes occur in the breeding season, but chocolate brown mottling and ear tab tend to be darker in males than in females. Young may have up to 15 thin stripes along sides punctuated by dark pigment producing a somewhat spotted lateral pattern (Cashner *et al.* 1989; Page and Burr 1991; Pardue 1993; Jenkins and Burkhead 1994; Marcy *et al.* 2005).

Native range: The mud sunfish occurs primarily on the Atlantic Coastal Plain and in lower Piedmont drainages from Hudson River, New York, to St. Johns River, Florida, and also occupies the extreme eastern Gulf Coastal Plain drainages from the Suwannee to St. Marks rivers in northern Florida and Georgia (Page and Burr 1991).

Habitat: The mud sunfish is a decidedly lowland species, inhabiting sluggish waters of swamps, vegetated lakes, ponds, sloughs, and backwaters and pools of creeks and small to medium rivers. The species occurs across a broad range of pH (about 4–9) and in a study of New Jersey lakes was significantly more frequent in acidic waters (Graham 1993). The species is most often associated with plants, detritus, undercut banks, instream wood, and other cover (Page and Burr 1991; Pardue 1993; Jenkins and Burkhead 1994). In a North Carolina swamp, 70% of individuals recaptured (31 total) were within 0.2 km, and 30% moved 2.7 to 4.9 km from where they were marked. Increased movements occur from January to May, presumably in association with spawning activity, lower water temperatures, and higher water levels (Pardue 1993). Mud sunfish frequently invade intermittent tributaries and wetlands that dry infrequently (Snodgrass *et al.* 1996; Marcy *et al.* 2005).

Food: The mud sunfish is reputed to be active at night, maintaining close affinity with and resting head down in vegetative cover during daylight (e.g., Abbott 1870; Breder and Redmond 1929; Mansueti and Elser 1953; Laerm and Freeman 1986), but quantitative studies of diel activity or feeding are lacking. Decapods, amphipods, odonates, and coleopterans form the primary diet of juveniles and adults, but small fish begin to be included in the diet at least seasonally when individuals reach >105 mm TL (Pardue 1993).

Reproduction: Maturity is reached at age 1+ and a minimum size of 66 to 140 mm TL. Spent females, egg sizes, and gonad to body weight ratios suggest that the mud sunfish begins and completes spawning at temperatures as low as 7 to 10°C (Pardue 1993), which is lower than minima reported for other centrarchids. The spawning period apparently extends from December to May in North Carolina and into June in New Jersey at water temperatures of 7 to 20°C (Breder 1936; Pardue 1993). The ovaries enlarge in the early fall and continue developing over winter (Pardue 1993), which is likely an adaptation for early spawning. Reproductive behaviors are essentially unknown. Males have been observed or captured over small depressional nests near the shoreline of lakes or near the banks of headwater streams in water 15 to 30 cm deep (Fowler 1923; Marcy *et al.* 2005). Mud sunfish produce audible grunting noises (Gerald 1971), but linkage with reproduction is undocumented. Mature ovarian eggs range from 0.7 to 1.1 mm diameter (Pardue 1993). At a median size of 128 mm TL, a female can produce 2304 mature eggs (range: 1515 at 114 mm TL to 3812 at 144 mm TL; data from Pardue 1993), which is one of the lowest batch fecundities among centrarchids (see also *Ambloplites* and *Enneacanthus*). Female allocation of energy to reproduction is also low relative to most centrarchids with peak female gonad to somatic weight values of 3% (Pardue 1993). Mature ovarian egg size is similar to that in *Lepomis* and may indicate a similar duration of male care provided to the embryos and larvae (Gross and Sargent 1985), but the combination of low batch fecundity and low female energy allocated to reproduction differs from reproductive patterns observed in all other centrarchids.

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The mud sunfish is widely distributed but not common anywhere. The species appears to be secure where its lowland habitats are undisturbed, particularly in the central portions of its Atlantic Coastal Plain range (North and South Carolina). Populations to the north and south are considered possibly extirpated (New York), imperiled (Delaware and Maryland), or vulnerable (Virginia, Georgia, and Florida) (NatureServe 2006).

Similar species: All other centrarchids have ctenoid scales (cycloid in *Acantharchus*), and except for *Enneacanthus*, deeply to shallowly emarginate caudal fins (rounded in *Acantharchus* and *Enneacanthus*). *Enneacanthus* possess three anal fin spines (4–6 in *Acantharchus*).

Systematic notes: The phylogenetic relationships of the monotypic genus *Acantharchus* to other centrarchid genera is the least resolved within the family. Phylogenetic analyses place the species as sister to all other centrarchids or as resolved within a clade of all centrarchid genera but *Lepomis* and *Micropterus* (Roe *et al.* 2002; Near *et al.* 2004, 2005). The species shows evidence of polytypy. A subspecies described from the Okefenokee Swamp region (Suwannee River drainage, Georgia) as *A. pomotis mizelli* (Fowler 1945) was based on little comparative data. In an extensive study of geographic variation, several meristic characters of populations in eastern Gulf of Mexico drainages diverged significantly from those of populations in Atlantic Slope drainages. Multivariate analyses of morphological characters suggested that a contact zone between northern Atlantic Slope populations and Gulf Slope populations exists in Atlantic Slope drainages of Georgia and Florida (Cashner *et al.* 1989). Resolution of the evolutionary distinctiveness of the two geographic groups awaits molecular phylogeographic analysis.

Importance to humans: The mud sunfish is one of the least known of all centrarchids, even to avid sport fishers, fisheries biologists, and most ichthyologists. The species is apparently rarely taken by hook and line and can go uncaught and unnoticed by anglers even when it occurs in heavily fished ponds (Mansueti and Elser 1953). Unfortunately, so little is known about the species that its ecological function and value in lowland stream and wetland ecosystems cannot be evaluated, but its adaptability to such habitats and distribution across a broad latitudinal band suggest a long evolutionary history in those environments and a potentially important functional role. The basal phylogenetic relationship of *Acantharchus* within the centrarchids may provide an important key for unraveling the relationship of the centrarchids to other percoid fishes, a relationship that is currently unknown. Likewise, study of its reproductive biology and behavior could illuminate the evolutionary history of complex reproductive strategies and associated behaviors observed in other centrarchids.

13.4 *Ambloplites* Rafinesque

The monophyletic genus *Ambloplites*, often referred to collectively as rock basses, is endemic to eastern North America and contains four species consisting of two sister group pairs: *Ambloplites ariommus* (shadow bass) and *Ambloplites rupestris* (rock bass) form one sister pair and *Ambloplites cavifrons* (Roanoke bass) and *Ambloplites constellatus* (Ozark bass), the other. *Ambloplites* is sister to the monotypic genus *Archoplites*, represented by the Sacramento perch, and these two genera are sister to the genus *Pomoxis* (Near *et al.* 2004, 2005). The genus is distributed broadly across eastern North America, mostly east of the Great Plains, from southern Canada to the Gulf Coastal Plain, but the natural ranges of all four species are allopatric within this region. The Roanoke bass–Ozark bass sister pair occupies some of the smallest ranges of any North American sport fish. The Roanoke bass is endemic to Atlantic Coast drainages of Virginia and North Carolina and the Ozark bass mostly to the White River of Arkansas and Missouri. The range of the shadow bass is essentially disjunct; part of the range includes drainages of the eastern Gulf Slope and lower Mississippi River and the remainder includes drainages of the Ouachita Mountains, Arkansas River Valley, and Ozark Plateau. The rock bass, the most broadly distributed member of the genus, has been introduced and is widely established outside its native range in both eastern and western North America (Cashner and Suttkus 1977; Fuller *et al.* 1999). Intentional (or suspected) introductions of rock bass and other species of *Ambloplites* into the ranges of congeners has obscured natural ranges, has produced introgressed populations, and threatens the genetic integrity of species within the genus, particularly the range-restricted endemics (Cashner and Suttkus 1977; Cashner and Jenkins 1982; Jenkins and Burkhead 1994; Koppelman *et al.* 2000).

Ambloplites appear to differ from most other centrarchids, except their sister genus *Pomoxis*, in several aspects of reproductive behavior, but detailed, multiple observations are available only for rock bass. Male *Ambloplites* apparently do not use caudal sweeping to clear nesting areas as is common in most other centrarchid males (Miller 1963). *Ambloplites* males use a combination of behaviors to construct the nest, including undulations of the anal fin, sweeping of the pectoral fins, and pushing material forward with outstretched pectoral fins (bulldozing, Gross and Nowell 1980; Petrimoulx 1984; Noltie and Keenleyside 1987b). Males orient slightly head downward and use alternating strokes of the pectoral fins for fanning the eggs, similar to *Pomoxis*, rather than the horizontally oriented and primarily caudal- fin fanning as described for *Lepomis* or *Micropterus* (Carr 1942; Miller 1963; Gross and Nowell 1980; Noltie and Keenleyside 1987b). Males show no overt courtship of females, and mate choice appears to be restricted to male acceptance of females (Gross and Nowell 1980; Petrimoulx 1984). Males aggressively and persistently repel and even attack females approaching the nest, spawning only with the most persistent, submissive females, behaviors in contrast to the active leading or guiding behaviors of nest-defending males toward females in other genera (e.g., *Lepomis* and *Micropterus*). The relative position of the male to the female during spawning also appears to differ in, and perhaps among, *Ambloplites*. The male of the Roanoke and Ozark bass occupies a central nest position during pairings with females rather than a position outside the female (toward the nest rim); the rock bass male takes an outside nest position in spawning if circling occurs, but occupies a central position when no nest circling occurs (Gross and Nowell 1980; Petrimoulx 1984; Noltie and Keenleyside 1987b; Walters *et al.* 2000).

Members of *Ambloplites* are popular sport and food fishes and are commonly taken by anglers. In Missouri, three species, the shadow bass, rock bass, and Ozark bass, comprise 10% of the catch and harvest of fishes in streams (Koppelman *et al.* 2000). Many individuals are caught incidentally with the same lures and tackle used by anglers seeking smallmouth, spotted, and redeye basses, which frequently co-occur with species of *Ambloplites*. Anglers specifically seeking rock basses use small lures and spinners, lures imitating minnows, or live bait, particularly dobsonfly larvae (hellgrammites) and small crayfishes (Nielsen and Orth 1988; Ross 2001). Anglers often refer to these fishes as "redeyes" because of the conspicuous red pigment in their iris or "goggle eyes" because of their relatively large and conspicuous eyes (Etnier and Starnes 1993; Koppelman *et al.* 2000).

Generic characteristics: Moderately compressed, elongate body, depth <0.5 of SL; compressed when young, becoming thicker as adults. Large oblique mouth, lower jaw slightly projecting, supramaxilla large (≤2 times maxilla length), upper jaw extending under eye pupil. Black or dusky oblique teardrop; prominent, large eye (≥0.25 of head length) with red iris. No bright red, orange, blue, or green colors. Young camouflaged with large, irregularly shaped, dark blotches alternating with lighter areas on body. Young and adults capable of rapid chameleon-like changes in pigmentation, providing effective camouflage under varying light and background conditions (Viosca 1936; Petrimoulx 1984; Noltie and Keenleyside 1987b). Opercle with two flat projections; dusky to dark opercular spot with light edge. Preopercle posterior margin variable in degree and kind of serrations. Dorsal, caudal, and anal fins with dusky spots and brown wavy lines. Long dorsal fin, usually 11 or 12 spines, 10 to 12 rays, 22 or 23 total; and moderate anal fin, usually 6 spines, 10 or 11 rays, 16 or 17 total. Dorsal fin base about 1.7 to 2.0 times longer than anal fin base. Dorsal fin continuous with a shallow gap between spines and rays. Short, rounded pectoral fin. Emarginate caudal fin. Moderately long gill rakers, 12 to 16. Ctenoid scales. Branchiostegal rays, usually 6; pectoral rays, 14 or 15; vertebrae, 31 (13 + 18). Complete lateral line. Teeth on endopterygoid, ectopterygoid, palatine (villiform), and glossohyal (tongue, one or two circular patches) bones (Bailey 1938; Cashner 1974; Page and Burr 1991; Mabee 1993; Boschung and Mayden 2004).

Similar species: The warmouth has somewhat similar overall body shape and body mottling but has only three anal spines and dark lines radiating from the eyes (Page and Burr 1991).

13.4.1 Ambloplites ariommus *Viosca*

13.4.1.1 Shadow bass

Characteristics: See generic account for general characteristics. Relatively small, compressed, and deepest-bodied member of genus; body depth usually >0.42 of SL. Eye large, diameter typically >0.30 of head length. The pattern of dark blotches alternating with lighter areas on body in young is retained in adults, so that adults and young resemble the appearance of young *A. rupestris*. Preopercle sharply serrate to weakly crenate to entire at the angle. Dorsal fin elements, (20)22 to 23(24); anal fin elements, (15)16 or 17(18). Cheeks fully scaled with large, exposed scales. Cheek scale rows, (5)6 or 7(8); lateral line scales, (34)38 to 43(45); scale rows above lateral line, (5)6 or 7(8); scale rows below lateral line, (11)13 to 15(16); diagonal scale rows, (18)22 or 23(24); and breast scale rows, (13)16 to 18(20). One circular patch of teeth on tongue (Cashner 1974; Cashner and Suttkus 1977; Page and Burr 1991).

Size and age: Typically reach 40 to 120 mm TL at age 1. Large individuals measure 160 to 203 mm TL, rarely exceed 340 g, and reach age 6+ to 9+ (maximum 220 mm TL); Missouri and Arkansas populations can apparently reach larger sizes (at least 254 mm TL) than other populations (Viosca 1936; Robison and Buchanan 1984; Page and Burr 1991; Pflieger 1997; C. S. Schieble, University of New Orleans, personal communication). World angling record, 820 g, Arkansas (IGFA 2006). Females may outlive males, and males slightly exceed females in average maximum size and weight, but growth curves for the sexes are similar (C. S. Schieble, University of New Orleans, personal communication).

Coloration: Light green to brown on sides with irregular marbling of brown or gray dark blotches alternating with lighter areas, blotches often joined dorsally to form saddles. Scales on sides bear a dark, triangular spot at the base (apex forward), producing a pattern of longitudinal lines that run through but are often obscured by the light and dark pigmented areas. Lower sides and belly transitioning to straw color (Viosca 1936; Cashner 1974; Page and Burr 1991). Large breeding males have a distinct darkening of the membranes in the pelvic and anal fins from the fin tips to the base and distinct black, threadlike filaments on their pelvic fins. These filaments are yellow to white in females (C. S. Schieble, University of New Orleans, personal communication).

Native range: The range of the shadow bass is disjunct. The species occupies Gulf Slope drainages from the Apalachicola River west to the lower Mississippi River, including the Mobile Basin, and also occurs in the Red, Ouachita, Arkansas, St. Francis, and Black rivers (Page and Burr 1991).

Habitat: The shadow bass inhabits gravel, sand, and mud-bottomed creeks and small to medium rivers with low levels of turbidity and sedimentation. The species is almost always associated with pools and cover of boulders, logs, log complexes, or rootwads; water willow or other aquatic vegetation in shallow water often harbors young-of-the-year (Probst *et al.* 1984; McClendon and Rabeni 1987; Page and Burr 1991; Pflieger 1997, reported as rock bass; C. S. Schieble, University of New Orleans, personal communication). In a large-scale tagging study (Funk 1957), shadow bass (reported as rock bass) were regarded as sedentary, but 48% and 31% of recaptured individuals moved at least 1.6 km from the original point of tagging in the Black and Current rivers, Missouri, respectively. Measures of biomass and fish size indicated that adult shadow bass emigrated from the Current River to a large near-constant temperature spring (13.5°C) during cold winter months when river temperatures dropped below the spring temperatures. Individuals reentered the river during warm periods when river temperatures exceeded spring temperatures. During high use of the spring in cold periods, shadow bass in the spring had significantly higher relative stomach fullness and larger eggs than conspecifics in the river, suggesting that an energy subsidy was conferred on fishes that used the spring seasonally (Peterson and Rabeni 1996, reported as rock bass).

Food: The shadow bass is primarily a benthic feeder. An extensive diet study in Missouri indicated that crayfish were by far the most important prey item in shadow bass >100 mm TL. Young-of-the-year initially relied on invertebrates, particularly chironomids and mayflies as prey, but began consuming crayfish at about 25 mm TL and increased consumption with growth. About 70% of usable energy of adult shadow bass was derived from consumption of crayfish. Shadow bass consumed crayfish species in proportion to their abundance in the river, were size selective for crayfish 30 to 44 mm in length, and showed no seasonal shifts in diet. Fish, primarily stonerollers, and other invertebrates, particularly mayflies and stoneflies, were additional, but less important, adult diet items (Probst *et al.* 1984; Rabeni 1992, reported as rock bass). A limited analysis of shadow bass diets in a small, sand-bottomed Gulf Coastal Plain stream in Louisiana indicated high consumption of benthic fish prey (e.g., darters, madtom catfish, shiners) and insects (e.g., dragonflies, stoneflies, caddisflies) but limited predation on crayfish (Viosca 1936). Diel activity and feeding studies are unavailable, but the absence of shadow bass at night from their daytime haunts suggests a nocturnal component in activity and perhaps foraging (or at least a nocturnal shift in habitat use) (Probst *et al.* 1984).

Reproduction: Maturity is reached at age 1+ and a minimum size of 87 mm TL in females and 108 mm TL in males (C. S. Schieble, University of New Orleans, personal communication). Nest building has not been described, but an extensive examination of reproductive biology is available for southern populations in Lake Pontchartrain, Pearl River, and Mississippi River tributaries (C. S. Schieble, University of New Orleans, personal communication). Based on ovarian condition and ovary to body weight ratios, southern populations have a protracted spawning period extending from January or February to May or June, corresponding to water temperatures ranging from 15 to 26°C. Peak ovarian condition occurs at about 23°C. Mature ovarian eggs average 0.98 mm diameter (range, 0.56–1.7 mm), suggesting a somewhat smaller average mature ova size than in rock bass, but maximum sizes are comparable (Gross and Nowell 1980). Two size classes of vitellogenic ova are reported in mature females, and these are present from January through May, suggesting production of multiple batches of eggs. At a mean size of about 120 mm SL, a female can potentially produce 1311 mature eggs (range: 161 eggs at 85 mm SL to 4113 eggs at 156 mm SL) in a single spawning event. Peak female ovary to body weight ratios average 4.1% in February and March and 2.7% in March through May. Female ovary to body weight ratios, mean total ova, and mean ova diameters decrease substantially in June and subsequent months (C. S. Schieble, University of New Orleans, personal communication).

Nest associates: None known.

Freshwater mussel host: None documented, but see account on *A. constellatus*.

Conservation status: The shadow bass appears to be secure throughout its range (Warren *et al.* 2000), but is considered vulnerable in Louisiana (NatureServe 2006) where it is confined to the southeastern portion of the state. Increased sedimentation and turbidity in formerly clear, relatively fast-flowing Gulf Coastal Plain and Mississippi Alluvial Valley streams could and likely have reduced available habitat for this species (Pflieger 1997; C. S. Schieble, University of New Orleans, personal communication).

Similar species: Color pattern of sides of adult Ozark bass and rock bass (>100 mm TL) are irregularly arranged freckles or rows of blackish spots, lacking the usually conspicuous, alternating light and dark blotches of adult shadow bass. Juveniles of all three species are similarly patterned (Pflieger 1997).

Systematic notes: Patterns of differentiation in the Ozark populations of *A. ariommus* and its sister species, *A. rupestris*, can render identification difficult, irrespective of whether morphological criteria or allozyme-derived genetic data are used. Some suggest that the patterns of differentiation indicate a north-to-south cline between *A. rupestris* and Ozarkian *A. ariommus* populations that are indicative of conspecificity, but the observed patterns are confounded by known or suspected introductions of both species into various drainages in the region. For example, populations of *Ambloplites* in the Gasconade River and Charette Creek (both Missouri River drainage) display allozyme-derived genetic distances intermediate between *A. rupestris* and *A. ariommus*, which are likely attributable to past introductions (Koppelman *et al.* 2000). Even in naturally occurring populations, intermediacy is not positive proof of conspecificity of *A. rupestris* and *A. ariommus* because long-term evolutionary retention of ancestral polymorphisms after divergence of sister species is common in centrarchids (Near *et al.* 2005). Further, morphological differences between the two species in the Ozarks are supported (e.g., cheek and breast scales, adult color patterns) (Koppelman *et al.* 2000). At this time, field identification of *A. ariommus* in the Ozarks appears to be best accomplished on the basis of adult body coloration, body depth to length ratio, aspects of squamation, and geography (Pflieger 1997; Koppelman *et al.* 2000). Notwithstanding the Ozarkian populations, extensive morphological comparisons and limited population sampling of allozymes indicate that *A. ariommus* is polytypic. Populations in drainages of the Florida Panhandle and perhaps the Mobile Basin may be distinct (Cashner 1974; Koppelman *et al.* 2000), but resolution of the nature of the differentiation awaits a rangewide phylogeographic analysis of the species.

Importance to humans: The shadow bass has many desirable qualities as a sport fish although the relatively small maximum size limits angler interest in some parts of its range. The species readily takes a lure or natural baits and is a popular catch for anglers using ultralight gear or fly rods in streams and rivers of the Coastal Plain of Mississippi and the Ozark and Ouachita Mountains of Missouri and Arkansas (Robison and Buchanan 1984; Probst *et al.* 1984; Ross 2001). Creel surveys in the Pascagoula and Pearl rivers of Mississippi indicated that shadow bass constituted 1% and 0.6% of the total catch by weight, respectively (Ross 2001). The flavor and texture of the flesh of the shadow bass is similar to other centrarchids such as spotted bass and bluegill (Viosca 1936).

13.4.2 Ambloplites cavifrons *Cope*

13.4.2.1 Roanoke bass

Characteristics: See generic account for general characteristics. Relatively large, elongate body; body depth >0.41 of SL. Eye large, diameter about 0.25 of head length. Body pattern similar to that of *A. rupestris* but with freckled pattern (scattered, dark brown spots) on side of body and head. Adults with unique color pattern of numerous iridescent gold to white spots on upper body and head. Preopercle strongly serrate at the angle. Dorsal fin elements, (22)23(24); anal fin elements, (16)17(18). Cheeks naked or incompletely scaled with small, deeply imbedded scales. Lateral line scales, (39)42 to 46(49); scale rows above lateral line, (8)9 or 10(12); scale rows below lateral line, (13)14 or 15(16); diagonal scale rows, 23 to 26(27); and breast scale rows, (26)30 to 34(36). One or two oval patches of teeth on tongue (Bailey 1938; Cashner 1974; Cashner and Jenkins 1982; Page and Burr 1991; Mabee 1993).

Size and age: Typically reach 42 to 89 mm TL at age 1. Large individuals measure 250 to 296 mm TL, weigh 770 g, and reach age 4+ to 9+ (355 mm TL) (Smith 1971; Carlander 1977; Petrimoulx 1983; Jenkins and Burkhead 1994). World angling record, 620 g, Virginia (IGFA 2006). State records in Virginia and North Carolina are 1.12 and 1.13 kg, respectively. The Roanoke bass is the largest species in the genus with many plausible historical accounts of individuals weighing >1.0 kg (Jenkins and Burkhead 1994).

Coloration: Numerous iridescent gold to white spots on upper side of body and head. Ground colors variable, ranging from olive to tan to black to cream or blends of lighter and darker shades. Lateral pattern may consist of parallel rows of black spots, formed by scales darkened at bases, producing a lined pattern or indistinct dark and light blotches. Sides transition to white to bronze on breast and belly. All fins with some degree of yellow pigment, but median fins tend to be more olive and may be mottled or barred. Membranes of anal fin of breeding males dusky to dark but lack dark marginal band (Cashner 1974; Cashner and Jenkins 1982; Page and Burr 1991). Sexual dimorphism in color is minimal, but during nest guarding and spawning, the male darkens intensively and the pale spots become more evident (Petrimoulx 1984).

Native range: The Roanoke bass is endemic to the Neuse, Tar, Roanoke, and Chowan river drainages, North Carolina, and Virginia (Page and Burr 1991).

Habitat: The Roanoke bass occurs across a broad range of stream types in the upper Coastal Plain, Piedmont, Blue Ridge, and Ridge and Valley. The species is most common in flowing, rocky, and sandy creeks and small to medium rivers above the Fall Line, where it is often associated with deep runs. Roanoke bass appear to frequent faster currents than congeners (Smith 1971; Petrimoulx 1983; Jenkins and Burkhead 1994).

Food: The Roanoke bass is primarily a benthic feeder. Crayfish are the most important prey item for adults (>150 mm TL), augmented by small fish (e.g., darters, catfish, shiners) and various aquatic insects, particularly mayflies and caddisflies (Smith 1969, 1971; McBride *et al.* 1982; Petrimoulx 1983). Fish are less important in the diet in spring than in summer or fall, but overall, 75% of the food volume of adults consists of crayfishes, and the remaining 25% is primarily fishes (Petrimoulx 1983). Young fish (<100 mm TL) transition at 100 to 150 mm TL from a diet of mayflies, amphipods, and other small invertebrates to one predominated by crayfish, mayflies, and small fish. A high frequency of river weed (*Podostemum* sp.) and associated invertebrates in stomachs of Roanoke bass suggests that foraging occurs in areas of considerable current (McBride *et al.* 1982; Jenkins and Burkhead 1994).

Reproduction: Matures at age 2+ if a minimum size of 150 mm TL and 75 to 100 g body weight is reached (Smith 1971; Petrimoulx 1983). Based on ovarian condition and spawning observations, Roanoke bass spawn in May and June (perhaps as late as early July) at water temperatures of 20 to <25°C; postreproductive females first appear in samples in late July (Smith 1969, 1971; Petrimoulx 1983, 1984). Males (280–330 mm TL) initiated and completed nest building in 1 day as water temperatures approached 20°C in a hatchery pond in Virginia (Petrimoulx 1984). Substrate preparation was minimal, except that the guardian male removed snails and pebbles from the center of the nest by mouth and expelled them outside the nest; fanning, nest sweeping, or plant uprooting was never observed. The firm substrate of the pond may have limited the need for extensive nest preparation. Nests are solitary (≥1.3 m apart), 305 to 330 mm in diameter, 25 to 75 mm deep, at water depths of 30 to 60 cm, and excavated in gravel (<2.5 cm diameter) substrates if available (Smith 1969; Petrimoulx 1983). The male aggressively drives females away from the nest, but after about 45 minutes, when the female refuses to be driven off, the pair circles the nest, and spawning ensues with the male (in a central position) and female (outside position) in a broadside, face-to-face position. Spawning with each female lasts about 2.5 hours. In the observation pond, males spawned with two females simultaneously, but this may reflect low numbers of guardian males in the observation pond (Petrimoulx 1984). Mature ovarian eggs range from 1.3 to 2.0 mm in diameter (Smith 1969) and are among the largest reported for centrarchids. Two size classes of maturing ova are reported in females (vitellogenic and mature), suggesting two potential batches of eggs (Smith 1969; Petrimoulx 1983). In a North Carolina pond, the occurrence of two size classes of young-of-the-year also suggested at least two spawnings (Smith 1969), but renesting was not observed in the Virginia pond (Petrimoulx 1984). The relationship between total number of maturing ova (Y) and TL (X) is described by the linear function $Y = -3937.1 + 36.7$ TL ($n = 16, R^2 = 0.70$, equation from Petrimoulx 1983). At a median size of about 193 mm TL, a female can potentially produce 3256 vitellogenic and mature eggs (range: 2440 eggs at 136 mm TL to 6476 eggs at 250 mm TL). At about 20°C, eggs hatch in 2 to 3 days, larvae reach swim-up 2 to 3 days later, and larvae disperse from the nest over a 3- to 4-day period. The male guards the nest until larvae reach the swim-up stage, gradually reducing holding time over the nest as larvae disperse (Petrimoulx 1984). Young Roanoke bass are apparently extremely wary and seek cover in thick vegetation (Smith 1969, 1971; Petrimoulx 1984).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The Roanoke bass is considered vulnerable throughout its range (Warren *et al.* 2000; NatureServe 2006). In Virginia, the species is generally rare, and most extant populations are small. In North Carolina, the species is sparsely distributed but locally common (Smith 1969; Jenkins and Burkhead 1994). The Roanoke bass has been extirpated from portions of its former range (e.g., upper Roanoke River), and many populations appear to be persisting in marginal habitats where recruitment is poor (Petrimoulx 1983; Jenkins and Burkhead 1994). Losses and declines of populations are attributed to interactions with introduced rock bass, habitat degradation, and impoundments (Cashner and Jenkins 1982; Jenkins and Burkhead 1994). Establishment of additional populations by stocking in heavily silted streams had no apparent success in Virginia or North Carolina, but carefully planned stocking in suitable, high-quality habitats lacking potential nonnative competitors (e.g., rock bass, spotted bass) might produce additional populations (McBride *et al*. 1982; Jenkins and Burkhead 1994).

Similar species: The rock bass has cheeks that are conspicuously scaled with relatively large scales that are only slightly to moderately embedded; the body lacks distinct, round pale spots; and the anal fin is marked by a dusky or black edge that contrasts with the rest of the fin. In the Roanoke bass the cheek is unscaled or partially scaled with tiny deeply embedded scales; the body is marked with distinct, round pale spots; and a dark margin on the anal fin is usually absent, rarely slightly developed, but never distinctly contrasting with the rest of the fin (Cashner and Jenkins 1982; Jenkins and Burkhead 1994).

Systematic notes: *Ambloplites cavifrons* forms a sister pair with *A. constellatus* (Near *et al*. 2004, 2005). Until the late twentieth century *A. cavifrons* was often considered a subspecies of *A. rupestris* and was not differentiated from that widespread species by fisheries agencies. Cashner and Jenkins (1982) provided a clear morphological diagnosis of *A. cavifrons*, delimited the restricted range, reviewed the confused taxonomic history and resulting repeated stockings of *A. rupestris* in rivers and streams with native *A. cavifrons*, and provided morphological evidence of extremely limited hybridization of nonnative *A. rupestris* with native *A. cavifrons*. Mitochondrial and nuclear DNA analyses provide further evidence of the distinctiveness of *A. cavifrons* from congeners and its relatively distant evolutionary relationship to *A. rupestris* (Roe *et al*. 2002; Near *et al*. 2004, 2005).

Importance to humans: Although long unrecognized as distinct among *Ambloplites*, the Roanoke bass possesses qualities of a first-class sport fish. The species is the largest member of the genus, is regionally unique, and is highly palatable (Jenkins and Burkhead 1994). A review of anglers' catches (1964–1977, 1983) revealed that the majority of the Virginia citations for trophy *Ambloplites* (species not distinguished, 0.45 kg, 304 mm TL) were almost certainly Roanoke bass (Jenkins and Burkhead 1994). The sport fishery for the Roanoke bass is specialized, but the species is ardently sought by the few anglers in Virginia and North Carolina knowing where and how to fish for it (Smith 1969; Jenkins and Burkhead 1994). Increased emphasis on developing the sports fishery for this unique, range-restricted fish would diffuse knowledge of the species among anglers and, in turn, enhance its chances for long-term viability.

13.4.3 Ambloplites constellatus *Cashner and Suttkus*

13.4.3.1 Ozark bass

Characteristics: See generic account for general characteristics. Relatively large, elongate body, depth usually <0.42 of SL. Eye large, diameter ≤0.27 of head length. Body pattern similar to that of *A. rupestris* but with freckling (scattered dark brown spots) on side of body and head. Preopercle strongly serrate to weakly crenate at the angle. Dorsal fin elements, (22)23(24); anal fin elements, (15)17(18). Cheeks fully scaled with large, exposed scales. Cheek scale rows, (6)9(11); lateral line scales, (38)43 or 44(48); scale rows above lateral line, (6)8 or 9(10); scale rows below lateral line, (11)12 or 13(14); diagonal scale rows, (21)22 to 24; and breast scale rows, (20)22. One circular patch of teeth on tongue (Cashner 1974; Cashner and Suttkus 1977; Page and Burr 1991).

Size and age: Typically reaches 41 mm TL at age 1. Large individuals measure 180 to 213 mm TL and reach age 6+ to 11+ (maximum 259 mm TL) (Cashner and Suttkus 1977; Page and Burr 1991; Pflieger 1997). World angling record, 450 g, Arkansas (IGFA 2006). State record in Arkansas, 681 g (AGFC 2007).

Coloration: General coloration similar to that of shadow bass and rock bass, but ground color of olive to tan above and below the lateral line is more uniform on the body and among individuals. Sides of body, cheek, opercle, and preopercle are dominated by a freckled pattern of irregularly arranged dark spots. In a lateral scale row, one to three scales are darkened at the anterior base and followed by a series of scales lacking the dark spots, producing the freckled pattern. On the body, the freckled pattern is most evident below the lateral line. Above the lateral line, four or five saddle-like blotches may be visible, but these are never dark enough to obscure the freckling or spotted pattern on the scales (Cashner and Suttkus 1977; Page and Burr 1991). Fins usually olive green, and no black marginal band develops on the anal fin. Sexual dimorphism in color is minimal, but males become nearly black and females grey during courtship and spawning (Walters *et al*. 2000).

Native range: The Ozark bass is endemic to the upper White River of Missouri and Arkansas. The species drops almost completely out of the White River fauna at the physiographic border between the Ozark Plateau and the Mississippi Alluvial Valley. Isolated populations in the upper Osage River may be the result of introduction (Pflieger 1997; Koppelman *et al*. 2000).

Habitat: The Ozark bass is abundant in clear, rocky pools of upland creeks and small to medium rivers in the White River drainage of the Ozark Plateau. The species also occurs in reservoirs. Ozark bass are often associated with cover of banks, boulders, or logs usually located away from the swiftest main channel currents (Cashner and Suttkus 1977; Robison and Buchanan 1984; Pflieger 1997).

Food: The food of the Ozark bass has not been detailed, but the diet is likely similar to that of the rock bass and shadow bass.

Reproduction: Knowledge of the reproductive biology of the Ozark bass is limited to a published account detailing aspects of nest sites and nesting chronology over two spawning seasons and describing behaviors of a single spawning pair in the Buffalo River, Arkansas (Walters *et al*. 2000). Asynchronous egg deposition and male nest guarding occurred over 4- to 5-week periods from mid-May to mid-June at water temperatures of 17 to 23.5°C. Nests were located in gravel and cobble substrates at depths of 0.5 to 2.9 m, and guarded by males ranging in size from 150 to 230 mm TL. Most nests (>74%) were <1 m from cover and were usually downstream of cover (e.g., boulders, logs). The majority of small nest-guarding males (<200 mm TL) were observed more than 2 weeks after initiation of spawning, but significant correlations of size of nest-guarding males and time since the beginning of spawning were not detected. During courtship, the male rarely directed or pushed the female into the nest; both sexes waved their soft dorsal, caudal, and pectoral fins almost constantly while keeping the spiny dorsal fin flat. Before each egg deposition, the male and female pair circled the nest several times, the female sometimes over the male and the male occasionally nipping the female near the caudal peduncle. Spawning ensued, with the pair dropping to the nest with the male (usually in a central position) and female (usually outside position) in a broadside, face-to-face position over the nest. Eighty-eight spawning bouts occurred in 2 hours, the pair drifting up from the nest between bouts. The female remained in or near the nest during this time. No postspawning aggression of the male toward the female was observed. A pair of Ozark bass were spawning at the same nest an hour later, but it is unknown if it was the same or another female. High water events were associated with renesting (nests with embryos), but new nests with embryos were found throughout the spawning season. At a mean temperature of 21°C, eggs hatched in $\geq$5 days, and larvae remained in the nest for 5 to 7 days. Dispersing young were grey. During the nesting period, no Ozark bass fry were observed outside areas guarded by males. No young-of-the-year were observed in daytime snorkeling transects, and few were caught in daytime seine hauls. In contrast, young-of-the-year were caught in larger numbers in nighttime seine samples, suggesting nocturnal activity in Ozark bass young (Walters *et al*. 2000).

Nest associates: None known.

Freshwater mussel host: None documented, but Ozark bass populations co-occur with populations of *Villosa iris*. Gravid females of *V. iris* possess highly modified mantle lures that, at least in Ozarkian populations, mimic the appearance and movement of small crayfishes (Barnhart 2006). The prominence of crayfish in the diet of some *Ambloplites* and the host relationship of *A. rupestris* (and other large centrarchids) with *Villosa* spp., suggest a potentially fascinating, but as yet unstudied, host–fish relationship.

Conservation status: The Ozark bass is considered currently stable throughout its range (Warren *et al*. 2000; NatureServe 2006).

Similar species: Other species of *Ambloplites* lack the distinctive freckled pattern of Ozark bass (Cashner and Suttkus 1977; Page and Burr 1991). In addition, the body depths in adult shadow bass and rock bass (>150 mm SL) are typically >0.41 of the SL and <0.41 of SL in Ozark bass (Koppelman *et al*. 2000).

Systematic notes: Morphological and genetic evidence support long-term divergence and distinctiveness of *A. constellatus* from its sister species *A. cavifrons* and congeners (Cashner and Suttkus 1977; Koppelman *et al*. 2000; Near *et al*. 2004, 2005; Bolnick and Near 2005). Nevertheless, *A. constellatus* was not diagnosed and clearly differentiated from congeners until late in the twentieth century (Cashner and Suttkus 1977; Koppelman *et al*. 2000) and consequently was not recognized as distinct until relatively recently by fisheries managers. Early efforts to establish "rock bass" in Missouri and Arkansas streams involved brood stock taken from the upper White River, the range of *A. constellatus* (Cashner and Suttkus 1977; Robison and Buchanan 1984; Koppelman *et al*. 2000). These hatchery-based efforts were particularly intense in the 1930s and 1940s in Missouri (Pflieger 1997). Populations of *Ambloplites* in the Pomme de Terre and Sac rivers (upper Osage River, Missouri River drainage) are essentially identical to White River (Mississippi River drainage) populations of *A. constellatus* as evidenced by diagnostic allozyme loci, genetic distance, and phenotype (Cashner and Suttkus 1977; Pflieger 1997; Koppelman *et al*. 2000). In contrast, similar data suggest that the population in the Niangua River (middle Osage River) consists of non-F_1 hybrids between *A. constellatus* and *A. rupestris*. No historical records are available before 1960 of the *A. constellatus* occurring anywhere in the Osage River. Similarly, no records of *A. rupestris* in the Niangua River drainage are known before 1940, and first documented records for the lower Osage River are from 1964 (Pflieger 1997). The populations of these species now established in the Osage drainage are likely the result of introduction of both species (Pflieger 1997), which may have produced the spatially limited hybridization as evidenced in the Niangua River (Koppelman *et al*. 2000). Impoundments in the upper Osage River appear to have limited dispersal of *A. constellatus* in the system, producing the essentially isolated populations in the Sac and Pomme de Terre rivers.

Importance to humans: The Ozark bass is an abundant, popular, and sought-after sport fish in the upper White River of Missouri and Arkansas (Pflieger 1997; Koppelman *et al*. 2000).

13.4.4 **Ambloplites rupestris** *(Rafinesque)*

13.4.4.1 Rock bass

Characteristics: See generic account for general characteristics. Relatively large, robust, elongate body, depth variable, usually >0.41 of SL. Eye large, diameter ≤0.30 of head length. Adults with rows of brown-black spots along side, forming horizontal lines. Preopercle strongly serrate to weakly crenate, but always a few teeth at angle. Dorsal fin elements, (20)22(24); anal fin elements, (15)16(17). Cheeks fully scaled with large, exposed scales. Cheek scale rows, (5)8 or 9(10); lateral line scales, (35)38 to 42(47); scale rows above lateral line, (6)7 or 8(10); scale rows below lateral line, 12 to 14(16); diagonal scale rows, (19)20 to 24(25); and breast scale rows, (18)21 to 24(27). One circular patch of teeth on tongue (Bailey 1938; Keast and Webb 1966; Cashner 1974; Cashner and Suttkus 1977; Cashner and Jenkins 1982; Page and Burr 1991).

Size and age: Typically 42 to 102 mm TL at age 1. Large individuals measure 180 to 290 mm TL, weigh 200 to 454 g, and reach age 10+ to 14+ (maximum 430 mm TL) (Carlander 1977; Page and Burr 1991). World angling record, 1.36 kg, Pennsylvania and Ontario (IGFA 2006). Growth shows a latitudinal component in stream-dwelling rock bass such that northern populations grow more slowly than midlatitude populations. Among northern populations, maximum size and age of stream-dwelling rock bass are less than those of lake-dwelling rock bass, likely reflecting higher mortality in variable stream environments (Noltie 1988). In addition, subtle but significant differences occur in body form and relative fin sizes between northern lake and stream populations (Brinsmead and Fox 2002). Male rock bass can weigh more and reach longer lengths at age than females, but females can live longer (Ricker 1947; Carlander 1977; Noltie 1988).

Coloration: Ground color of olive to tan above and on sides, fading to lighter, white to bronze, on breast and belly; brassy yellow flecks on sides; however, general coloration and shading highly variable among individuals and populations. If not obscured by darkened ground color, sides of body are dominated by a spotted pattern of regularly arranged dark spots, forming dark, uninterrupted horizontal lines. In a lateral scale row, scales are darkened by a spot at the anterior base, producing the horizontal striping effect. Light areas on the scales above and below the spot often give the appearance of light horizontal lines and together produce a pattern of alternating light and dark lines. The lined pattern is most evident below the lateral line. Four or five dorsal saddles may be visible, extending down to or just below the lateral line. Anal fin has a distinct, black marginal band that extends across the spiny portion to the fifth or sixth soft ray (Cashner 1974;

Page and Burr 1991). Breeding males darken dramatically during the spawning period and develop black pigmentation along the spine and first ray of the pelvic fin or darken the entire fin (Cashner 1974; Gross and Nowell 1980; Noltie and Keenleyside 1987b). The pelvic fin margins of breeding female rock bass are yellowish white (Noltie 1985). External appearance of the genitalia (presence of the genital papillae in females) can be used as a reliable means of separating sexes during the breeding season (Noltie 1985).

Native range: The rock bass has the largest native range in the genus occurring in the St. Lawrence River-Great Lakes, Hudson Bay (Red River), and Mississippi River Basins. Rock bass have been widely introduced and are established in Atlantic Slope drainages as far south as the Roanoke River, Virginia, and in the Missouri and Arkansas River drainages. The species is also established in several western states (Page and Burr 1991; Fuller *et al.* 1999).

Habitat: The rock bass frequents cover in pools of creeks to small and medium rivers and the rocky and vegetated margins of lakes, being most common in silt-free rocky streams. Individuals in lakes frequent cover during the day (e.g., aquatic vegetation, rocky shelves, boulders) but disperse from these areas at night to feed (Keast 1977).

Rock bass movements of >161 km (Funk 1957; Storr *et al.* 1983) are documented and populations may or may not show restricted summer home ranges. In Lake Erie, recaptured, tagged rock bass were taken from ≤3 km of their original location (MacLean and Teleki 1977). In Lake Ontario, postspawning rock bass showed less dispersion along the shoreline than prespawning individuals, but the degree of dispersal in both periods (about 2 weeks on average) was large (average 3.5 km versus 11.2 km, respectively; Storr *et al.* 1983). Overall average movement from April to June in tributaries to Lake Ontario was 500 m/d and maximal hourly movement was 200 m/h (Gerber and Haynes 1988). Summer home range in an Indiana stream was estimated at about 66 linear meters (Gerking 1950), and seasonal, multiyear samples in Tennessee streams revealed that 90% of recaptured rock bass remained in the same 500-m segment, and more than 50% were within the same 100-m segment (Gatz and Adams 1994).

Some populations of rock bass migrate to wintering areas. In Lake Ontario, catches of tagged rock bass and dispersion models suggested movement from shoreline habitats to overwintering areas in deeper water (Storr *et al.* 1983), and littoral zone samples in Wisconsin lakes also indicated offshore movement in fall (Hatzenbeler *et al.* 2000). In small Virginia streams, fish in headwaters emigrated downstream in the fall, and in winter, fish used the deepest pools available (Pajak and Neves 1987). The presence of rock bass in a small North Carolina stream almost exclusively from autumn to spring over 10 years of sampling indicates that some populations migrate upstream to overwintering areas in fall and return downstream the following winter or spring (Grossman *et al.* 1995).

Rock bass are sensitive to acidification, but sensitivity varies among life stages. Faunal analyses of northern lakes, *in situ* tests in lakes, and laboratory tests indicate that rock bass are negatively affected at pH 4.5 to 5.5 (Rahel and Magnuson 1983; Magnuson *et al.* 1984; McCormick *et al.* 1989; Eaton *et al.* 1992). Rock bass embryos, but not larvae, survived in an experimentally acidified lake at pH 5.1, recruitment was greatly reduced at pH 5.6, and high adult mortality occurred at pH 4.7. In the laboratory, survival of embryos and larvae (to 7-day post hatching) decreased by 40 to 50% at pH 5.0 and was near zero at pH 4.5. Larval survival also showed a dose-correlated decrease with decreasing pH (7.0 to 5.0) and increased Al (<0.6 to 56 μg/l) (Eaton *et al.* 1992). In a related laboratory study, juvenile rock bass (5.3 g) osmoregulated and survived up to 30 days at pH ≥4.5 but lost osmoregulatory control at pH 4.0 and died in ≤29 days (McCormick *et al.* 1989).

Food: The rock bass is primarily a benthic feeder. Large invertebrates, such as crayfish, dragonfly nymphs, mayfly larvae, and caddisfly larvae are the primary diet items of adults (Keast and Welsh 1968; Keast 1977, 1985c; Johnson and Dropkin 1993; Roell and Orth 1993). In the New River, Virginia, where crayfish constitute more than 50% of the wet weight diet of individuals >100 mm TL, rock bass consume an estimated 31% of the annual production of crayfish of age 1 or 2 in the river (Roell and Orth 1993). Predation by rock bass is implicated in shifts in longitudinal distribution and species composition of juvenile crayfishes in headwaters of the New River, North Carolina (Fortino and Creed 2007). Small fish are taken during the second summer of life but contribute substantially to the diet only in larger adults (Keast 1977, 1985c; Elrod *et al.* 1981). Young-of-the-year feed heavily on cladocerans, isopods, amphipods, and chironomids; various aquatic insect larvae also contribute to the diet in the first summer (Keast 1977, 1980; George and Hadley 1979). The eyes of the rock bass are well equipped to allow successful capture of invertebrates in dimly lit bottom habitats. Lens quality increases until age 5, the distance of contraction and relaxation is high (≤28 diopters), and the ability to retain focus on approaching a target (93 diopters/s) is almost an order of magnitude greater than that reported for humans (Sivak 1973, 1990; Sivak and

Howland 1973). The relatively large retina contains a temporal dorsal area of highest double cone densities that correlates with ability to detect prey below the horizontal plane (Williamson and Keast 1988). In the spring, diel studies indicate about equal feeding from mid-morning until noon and again from late afternoon to midnight (Keast and Welsh 1968) and in the fall, low levels of feeding during daylight hours with peak feeding between 2000 and 0400 hours (Johnson and Dropkin 1993). Diel movement of radio-tagged individuals in summer in Lake Ontario suggested higher diurnal than nocturnal activity. Activity was highest from 0900 to 2000 hours, decreasing substantially by 2200 hours; no diel patterns in activity were discerned in fish in tributaries to the lake (Gerber and Haynes 1988). Underwater observation in two lakes revealed an intensification of activity and feeding 30 minutes to 2 hours before darkness. During that time, large rock bass that aggregated in daytime resting areas near cover (1–8 m depth) moved as individuals or small groups into shallow water (Emery 1973; Helfman 1981). After darkness, individuals continued to be active in one lake, but in the other, individuals settled into and rested on rocks, logs, or plants. Underwater observations in a river indicated that rock bass are more active at night, tending to move from daytime cover to presumably feed in riffle and run habitats (Lobb and Orth 1991). Rock bass show active shoaling preferences for conspecifics and benefit from social enhancement of foraging (Brown and Colgan 1986; Templeton 1987; Brown and Laland 2003).

Reproduction: Age at maturity is highly variable ranging from age 2+ to 7+ or even 9+ (about 125–150 mm TL) (Gross and Nowell 1980; Noltie 1988). Rock bass along the northern shore of Lake Erie make a 35- to 40-km spring migration to spawning grounds in an inner bay (MacLean and Teleki 1977), and other northern populations regularly ascend streams for spawning, moving up to 11 km/d (average 2.9 km/d), after overwintering in deeper waters (Noltie and Keenleyside 1987a; Gerber and Haynes 1988). Nest-site fidelity is high in some populations. Over 85% of recaptured rock bass in a northern lake nested within 50 m of their nest site in the previous year (Sabat 1994a), but in a Lake Ontario study, only 3 of 25 rock bass tagged during a spawning season and recaptured during subsequent spawning seasons were taken at the same site. The others were recaptured 28 to 185 km from the original tagging site (Storr *et al.* 1983). Males initiate nest building in late spring or early summer at temperatures as low as 14.0°C, and spawning temperatures range from about 18 to 23°C. Nests are circular in lakes (average 27 cm diameter) and elliptical in streams (37 cm wide, 43 cm long), about 5 to 7 cm deep, at water depths of 50 to 70 cm, and are typically excavated over coarse substrates (0.9–2.4 cm diameter). The spawning period can last from 6 to 8 weeks, but most reproductive activity occurs over a 3- to 4-week period; spawning tends to be synchronous in lakes and asynchronous in streams (Gross and Nowell 1980; Noltie and Keenleyside 1987a; Sabat 1994a). Large, older male rock bass (>100 g) nest and spawn 2 to 4 weeks earlier than smaller, younger males, and male size and number of eggs acquired are correlated positively, presumably reflecting female choice of mates (Noltie and Keenleyside 1987a; Sabat 1994b). In streams, nests are spaced widely (average 7.7 m apart) and near cover, but in lakes, nests are more closely spaced (average 1.6 m apart) with no apparent relation to cover (Gross and Nowell 1980; Noltie and Keenleyside 1987a). Circling of the nest by the male and female before spawning may occur for several minutes, or spawning may proceed without circling (Gross and Nowell 1980; Noltie and Keenleyside 1987b). A complete spawning bout can last 3.5 hours (average 2 h) and on average involves 120 separate egg releases (about 3–5 eggs per release); after each release, the female is often aggressively driven from the nest by the male for periods of 15 seconds to several minutes before returning for another bout (Gross and Nowell 1980). In synchronously spawning lake populations, females may spawn with more than one male, and males may spawn serially with alternating females (Gross and Nowell 1980), but in asynchronously nesting stream populations, males and females appear to be nearly monogamous (Noltie and Keenleyside 1987a,b). Mature ovarian eggs range from about 1.2 to 2.1 mm in diameter. Two size classes of ova are reported in females (modes, 1.65 mm and 0.44 mm) (Gross and Nowell 1980). Temporal changes in frequencies of egg diameter classes in lake-dwelling rock bass are coincident with spawning of two batches separated by a 16-day interval (Gross and Nowell 1980), and up to three discrete egg-laying bouts may occur over a 6- to 8-week period (Sabat 1994a,b). Information on numbers of mature ova in spawning-ready females is unavailable, but total fecundity is related positively to length (Carlander 1977). Based on observations of ovipositing females and numbers of larvae in nests, females appear to deposit about 400 to 500 eggs in a spawning bout (Gross and Nowell 1980). At a mean temperature of 22.5°C (range 16–22°C), eggs hatch in 5 days, and larvae disperse from nests 9 days later. Large older males may renest one or more times over the breeding season (Gross and Nowell 1980; Noltie and Keenleyside 1986; Sabat 1994b). Flooding, predation, and fouling of nests by algae are major causes of brood failure in stream-dwelling populations, resulting in frequent renesting attempts by males (Noltie and Keenleyside 1986). Parental males fan the eggs and defend the embryos and larvae (344 to 1758/nest) for an average of 14 days, abandoning the nest as the fry disperse (Carbine 1939; Gross and Nowell 1980; Noltie and Keenleyside 1986). Body weight of males can decline by 5 to 24% during the parental care period (Noltie and Keenleyside 1986; Sabat 1994a). Increased weight loss of parental male rock bass reduced probability of recapture in subsequent years (Sabat 1994a), suggesting a link between weight loss due to nesting and subsequent survivability of males. Free-swimming rock bass fry show no swarming behavior, begin agonistic behaviors sooner and at a smaller size (36 days post swim-up, 21 mm TL) than either *Lepomis* or *Micropterus*, and begin predator avoidance responses at 1 week of age (Brown 1984; Brown and Colgan 1985a).

Freshwater mussel host: Confirmed host to *Actinonaias ligamentina* (Lefevre and Curtis 1910), *Arcidens confragosus* (Surber 1913), *Pyganodon grandis, Utterbackia imbecillis* (Tucker 1928; Trdan and Hoeh 1982), *Strophitus undulatus* (Van Snik Gray *et al*. 2002), *V. iris* (Zale and Neves 1982, as *Villosa nebulosa*; O'Connell and Neves 1999), and *Villosa taeniata* (Gordon *et al*. 1994). Putative host to *Amblema plicata*, *Epioblasma obliquata*, *Lampsilis reeveiana*, *Lasmigona holstonia*, *Ligumia recta*, *Pyganodon cataracta*, and *Villosa constricta* (unpublished sources in OSUDM 2006).

Conservation status: The rock bass is currently considered stable throughout its range (Warren *et al*. 2000; NatureServe 2006). Introduction of rock bass into northern lakes where it is not native is implicated in declines in littoral zone fishes with potentially severe consequences for native lake trout populations dependent on those fishes for forage (Vander Zanden *et al*. 1999).

Similar species: Other species of *Ambloplites*, except the Roanoke bass, lack the distinctive rows of spots of rock bass; the Roanoke bass has unscaled or partly scaled cheeks and iridescent gold to white spots on the upper side and head (Cashner and Jenkins 1982; Page and Burr 1991).

Systematic notes: See accounts on *A. ariommus, A. constellatus,* and *A. cavifrons.*

Importance to humans: Although underappreciated by many anglers, the rock bass is a feisty sport fish with firm, excellent-tasting flesh. As recently as the 1970s, rock bass contributed substantially to the commercial fishery and sport fishery catch in several Great Lakes (Scott and Crossman 1973; MacLean and Teleki 1977).

13.5 *Archoplites interruptus* (Girard)

13.5.0.1 Sacramento perch

Characteristics: Moderately compressed, deep but somewhat elongate body, depth about 0.4 of SL. Large, oblique mouth, lower jaw projecting, supramaxilla large ($\leq$2 times maxilla length), upper jaw extending under pupil of the eye. Opercle varies from two flat extensions to broadly rounded; dusky to dark opercular spot. Preopercle posterior margin sharply serrate. Long dorsal fin, 12 to 14 spines, 10 to 11 rays, 22 to 25 total; and moderate anal fin, 6 to 8 spines, 10 to 11 rays, 16 to 18 total. Dorsal fin base about twice as long as anal fin base. Dorsal fin continuous with shallow gap between spines and rays. Emarginate caudal fin. Rounded pectoral fins. Long, slender gill rakers, 25 to 30. Strongly ctenoid scales. Lateral line scales, 38 to 48; cheek scale rows, 6 to 9; branchiostegal rays, 7; pectoral rays, (13)14(15); vertebrae, 31(13 + 18). Teeth on entopterygoid, ectopterygoid, palatine (villiform), and glossohyal (tongue, two elongate patches) bones (Bailey 1938; Page and Burr 1991; Mabee 1993; Moyle 2002; C. M. Woodley, University of California-Davis, personal communication).

Size and age: Typically 60 to 130 mm TL at the end of year one, depending largely on food availability and water temperature (C. M. Woodley, University of California-Davis, personal communication). Large individuals measure 370 to 400 mm TL, weigh 1.2 kg, and age 9+ (maximum, 610–730 mm TL and 3.6 kg) (Page and Burr 1991; Moyle 2002). World angling record, 1.44 kg, California (IGFA 2006). Females grow faster, reach larger sizes, and live longer than males (Mathews 1962; Aceituno and Vanicek 1976; Moyle 2002).

Coloration: Olive brown above with 6 to 7 irregular dark bars on the upper side extending ventrally to the lateral line. Depending on habitat, varies from silver-green to purple sheen on mottled black and white side to silvery with dark barring; white ventrally. Breeding colors are variable. Males can be darker than females with purple opercula and a distinctive silvery spotting showing through the darker sides and can have a conspicuous darkened patch on top of their head; breeding females tend to be more uniform in color (Page and Burr 1991; Moyle 2002; C. M. Woodley, University of California-Davis, personal communication).

Native range: The Sacramento perch is the only centrarchid with a native range west of the Rocky Mountains, where it was common and often abundant historically throughout the Central Valley of California (San Joaquin-Sacramento rivers), the Pajaro and Salinas rivers, and Clear Lake at elevations below 100 m. Currently, the only population that represents continuous occupation within the native range persists in Alameda Creek (Moyle 2002), but that population is considered unstable, the last record being of a single individual taken in 1999 in Calveras Reservoir (P. Crain and C. M. Woodley, University of California-Davis, personal communication). The species was introduced extensively outside its native range in the western United States between the 1870s and 1960s as a potential sportfish (McCarraher and Gregory 1970; Fuller *et al.* 1999) but now occurs outside the native range only in lakes, reservoirs, and associated streams in California, Nevada, Utah, and Oregon. Few of these populations are considered stable (Moyle 2002; Schwartz and May 2004; P. Crain, R. Schwartz, and C. M. Woodley, University of California-Davis, personal communications).

Habitat: The Sacramento perch was formerly common in sloughs, slow-moving rivers, and lakes. The species often is associated with vegetation beds, which may be an essential habitat for young-of-the-year. Now, the species most commonly occurs in reservoirs and farm ponds. Because the original habitat was subject to extreme drought and flooding, Sacramento perch are notably tolerant of high turbidity, temperatures, alkalinity, chloride–sulfate salinity, and dissolved solids (Moyle 2002). Temperatures ≤30°C are readily tolerated (Moyle 2002). Recent work indicates the species is a cool-water centrarchid, with the preferred temperature ranging from 16 to 19°C; similarly, physiological optima appear to lie between 18 and 23°C (C. M. Woodley, University of California-Davis, personal communication). The species survived ≥12 months at pH >9 and maximal alkalinities >2000 mg/l in alklai lakes of Nebraska. Other centrarchids introduced in these habitats survived from a few hours to less than a month (McCarraher and Gregory 1970; McCarraher 1971). The species can reproduce in ponds with maximal pH and dissolved solids of 8.8 and 19,248 mg/l, respectively (Imler *et al.* 1975), and chloride–sulfate alkalinities of 17 ppt (McCarraher and Gregory 1970).

Food: The Sacramento perch is a sluggish, slow-stalking, highly opportunistic suction-feeding carnivore (Vinyard 1982; Moyle 2002). It feeds primarily by "inhaling" organisms off the bottom or aquatic plants and by capturing zooplankton, fish, or emerging insects in midwater (Moyle *et al.* 1974). The species has numerous, long gill rakers that likely play an important functional role in the extended (<90 mm TL) feeding on zooplankton and other microcrustaceans. Although slight peaks in foraging occur at dawn and dusk, Sacramento perch show no obvious diel feeding periodicity, feeding at all times of the day and night (Moyle *et al.* 1974; Moyle 2002). Large individuals (>90 mm TL) in an introduced population (Pyramid Lake, Nevada) switched almost exclusively to piscivory, but in many populations, microcrustaceans and aquatic insect larvae and pupae continue as important components of the adult diet (Moyle *et al.* 1974; Imler *et al.* 1975; Aceituno and Vanicek 1976).

Reproduction: Maturity is reached at age 2 to 3+ at a minimum size of about 120 mm fork length (FL). Spawning occurs at water temperatures of 18 to 29°C and can extend from March through early August with peaks in late May to early June (Murphy 1948; Mathews 1962; McCarraher and Gregory 1970; Aceituno and Vanicek 1976; Moyle 2002). Published accounts of reproductive behaviors are few, somewhat inconsistent, and based on limited observations. Although some observations suggested definite male territory defense (about 40 cm diameter) without preparation of the substrate, more recent extensive observations indicate male digging of nests with the caudal fin and subsequent defense of obvious cleared, depressions (C. M. Woodley, University of California-Davis, personal communication). Territories and nests are often associated with vegetation or filamentous algae beds in shallow water (20–50 cm deep) and over substrates of mud, clay, or rocks; rock piles or other cover may also attract spawning individuals (Murphy 1948; Mathews 1962, 1965; Aceituno and Vanicek 1976; Moyle 2002; C. M. Woodley, University of California-Davis, personal communication). Nest preparation may span several days (Moyle 2002). Some observed nests were arranged linearly along shorelines, but others were suggestive of colonies (Murphy 1948; Aceituno and Vanicek 1976; Moyle 2002). Tail quivering occurs in territorial males, a behavior which appears distinct from the nest sweeping behavior of other centrarchids (caudal sweeping, Miller 1963; Mathews 1965). The male remains stationary over the nest with the head down and pectoral fins out and rapidly oscillates the tail back and forth in small arcs, at 3 to 5 oscillations per second, ending with the head up and nearly perpendicular to the nest. After several seconds the male rests, then repeats the behavior, which intensifies during courtship and spawning. Territorial males repeatedly repulse approaching females (Mathews 1965). After repeated attempts to repulse the female (≤1 hour), the male swims stiffly to the ready female and nips at the vent (Moyle 2002). Pairs of Sacramento perch spend up to 30 minutes on the nest before spawning, during which time the male nips or nudges the female and both substrate bite, undulate, and contort their bodies, and jaw gape. Females may mate with more than one nesting male (Moyle 2002). In a natural setting, a male and female in the nest oriented broadside during spawning, but in opposite directions, unlike the head-to-head spawning position typical of other centrarchids. They made tight circles during gamete release as is typical of many centrarchids, but both the male and female tilted away from one another at the moment of release, another apparent departure from typical centrarchid gamete release (Mathews 1965; see also Bolnick and Miller 2006). Eggs are demersal, slightly adhesive, and upon deposition, adhere to surrounding vegetation or substrate in the bottom of the nest. Sacramento perch have among the smallest mature eggs among centrarchids (0.67 mm diameter) (Mathews 1962) and one of the highest batch fecundities among centrarchids (see *Centrarchus macropterus* and *Pomoxis*). Descriptive accounts indicate a unimodal distribution of mature or ripening ova sizes in mature females (Mathews 1962), suggesting release of a single batch of eggs. The relationship between number of mature eggs (Y) and TL (X) is described by the power function $Y = 0.0279X^{2.6148}$ ($n = 32$, $R^2 = 0.89$, data from Mathews 1962, FL converted to TL, see Aceituno and Vanicek 1976). At a mean size of 200 mm TL, a female can produce 29,003 mature eggs (range: 9820 eggs at 117 mm TL to 121,570 eggs at 330 mm TL, Mathews 1962). Hatching occurs in 51 hours and larval swim-up between 4 and 6 days at 22°C (Mathews 1962). From a single nest observation, male parental care is oft-cited as lasting only 3.5 days at water temperatures between 22 and 24°C, which is a short period of parental care relative to other centrarchids (Mathews 1965). More extensive observations at cooler water temperatures indicate that males stay at the nest for 5 to 7 days, apparently abandoning the nest only after larvae swim-up and move out of the nest area (Mathews 1962, 1965; C. M. Woodley, University of California-Davis, personal communication).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: Although tolerant of a range of physicochemical conditions, the distribution and abundance of native populations of the Sacramento perch has declined gradually since the nineteenth century. Declines are attributed to habitat alteration, embryo predation, and interspecific competition, particularly from nonnative centrarchids, such as bluegill and black crappie (Murphy 1948; Aceituno and Nicola 1976; Vanicek 1980; Marchetti 1999; Moyle 2002). In experiments with limited food resources, growth was depressed and habitat use shifted in the Sacramento perch in the presence of the more aggressive, dominating bluegill (Marchetti 1999). Native populations in the Pajaro and Salinas rivers and Clear Lake (Lake County) are extirpated (Gobalet 1990; Moyle 2002; Schwartz and May 2004). Within their native range the species persists primarily in ponds, reservoirs, and recreational lakes into which they were introduced, often upstream of native habitat (Moyle 2002). The species is considered of special concern in California rather than endangered because a few introduced populations appear secure (e.g., Garrison Reservior, Utah; Crowley Reservoir, California). However, even in many introduction sites in California and elsewhere, the species is uncommon, extremely rare, or extirpated (Moyle 2002; P. Crain and C. M. Woodley, University of California-Davis, personal communications; see section on native range).

Similar species: The anal fin base of the white crappie and black crappie is about as long as the dorsal fin base, and the dorsal fin in these species has six to eight spines.

Systematic notes: *Archoplites interruptus* is sister to the genus *Ambloplites*, and the *Archoplites–Ambloplites* pair are sister to *Pomoxis* (Roe *et al.* 2002; Near *et al.* 2004, 2005). Fossil representatives of the genus *Archoplites* are widespread west of the continental divide in Miocene to Early Pleistocene deposits (e.g., Idaho, Washington, Oregon, Utah, Nevada, and California) (Miller and Smith 1967; Smith and Miller 1985; Minckley *et al.* 1986; McPhail and Lindsey 1986; Near *et al.* 2005). Two other species, both extinct, are congeners: *A. clarki* Smith and Miller, from Miocene lacustrine deposits in northern Idaho (Smith and Miller 1985) and *A. taylori* Miller and Smith, from Late Pliocene to Early Pleistocene lacustrine deposits in southwestern Idaho (Miller and Smith 1967; Smith and Patterson 1994). Meristic variation among populations of *A. interruptus* is low, but some differences in color pattern exist (Hopkirk 1973; Moyle 2002). The population in Clear Lake probably is genetically distinct because of long isolation from other populations (Moyle 2002).

Importance to humans: Historically, the Sacramento perch was one of the most common fishes caught by native peoples of California. In the late nineteenth century, 18,144 to 195,954 kg (40,000 to 432,000 lb) were sold annually in San Francisco (Gobalet and Jones 1995; Moyle 2002).

13.6 *Centrarchus macropterus* (Lacépède)

13.6.0.2 Flier

Characteristics: Deep, extremely compressed body, depth about half of SL. Small, supraterminal, oblique mouth, lower jaw projecting, supramaxilla moderate (2.1 to ≤3 times into length of maxilla), upper jaw not reaching past middle of eye. Eye large, diameter equal or greater than snout length. Large black teardrop. Interrupted rows of dark spots along the side. Juveniles (≤65 mm SL) with red-orange halo encircling black spot on posterior of soft dorsal fin. Opercle lacks flat extensions; opercular spot black. Preopercle posterior margin finely serrate. Long dorsal fin, 11 to 14 spines, 12 to 15 rays, 25 to 27 total; and long anal fin, 7 to 9 spines, 13 to 17 rays, 22 to 24 total. Dorsal fin base about 1.1 to 1.3 times longer than anal fin base. Spiny and soft dorsal fins continuous and smoothly rounded. Emarginate caudal fin. Long, pointed pectoral fin. Long, slender gill rakers, 30 to 40. Ctenoid scales. Lateral line scales 36 to 44; cheek scale rows, 4 to 7; branchiostegal rays, 7; pectoral rays, (12)13(14); vertebrae, 31(13 + 18). Teeth on entopterygoid, ectopterygoid, palatine (villiform), and glossohyal (tongue, two patches) bones (Bailey 1938; Page and Burr 1991; Mabee 1993; Jenkins and Burkhead 1994; Boschung and Mayden 2004).

Size and age: Typically reach 55 to 72 mm TL at age 1. Large individuals measure 210 mm TL, weigh 156 to 197 g, and reach age 7+ to 8+ (maximum 250–356 mm TL) (Conley 1966; Geaghan 1978; Etnier and Starnes 1993; Jenkins and Burkhead 1994; Pflieger 1997). World angling record, 560 g, Georgia and North Carolina (IGFA 2006). Females can reach larger sizes and live longer than males (Conley 1966; Geaghan and Huish 1981).

Coloration: Olive green to olive brown above; sides brassy yellow or silver with green and bronze flecks; rows of brown spots on sides forming horizontal lines. Brown-black spots on medial fins often form wavy bands or bars. Iris with vertical black bar continuing as tear drop. Young with four to five broad dark bars on side (Page and Burr 1991; Jenkins and Burkhead 1994; Pflieger 1997; Boschung and Mayden 2004).

Native range: The flier occurs primarily on the Coastal Plain from the Potomac River drainage, Maryland, to central Florida, and west to the Trinity River, Texas. The species penetrates the Mississippi Embayment to southern Illinois and southern Indiana, where it occurs above the Fall Line (Page and Burr 1991).

Habitat: The flier is a decidedly lowland species, inhabiting swamps, vegetated lakes, ponds, sloughs, and backwaters and pools of small creeks and small rivers. The species is usually associated with densely vegetated, clear waters (Page and Burr 1991; Jenkins and Burkhead 1994; Pflieger 1997; Boschung and Mayden 2004). Relative abundances were highest in hypoxic habitats in the Atchafalaya River Basin, Louisiana, where most fishes occurred in low relative abundances (Rutherford *et al.* 2001). The species also occurs in acid waters (pH 3.7 to 4.8), although growth appears to be diminished at low pH (Geaghan 1978); it is the most common sunfish in the acidic Okefenokee Swamp (Laerm and Freeman 1986). Movements of 12.7 km are documented, but ≥75% of individuals recaptured within 90 days of marking were found <200 m from their release site (Whitehurst 1981), suggesting fidelity to limited activity areas over extended periods. Increased movements occur in spring, presumably in association with spawning (Holder 1970; Whitehurst 1981).

Food: The flier is a primarily nocturnal feeder with feeding practically ceasing during daylight hours (Conley 1966). The diet varies considerably with size, but zooplanktivory is continued to relatively large sizes and is likely associated with the possession of numerous, long gill rakers. Young (<22 mm TL) feed exclusively on copepods. Small crustaceans (primarily copepods and cladocerans), augmented with aquatic insects, form the bulk of the diet of individuals <175 mm TL. At larger sizes, insects are of primary importance, but small fish (mainly young bluegills) and crustaceans are also taken (Chable 1947; Conley 1966; Geaghan 1978; Jenkins and Burkhead 1994; Pflieger 1997).

Reproduction: Maturity is reached at age 1+ and a minimum size of about 70 to 75 mm TL. Fliers are among the earliest, lowest temperature spawners in the family. The ovaries enlarge and continue developing in the fall and over winter (Conley 1966), which is likely an adaptation for early spawning. Nest building is initiated at 14°C and the brief 10- to 14-day spawning period begins at water temperatures of 17°C in March and April (Dickson 1949; Conley 1966; Pflieger 1997). Only a single anecdotal account of reproductive behaviors is available (Dickson 1949). The male establishes and defends a territory and prepares a typical, saucer-shaped depressional nest using his mouth and fins. Nesting occurs in shallow water (0.3–1.2 m depth) and is apparently colonial (2–15 closely spaced nests, similar to bluegill). Males remain relatively motionless over the nest and are quick to flee on approach and exceedingly slow to return to the nest (Dickson 1949). The male leads the female to the nest. On entering the nest, the female remains motionless in the nest as the male circles several times; biting is mutual during spawning. Females may mate with more than one nesting male (Dickson 1949). Eggs are demersal, adhesive, and golden yellow. Mature ovarian eggs are the smallest of all centrarchids (0.300–0.434 mm diameter) (Dickson 1949; Conley 1966), and size-adjusted batch fecundities are high for a centrarchid (see *Archoplites* and *Pomoxis*). Only one size class of maturing ova is reported in mature females, and postspawning females did not retain mature or maturing eggs (Conley 1966), suggesting production of a single batch of eggs. The relationship between number of mature eggs (Y) and TL (X) is described by the power function $Y = 0.0230X^{2.7525}$ ($n = 63$, $R^2 = 0.79$, data from Dickson 1949, Alabama; Conley 1966, Missouri). At a mean size of 114 mm TL, a female can produce 10,552 mature eggs (range: 4412 eggs at 70 mm TL to 48,254 eggs at 205 mm TL). Peak spawning female ovary to body weight ratios are among the highest of any centrarchid (see *Enneacanthus* and *Lepomis*), reaching 12.5% in early spring (Conley 1966). The tiny eggs suggest that the flier lies close to *Pomoxis* or *Archoplites* on the male parental care continuum (Gross and Sargent 1985). Hatching occurs in 7 to 8 days at about 19°C. One (or few) anecdotal observation suggested that the male leaves the nest and eggs before hatching (Dickson 1949), which, if true, is a notable departure from centrarchid male reproductive behavior. Detailed study of parental care and other aspects of the reproductive biology of the flier could provide insight into evolution of these traits in other Centrarchinae.

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The flier appears to be secure where its lowland habitats are undisturbed (Warren *et al.* 2000) but its conservation is of concern at the periphery of its range (vulnerable, Illinois, Missouri, and Oklahoma; critically imperiled, Maryland) (NatureServe 2006).

Similar species: The white crappie and black crappie lack the dark teardrop and rows of spots on the sides and have 6 to 8 dorsal fin spines.

Systematic notes: *Centrarchus* is a monotypic genus that is basal to a clade comprised of the genera *Enneacanthus, Pomoxis, Archoplites*, and *Ambloplites* (Roe *et al.* 2002; Near *et al.* 2004, 2005). Comparative studies of variation across the range of *C. macropterus* are lacking.

Importance to humans: The flier is too small and localized in distribution to contribute to most sport fisheries. The species is a popular sport fish in the Okefenokee Swamp, where it makes up a considerable portion of the sunfish creel (Laerm and Freeman 1986). The flier rapidly seizes live or artificial bait and often leaps out of the water (hence, the name flier). The flesh is likened to that of bluegill (Dickson 1949).

13.7 *Enneacanthus* Gill

The genus *Enneacanthus* consists of a clade of three diminutive species in which *Enneacanthus chaetodon*, the blackbanded sunfish, is sister to *Enneacanthus gloriosus*, the bluespotted sunfish, and *Enneacanthus obesus*, the banded sunfish. *Enneacanthus* is sister to a clade comprised of the genera *Pomoxis, Archoplites*, and *Ambloplites* (Near *et al.* 2004, 2005). The genus is distributed in the lower Piedmont and Coastal Plain drainages of the Atlantic Slope and eastern Gulf of Mexico from New Hampshire to Mississippi. With the exception of the bantam sunfish, *Lepomis symmetricus*, species of *Enneacanthus* are the smallest centrarchids (Page and Burr 1991). All three species are adapted to lowland habitats with abundant aquatic vegetation in which individuals aggregate. Their rounded caudal fins and deep, compressed bodies likely help these fishes navigate in thick aquatic vegetation. The genus *Enneacanthus* also shows extreme tolerance and adaptations to low pH in wetland habitats. Each species in the genus occurs in acid, dystrophic waters (e.g., bogs, swamps), but a gradient in tolerance exists from the most (banded sunfish) to the least tolerant (blackbanded sunfish) (Gonzalez and Dunson 1989a,b,c, 1991). Differential pH tolerance within the genus apparently exerts a strong effect on local distribution in areas of overlap (Graham and Hastings 1984; Gonzalez and Dunson 1991; Graham 1993), and in banded sunfish, it is rooted in highly specialized physiological adaptations (Gonzalez and Dunson 1989a,b,c, 1991).

Characteristics: Deep, compressed body, depth >0.4 of SL. Mouth small, jaws equal, supramaxilla small (>3 times into length of maxilla), upper jaw not extending beyond front of eye. Eye large, diameter greater than snout length. Black teardrop. Opercle with two flat extensions. Rounded, truncate, or slightly emarginate caudal fin. Dorsal fins continuous. Long dorsal fin, (7)9 to 10(11) spines, 10 to 12 rays, usually 21 total, and short anal fin, 3 spines, 9 to 13 rays, 13 to 16 total. Preopercle margin entire. Long gill rakers, 11 to 14. Ctenoid scales. Vertebrae, 28 (12 + 16). Branchiostegal rays, 6. Teeth present or absent on palatine. No teeth on entopterygoid, ectopterygoid, or glossohyal (tongue) bones (Bailey 1938; Page and Burr 1991; Mabee 1993; Jenkins and Burkhead 1994).

Similar species: See generic account for *Lepomis* and *Micropterus*.

13.7.1 Enneacanthus chaetodon *(Baird)*

13.7.1.1 Blackbanded sunfish

Characteristics: See generic account for general characteristics. Deep, compressed body, depth ≥0.55 of SL. Mouth small, terminal. Eye large, diameter >1.2 of snout length. Six bold, black bars on sides, the first passes through the eye, the third extends dorsally through anterior spiny dorsal fin and ventrally through medial portion of pelvic fin, and the sixth through the caudal peduncle (often faint). Opercular spot dark with pale medial crescent. Rounded or slightly truncate caudal fin in young and juvenile, becoming truncate or slightly emarginate in adults. Long dorsal fin, (8)10(11) spines, 11 to 12 rays, usually 21 total, and short anal fin, 3 spines, (11)12 to 13(14) rays, 14 to 16 total. Dorsal fin continuous with deep notch between spines and rays. Dorsal fin base about 1.5 times longer than anal fin base. Dorsal and caudal fins not enlarged in breeding male. Pectoral fin narrow, somewhat pointed. Lateral line complete. Lateral scales, (23)25 to 29(32); cheek scale rows, (2)3(4); caudal peduncle scale rows, (16)18 to 21(22); pectoral rays, (9)11(13). Teeth present or absent on palatine bone (Bailey 1938; Page and Burr 1991; Mabee 1993; Jenkins and Burkhead 1994).

Size and age: Typically reach 13 to 40 mm TL at age 1. Large individuals measure 40 to 60 mm TL (maximum 80 mm TL) and reach age 4+ (Schwartz 1961; Page and Burr 1991; Jenkins and Burkhead 1994). Length–weight relationships between males and females are similar in some populations (Schwartz 1961), but in a Delaware population females lived longer (age 3+) and reached larger maximum sizes (70 mm SL) than males (age 1+, <49 mm SL) (Wujtewicz 1982).

Coloration: Prominent black vertical bars on sides (see Characteristics). Dusky yellow-gray to brown or black above, light below with tiny yellow flecks on sides. Leading edges of pelvic fins red, orange, or pink; third membrane of spiny dorsal fin similarly colored. Dorsal, anal, and caudal fins with black mottling. Iris reddish orange (Page and Burr 1991; Jenkins and Burkhead 1994; Marcy *et al.* 2005).

Native range: The blackbanded sunfish is sporadically distributed below the Fall Line in Atlantic and Gulf Slope drainages from New Jersey to central Florida and west to the Flint River, Georgia. Large distributional gaps occur across the range (e.g., entire western Chesapeake basin), and populations in Georgia and Florida are isolated and widely scattered (Gilbert 1992b; Jenkins and Burkhead 1994). Four areas of concentration are evident. Three of these, the pine barrens of New Jersey, the sandhills in southeastern North Carolina, and the central highlands of Florida, are characterized by well-drained sandy soils with vegetation of pine and scrubby oak species and dystrophic, acidic waters. The fourth area is the acidic Okefenokee Swamp in Georgia (Gilbert 1992b). The broad gaps in the *E. chaetodon* distributional pattern may have arisen from prehistoric changes in sea levels, subtle ecological habitat differences, and competition with other fishes (Jenkins *et al.* 1975; T. Darden, South Carolina Department of Natural Resources, personal communication).

Habitat: The blackbanded sunfish inhabits vegetated lakes, ponds, and quiet sand- and mud-bottomed pools and backwaters of creeks and small to medium rivers (Page and Burr 1991). Distributional studies in New Jersey indicate that the species occurs most often in acidic lakes (pH range, 7.0 to 4.1) (Graham and Hastings 1984; Graham 1993) and is most frequent in streams with a pH between 5.0 and 4.5 (Zampella and Bunnell 1998). In spring samples of small, sandy North Carolina streams, the species occurred most often in active beaver ponds apparently avoiding unimpounded stream channels and abandoned beaver ponds (Snodgrass and Meffe 1998). Although certainly tolerant of acidic conditions, laboratory studies suggest it is less tolerant of low pH than congeners. At pH 4.0 and 3.5, the blackbanded sunfish experienced the greatest disturbance of net Na flux, an indicator of pH stress, among the three species of *Enneacanthus*. All individuals of the blackbanded sunfish survived and recovered from a 12-hour exposure at pH 4.0, but 60% of test animals died in <12 hours at pH 3.5 (Gonzalez and Dunson 1989a).

Food: The blackbanded sunfish apparently takes small invertebrates from the surface of vegetation, the water column, and the bottom (Reid 1950a; Schwartz 1961; Wujtewicz 1982). Aquatic insects (chironomid, caddisfly, and dragonfly larvae), amphipods, filamentous algae, and plant leaves dominate the diet; the algal and plant material are perhaps incidentally taken with invertebrates. The species apparently feeds throughout the day and perhaps even nocturnally (Schwartz 1961; Wujtewicz 1982).

Reproduction: Knowledge of the reproductive behavior and biology of the blackbanded sunfish is sketchy, limited largely to aquarium observations by hobbyists, and almost entirely based on anecdotal accounts and unpublished reports (summaries by Hardy 1978; Jenkins and Burkhead 1994). Females mature at 33 mm SL and age 1+, or perhaps age 0+; males presumably mature at age 1+ (Wujtewicz 1982). Breeding activity is associated with water temperatures of about 20 to 28°C (Breder and Rosen 1966; Wujtewicz 1982; Sternburg 1986), and spawning occurs as early as March in North Carolina (Smith 1907) and early May to late June in Delaware (Wujtewicz 1982). Adults in North Carolina streams migrate seasonally into beaver ponds to spawn, habitats which are also important for young-of-the-year (Snodgrass and Meffe 1999). The male may excavate and defend a small depressional nest (ca. 10 cm in diameter) in sand or gravel or push out hollows in filamentous algae beds or macrophytes in water about 30 cm deep (Breder 1936; Breder and Rosen 1966; Sternburg 1986). Movement of bottom materials during nest excavation has been attributed to using the mouth, body, tail, or just "finning" (Breder and Rosen 1966; Sternburg 1986; Jenkins and Burkhead 1994). Males lead the female to the nest by darting toward her, quivering, spreading the fins, and then swimming back to the nest (Breder 1936; Sternburg 1986). The pair releases gametes in the typical head-to-head, vent-to-vent centrarchid spawning position (Breder 1936; Sternburg 1986). Gamete release is repeated numerous times over about 1.5 hours with pauses of 10 to 30 seconds between bouts (Breder and Rosen 1966; Sternburg 1986). In an aquarium, two females spawned simultaneously with a single male (Sternburg 1986). Spawning in the species is apparently protracted. In aquaria, spawning occurs repeatedly over several weeks (Sternburg 1986; Rollo 1994), and in Delaware, females were gravid from early May through June (Wujtewicz 1982). Ripe eggs were 0.9 mm in diameter (Wujtewicz 1982). Eggs were small or absent in females in July in Maryland and averaged 0.3 mm in diameter in November (Schwartz 1961). Females contain 233 to 920 mature ova (33 to 52 mm SL, respectively) (Wujtewicz 1982), but all of these may not be deposited in a single spawning (Quinn 1988). Fertilized eggs are adhesive and sand colored (Hardy 1978). The male guards the eggs, which hatch in about 2 days (Breder 1936), and continues guarding the larvae until they are free swimming (about 4–5 days after hatching) (Sternburg 1986; Rollo 1994). A guardian male in an aquarium was observed picking up stray larvae in his mouth and "spitting" them back into the nest (Rollo 1994), a behavior at least unusual if not unique among centrarchids (Miller 1963). An anecdotal report of biparental care of eggs and fry also deserves further investigation (Quinn 1988).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The blackbanded sunfish is considered vulnerable to critically imperiled across most of its range (Warren *et al.* 2000; NatureServe 2006). The species is presumed extirpated in Pennsylvania, and only populations in New Jersey are considered secure (NatureServe 2006). The fragmented range and tendency for populations to be isolated, even though often locally common (e.g., Gilbert 1992b; Marcy *et al.* 2005), increase extirpation risk. Continuing urban, agricultural, and coastal development that involves drainage of small wetlands and ponds exacerbate the extinction risk imposed by fragmentation and isolation. Collection of specimens for aquaria may also adversely impact some low-density populations (Burkhead and Jenkins 1991).

Similar species: The banded sunfish and bluespotted sunfish lack the black pigment at the front of the dorsal fin. Small individuals of all three species are similar, but the blackbanded sunfish develops the distinctive adult markings early (about 10 mm TL) (Sternburg 1986).

Systematic notes: A southern subspecies, *E.c. elizabethae*, was described from limited samples from the Okefenokee Swamp and central Florida, based on differences in dorsal fin spine counts, caudal peduncle scale counts, and subtle aspects of pigmentation (Bailey 1941). Subsequent work suggested a north–south cline (Sweeney 1972), but larger sample sizes confirm reduced average counts in Florida and southern Georgia specimens (Gilbert 1992b).

Importance to humans: The handsome blackbanded sunfish has long been of interest to aquarists in southeast Asia, where it is cultured in large numbers and shipped back to enthusiasts in North America (Sternburg 1986; Quinn 1988; Schleser 1998) and in Germany, where it has been kept since 1897 (Jenkins and Burkhead 1994). The species is currently traded and sold on Internet websites by individuals and pet stores. Feeding, water conditioning, and breeding of the species are featured frequently in magazines and on websites of organizations promoting use of native fish in aquariums (e.g., North American Native Fish Association, The Native Fish Conservancy).

13.7.2 Enneacanthus gloriosus *(Holbrook)*

13.7.2.1 Bluespotted sunfish

Characteristics: See generic account for general characteristics. Deep, compressed body, depth 0.4 to 0.6 of SL. Mouth small, terminal, or supraterminal. Rows of blue or silver spots along sides of large young and adults; bars on sides indistinct in adults. Opercular spot dark, sometimes with pale medial crescent, usually <0.5 of eye diameter in specimens >25 mm SL. Rounded caudal fin. Long dorsal fin, (7)9(11) spines, (10)11(13) rays, usually 21 total, and short anal fin, 3 spines, (9)10(11) rays, 13 to 14 total. Dorsal fin continuous. Dorsal fin base about 1.5 to 1.7 times longer than anal fin base. Breeding male with enlarged second dorsal and anal fins; female lacks enlarged fins. Pectoral fin rounded. Lateral line may be lacking on several posterior scales. Lateral scales, (25)30 to 32(35); cheek scale rows, (3)4(5); caudal peduncle scale rows, (14)16 to 18(20); pectoral rays, (9)11 to 12(13). Teeth (cardiform) present on palatine bone (Bailey 1938; Sweeney 1972; Peterson and Ross 1987; Page and Burr 1991; Mabee 1993; Jenkins and Burkhead 1994).

Size and age: Typically reach 19 to 34 mm TL at age 1. Large individuals measure 52 to 63 mm TL (maximum 99 mm TL) and at least in northern populations reach age 5+ (Breder and Redmond 1929; Fox 1969; Werner 1972; Snyder and Peterson 1999b). In southern populations, individuals rarely live to age 4+ (Fox 1969; Snyder and Peterson 1999b). Maximal size in Gulf Coast populations is less than that in Atlantic Coast populations, a likely consequence of earlier maturity in the former (Peterson and VanderKooy 1997; Snyder and Peterson 1999b). Length to dry weight relationships did not differ for males and females in Mississippi populations (Snyder and Peterson 1999b), and older males were slightly heavier than same-age females in Florida (Fox 1969).

Coloration: Olive brown to olive or very dark midnight blue on body and head. Rows of round to oval, blue, green, silver, or gold spots along the sides of large young and adults (lacking in Mississippi populations), and extending onto head. Opercular spot black to pearly blue, often with medial blue-green crescentic mark. Spots on head and sides most developed on breeding males, which have a nearly black background with bright iridescent spots. Young and nonreproductive adults may have indistinct bars on sides. Soft dorsal, anal, and caudal fins may be pink or reddish; pale whitish spots in median fins. Iris dull red or gold (Page and Burr 1991; Jenkins and Burkhead 1994; Ross 2001; Marcy *et al.* 2005).

Native range: The bluespotted sunfish, the most wide-ranging *Enneacanthus*, occurs in the Coastal Plain and Piedmont of Atlantic and Gulf Slope drainages from southern New York south to southern Florida and westward to the Biloxi Bay drainages of southeastern Mississippi (Page and Burr 1991; Jenkins and Burkhead 1994; Ross 2001). An introduced population is established in the Black River drainage, Mississippi (Peterson and Ross 1987), and populations in the Lake Ontario drainage, New York, and Susquehanna River drainage, Pennsylvania, are of unknown provenance (Smith 1985; Fuller *et al.* 1999).

Habitat: The bluespotted sunfish inhabits vegetated lakes, ponds, and sluggish sand- and mud-bottomed pools and backwaters of creeks and small to large rivers (Fox 1969; Page and Burr 1991; Peterson and VanderKooy 1997; Snodgrass and Meffe 1998). In spring samples in North Carolina, the species occurred most often in beaver ponds rather than in unimpounded stream channels (Snodgrass and Meffe 1998). In coastal Mississippi drainages, the species almost exclusively used side ponds of oxbows, avoiding main channel habitats. In the side ponds, highest relative abundance was associated with decreased pH, decreased conductivity, and increased coverage of submergent and emergent vegetation; presence and absence of the species in the ponds was associated significantly with a mean pH of 5.6 and 6.5, respectively (Peterson and VanderKooy 1997). In New Jersey, the species was distributed independently of a color-pH gradient occurring across a pH range of about 9.0 to 4.0 (median 7.0) in lakes (Graham and Hastings 1984; Graham 1993), and in pineland streams the species occurred at a median pH between 5.0 and 4.5 (Zampella and Bunnell 1998). Growth is not affected negatively until pH declines below 4.5, but individuals survived up to 12 weeks at pH 4.0 (Gonzalez and Dunson 1989c).

Food: The bluespotted sunfish is an opportunistic diurnal forager on benthic, vegetational, and planktonic prey; adult diets are dominated by prey associated with submerged aquatic vegetation and associated sediments (Breder and Redmond 1929; Fox 1969; Graham 1989; Snyder and Peterson 1999a). Dominant adult food items are chironomid larvae (and other aquatic insects), gastropods, and small crustaceans (ostracods, copepods, cladocerans, amphipods). The young transition from a diet predominated by cladocerans, copepods, and chironomid larvae to the broader adult diet (Fox 1969; Graham 1989; Snyder and Peterson 1999a). In late summer, young-of-the-year stomachs were nearly empty at dawn, but stomach fullness and digestion of prey indicated that individuals began feeding at dawn and fed continuously until darkness (Graham 1986).

Reproduction: Maturity is reached in northern populations at age 2+ at a minimum size of about 53 mm TL (40 mm SL, Breder and Redmond 1929). Southern populations mature at age 1+ and show 50% maturity at 23 to 25 mm TL (Fox 1969; Snyder and Peterson 1999b), apparently the smallest size at maturity of any centrarchid. Spawning is protracted, and depending on latitude gravid females and small young occur from early spring through fall (Breder and Redmond 1929; Fox 1969; Wang and Kernehan 1979; Jenkins and Burkhead 1994; Snyder and Peterson 1999b; Doyle 2003). Female and male gonad to body weight ratios show initial increases as water temperatures rise above 15°C and remain high throughout much of the summer, but decline if temperatures remain above 27°C (Snyder and Peterson 1999b). Observations of nests are few and guardian male behaviors unknown, but the size, substrate, and placement of the nests are apparently similar to *E. chaetodon* (summary in Breder and Rosen 1966). Mature ova percentages increase throughout the summer, indicating continued recruitment from smaller ova classes. In Mississippi populations, there was no size–fecundity relationship (Snyder and Peterson 1999b), and the number of mature ova per female averaged 117. In Florida populations, the number of mature eggs increased from 67 to 80 in age 1+ females to an average of 400 and 500 mature eggs in age 2+ and 3+ females, respectively (Fox 1969). Mature eggs averaged 0.9 mm in diameter in freshly stripped eggs (Breder and Redmond 1929) and 0.68 mm in preserved females (Snyder and Peterson 1999b). Eggs are adhesive and demersal (Breder and Redmond 1929). Hatching occurs in 57 hours at 23°C, and length at hatching is 2.3 mm TL (Breder and Redmond 1929).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The bluespotted sunfish is considered currently stable over its range, but populations at the periphery of the range (Mississippi, Alabama, New York, and Maryland) are listed as vulnerable (Warren *et al.* 2000; NatureServe 2006).

Similar species: Pigmentation patterns of young bluespotted sunfish are virtually indistinguishable from banded sunfish, and even adults of the two species can be difficult to distinguish. In breeding male bluespotted sunfish the pale markings are nearly always present, are broadly oval, and are greenish yellow or gold in color; the body is often very dark, olive blue; and the dark lateral bars are absent or indistinct. In breeding male banded sunfish bright markings are sometimes present as gold-green crescentic flecks, the species never appears blue, and the lateral bars are dark and evident (Jenkins and Burkhead 1994). Average counts of caudal peduncle scale rows also appear to reliably separate the species, but traditionally used characteristics, such as completeness of the lateral line and relative size of the opercular spot, are not reliable across much of the range (Peterson and Ross 1987; Jenkins and Burkhead 1994).

Systematic notes: Evolutionary relationships among *E. gloriosus* populations and between *E. gloriosus* and *E. obesus* appear to be complex and not yet fully resolved. Phylogeographic analyses of mitochondrial DNA indicate that *E. gloriosus* and *E. obesus* are not monophyletic taxa and suggest either incomplete lineage sorting or a polyphyletic *E. obesus* (T. Darden, South Carolina Department of Natural Resources, personal communication). Introgression was detected using nuclear-encoded allozyme data in sympatric populations of the sister species pair *E. gloriosus* and *E. obesus* in New Jersey (Graham and Felley 1985). In areas of allopatry, hybridization was not detected, but appreciable introgression was present in co-occurring populations. Developmental instability was correlated positively with the degree of introgression (heterozygosity), indicating that hybridization may result in reduced fitness for the hybrid individuals (Graham and Felley 1985). Morphological variation in the two species in Virginia also shows considerable and curious overlap (Jenkins and Burkhead 1994). Phylogeographic analyses appear to support an Okefenokee Swamp–based center of dispersal for *E. gloriosus* and relatively long-term isolation and differentiation of Florida populations from other Atlantic Slope populations (T. Darden, South Carolina Department of Natural Resources, personal communication). In addition, populations in Mississippi are morphologically divergent from other *E. gloriosus* populations (Peterson and Ross 1987).

Importance to humans: The bluespotted sunfish, like its congener the blackbanded sunfish, has attracted the attention of aquarists. A perusal of Internet sites indicates that the species is regarded as an adaptable aquarium fish, although feeding and water conditioning can be challenging. The species is actively sold and traded by enthusiasts and retailers.

13.7.3 Enneacanthus obesus *(Girard)*

13.7.3.1 Banded sunfish

Characteristics: See generic account for general characteristics. Deep, compressed, somewhat thick body, depth 0.4 to 0.5 of SL. Mouth small, supraterminal, oblique. Rows of purple-gold crescentic flecks on sides; five to eight dark bars on sides. Opercular spot dark, usually >0.5 of eye diameter in specimens >25 mm SL. Rounded caudal fin. Long dorsal fin, (7)9(11) spines, (10)11(13) rays, usually 21 total, and short anal fin, 3 spines, (10)10 to 11(12), 13 to 14 total. Dorsal fin continuous. Dorsal fin base about 1.5 to 1.7 times longer than anal fin base. Breeding male with enlarged second dorsal and anal fins and longest pelvic rays distally filamentous; female lacks enlarged fins and filamentous extensions. Pectoral fin rounded. Lateral line usually interrupted or incomplete. Lateral scales, (27)30 to 32(35); cheek scale rows, (3)4(5); caudal peduncle scale rows, (17)19 to 22(24); pectoral rays, (10)11 to 12(13). Teeth (cardiform) present on palatine bone (Bailey 1938; Peterson and Ross 1987; Page and Burr 1991; Mabee 1993; Jenkins and Burkhead 1994).

Size and age: Reached 20 to 30 mm TL at age 1 in a Connecticut reservoir (Cohen 1977); age 0+ fish were 34 to 35 mm SL in October and 51 mm SL the following April in the Okefenokee Swamp (Freeman and Freeman 1985). Large individuals measure 55 mm TL (maximum 95 mm TL) and reach age 6+ (Cohen 1977; Page and Burr 1991). Males tend to live longer and grow slightly faster than females (Cohen 1977).

Coloration: Dusky olive above, light below, with olive-black or five to eight black bars on the sides that may vary in distinctiveness. Rows of purple-gold crescentic flecks along side. Opercular spot black, bordered with iridescent gold-green margin. Median fins dark with rows of blue to white spots. Breeding male, and to a lesser degree, breeding female with gold-green or blue flecks on head, body, and median fins, fin spines glowing white. Iris orange-red (Page and Burr 1991; Jenkins and Burkhead 1994). Aspects of subtle differences in coloration between *E. obesus* and *E. gloriosus* are summarized by Jenkins and Burkhead (1994).

Native range: The banded sunfish occurs primarily on the Coastal Plain of Atlantic and Gulf Slope drainages from southern New Hampshire south of central Florida and west of the Perdido River drainage of Alabama (Page and Burr 1991; Boschung and Mayden 2004). Across the range, the species can be rare to relatively common (Smith 1985; Laerm and Freeman 1986; Jenkins and Burkhead 1994; Boschung and Mayden 2004; Marcy *et al.* 2005). An introduced population is established in the Black River drainage of Mississippi (Peterson and Ross 1987).

Habitat: The banded sunfish inhabits heavily vegetated lakes, ponds, and sluggish sand- or mud-bottomed pools and backwaters of creeks and small to large rivers (Page and Burr 1991). The species is perhaps one of the most acid-tolerant fishes known (Gonzalez and Dunson 1987) and occurs in waters with pH 3.7 (e.g., New Jersey, Graham and Hastings 1984; Graham 1989; Georgia, Freeman and Freeman 1985). In multivariate studies in New Jersey, the banded sunfish was associated more strongly with acidic (pH 6.6–4.1), dystrophic habitats than either congener in lakes (Graham and Hastings 1984; Graham 1993) and in streams occurred most frequently between pH 5.0 and 4.5 (Zampella and Bunnell 1998). Individuals survived 2-week laboratory exposures to pH 3.5, and 60% of test individuals survived 3-week exposures to pH 3.3 after a gradual lowering from 3.5 over a 1-week period (Gonzalez and Dunson 1987). Growth was unaffected down to a pH of 3.75 (Gonzalez and Dunson 1989c). These findings suggest that the banded sunfish may have distinct competitive advantages over congeners and other sunfishes in low pH habitats (Gonzalez and Dunson 1991). Its tolerance of low pH is the result of complex adaptations for compensating for losses in body Na that would kill other fishes and involves the ability to limit branchial electrolyte permeability during acidic exposure (Gonzalez and Dunson 1987, 1989a,b,c). The gills of banded sunfish have a high affinity for Ca that reduces leaching by H+ and prevents high Na losses down to pH 3.5. In addition to limiting Na efflux, the species apparently can shift internal Na from osmotically inactive sources (e.g., bone) to plasma, which maintains Na concentrations of extracellular fluid. Although chronic acid exposure causes a large drop in body Na concentration (up to 52%, lethal to most fishes), these adaptations allow the banded sunfish to survive (Gonzalez and Dunson 1987, 1989a,b,c, 1991).

Food: The banded sunfish, like its sister species the bluespotted sunfish, is an opportunistic forager on benthic, vegetational, and planktonic prey; adult diets are dominated by prey associated with submerged aquatic vegetation (Chable 1947; Cohen 1977; Graham 1989). Although diets overlap substantially between the two species, the banded sunfish gleans more vegetational prey and eats less benthic and planktonic prey than the bluespotted sunfish where the two co-occur (Graham 1989). Dominant adult food items are chironomid larvae (and other aquatic insects) and small crustaceans (cladocerans, copepods, amphipods). The young transition from a diet predominated by cladocerans, copepods, and chironomid larvae to the broader adult diet (Graham 1989). In late summer, young-of-the-year stomachs were nearly empty at dawn, but stomach fullness and digestion of prey indicated that individuals began feeding at dawn, paused between late morning and midday, and then fed continuously until dark (Graham 1986).

Reproduction: Maturity is reached at age 2+ in females at a size of about 35 to 40 mm TL, but some smaller, age 1+ females are capable of spawning (Cohen 1977). Information on minimum size and age of maturity of males is lacking, but males are reproductively active by at least 59 mm TL (Harrington 1956). Gonadal development and associated nesting and spawning behaviors are controlled by increasing photoperiod and temperature (Harrington 1956). When males and females collected from ponds in fall were exposed in the laboratory to 15 hours of daylight and 21.7°C water temperature, ovary volume, ova size, testis volume, and male breeding colors developed rapidly (about 38 days), and nest building and spawning occurred. In contrast, in a parallel set of experiments at 21.7°C conducted under a fall photoperiod (9.2–11.6 hours daylight), individuals did not show gonadal enlargement or other reproduction-associated changes. In natural environments, spawning can be protracted. Gravid females and nuptial males occur from April to July in Virginia (Jenkins and Burkhead 1994), and capture of small young in Delaware suggests a late spring-through-summer breeding season (Wang and Kernehan 1979). In contrast, young-of-the-year only appeared in early June collections in a year-long sampling effort in the Okefenokee Swamp, Georgia (Freeman and Freeman 1985). Peak spawning and egg development occurred in June and July in a Connecticut reservoir at surface water temperatures of 23 to 27°C. Most details of reproductive biology, spawning behavior, and aspects of parental care are undocumented. In aquaria, breeding males establish territories, engage in threat postures and chasing, excavate depressional nests with their mouths, and vigorously defend the nest, eggs, and free-swimming larvae (Harrington 1956; Breder and Rosen 1966; Cohen 1977; Rollo 1994). One large male (52 mm SL) bred on 10 different days (of 26 days observed) and participated in 107 spawning acts under laboratory conditions (Harrington 1956). The interval between spawning acts was from 0 to 4 days. Mean fecundity, presumably based on total ova, increases with age (and size) ranging from 802 eggs at age 1 to 1400 eggs at age 6 (Cohen 1977). Mature ova are 0.6 mm in diameter. Fertilized eggs are adhesive and colorless, eggs hatch in about 3 days at 21.7°C, and larvae become free swimming about 5 days after hatching (Harrington 1956; Rollo 1994).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: Although not in danger of imminent extinction because of occupation of broad latitudinal range across many independent drainage systems, the banded sunfish is considered vulnerable to critically imperiled in many states within its range (New Hampshire, Rhode Island, Connecticut, Virginia, Alabama, Pennsylvania, New York) (Warren *et al.* 2000; NatureServe 2006).

Similar species: See account on bluespotted sunfish.

Systematic notes: See account on *E. gloriosus*.

Importance to humans: Like congeners, the banded sunfish is popular among enthusiasts interested in keeping and rearing native fishes (Rollo 1994; Schleser 1998). Although perhaps underappreciated, the ability of the species to tolerate waters of relatively high acidity should increase scientific interest in the species.

13.8 *Lepomis* Rafinesque

The genus *Lepomis* is a monophyletic clade of 13 species and is sister to the genus *Micropterus* (Near *et al.* 2004, 2005). The natural range encompasses most of eastern North America east of the Rocky Mountains, reaching northward to the Great Lakes, St. Lawrence River, and Hudson Bay drainages of Canada and eastward and southward in the Mississippi River Basin, Atlantic Slope, and Gulf of Mexico drainages west to the Rio Grande.

Breeding males of some *Lepomis* are among the most colorful of all North American native fishes, and the reproductive habits of several species are among the best-studied and most fascinating within the fish fauna. The literature is extensive and only a brief overview is presented here and in the individual accounts. *Lepomis* share many features common to centrarchid reproduction. Males establish territories, excavate nests, fan, and guard eggs and defend newly hatched larvae until the swim-up stage. In addition, many *Lepomis* develop brilliant breeding colors and possess highly complex reproductive behaviors that can involve motor, visual, and auditory signals, and several species have evolved alternative mating strategies. Territorial breeding males excavate the typical circular depressional nest of other centrarchids, but many distinctive behaviors and combinations of behaviors are documented, often being associated with nest defense, courtship, or both. The male is faced with defending a nesting territory using agonistic behaviors and successfully mating with a female using courtship behaviors, motivations that necessarily shift from moment to moment, particularly in colonial nesters, and often appear in conflict (Keenleyside 1967; Steele and Keenleyside 1971; Ballantyne and Colgan 1978a,b,c). Males over nests display to nearby or approaching males and females using combinations of nest hovering, dashes to the surface and back to the nest, nest sweeping with the caudal fin, fin spreading, mouth gapes, jaw snaps, lateral displays (males side-by-side with fins erect), breast displays, substrate biting, and opercular spreads. Males most frequently rush toward an interloper with a quick retreat to the nest (thrust, Miller 1963), but if the intruder does not retreat, males display or actually ram, push, bite, or jaw grasp the other male. Males may also engage in rim circling, in which males repeatedly and rapidly circle their nest (e.g., over 100 circles in 30 minutes) with fins displayed (Miller 1963; Hunter 1963; Huck and Gunning 1967; Boyer and Vogele 1971; Avila 1976; Colgan *et al.* 1979; Lukas and Orth 1993). The act likely makes the male more conspicuous to females (Miller 1963; Avila 1976) but also serves as a territorial advertisement to other males (Colgan *et al.* 1979). In courtship, as a spawning-ready *Lepomis* female approaches a male's nest, the male performs courtship circles by darting from the nest with fins spread, encircling the female and leading her toward the nest (Keenleyside 1967; Boyer and Vogele 1971; Avila 1976; Ballantyne and Colgan 1978a,b,c; Gross 1982). The male may courtship circle many times in rapid succession until the female follows him to the nest or leaves (Miller 1963; Keenleyside 1967).

Augmenting the motor behaviors and breeding colors developed on the body and head, males of some species also have exaggerated opercular flaps. The ear flaps (or ear tabs) are species specific in orientation, size, and color patterns and serve as sex ornaments (secondary sexual characteristics) that play a complex role in mate choice, species recognition, and aggression between rival males (Keenleyside 1971; Colgan and Gross 1977; Stacey and Chiszar 1977). Opercle flaring directed at females is frequent in courting males (Keenleyside 1967), and the flap apparently signals to the female the species, condition, and quality of the male (Childers 1967; Goddard and Mathis 2000). Females prefer males with larger opercular flaps (e.g., *Lepomis megalotis*), and larger flaps increase the probability of a male in attaining and holding central nesting sites in a colony, where females spawn preferentially relative to peripheral nests (e.g., *Lepomis macrochirus*) (Gross and MacMillan 1981; Côté and Gross 1993; Goddard and Mathis 1997; Ehlinger 1999). Aggressiveness and dominance also are closely linked to the opercular flap. Males of at least some *Lepomis* appear to assess the resource-holding power of rivals by their opercular flap size (Goddard and Mathis 2000). Out of age, size, and seven morphological features in male bluegill, opercular flap size was the only feature that corresponded significantly with male rank in a breeding territory dominance hierarchy in experimental tanks (Ehlinger 1999).

Some territorial, breeding male *Lepomis* further augment motor and visual reproductive signals with sound. On sighting a female near his nest, a nesting male rushes toward her and back toward his nest while producing a series of gruntlike

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sounds (bluegill, green sunfish, longear sunfish, and redspotted sunfish) or popping sounds (pumpkinseed and redear sunfish) (Gerald 1971; Ballantyne and Colgan 1978a,b,c). The sounds are also produced as males attack other males intruding into their nesting territory or in noncourtship agonistic contexts (Ballantyne and Colgan 1978a,b,c). Sound production is attributed to manipulation of the pharyngeal jaw pads, but in agonistic or courtship contexts is not associated with feeding (Ballantyne and Colgan 1978a,b,c). Sound characteristics suggest species specificity (Gerald 1971), and conspecific and heterospecific sounds elicit auditory brainstem responses in *Lepomis* (Wysocki and Ladich 2003), but individual variation in sound characteristics is high (Ballantyne and Colgan 1978a,b,c). Females are more responsive to conspecific than heterospecific sounds, but males respond to both (Gerald 1971; Ballantyne and Colgan 1978a,b,c). Sound production may facilitate location of nesting males by females in conditions of low visibility (Gerald 1971; Steele and Keenleyside 1971), but the behavior also appears to be part of a ritualized sequence of behaviors (e.g., jaw snaps and courtship circles), signaling that the male is both highly aggressively and sexually aroused (Ballantyne and Colgan 1978a).

Alternative male reproductive strategies are highly evolved in *Lepomis* (Gross 1982; Jennings and Philipp 1992a; Philipp and Gross 1994; Avise *et al*. 2002). In a nest takeover strategy, large guardian males permanently displace small guardian males, or in nesting colonies, neighboring guardian males may intrude temporarily in another male's nest to steal fertilizations with a female (Keenleyside 1972; Avila 1976; Dominey 1981; Gross 1982; Dupuis and Keenleyside 1988; Jennings and Philipp 1992b,c; DeWoody *et al*. 1998). Nesting male *Lepomis* habituate to the appearance of males on neighboring nests and become less aggressive toward them (Colgan *et al*. 1979), so unmated neighbors can more easily intrude and steal fertilizations (Keenleyside 1972; Jennings and Philipp 1992b). These strategies, however, appear to occur in relatively low frequencies (<5% of nests, DeWoody and Avise 2001; Neff 2001).

A more common parasitic reproductive strategy is used by cuckolder males of *Lepomis*, which do not invest in parental care, but do attempt to steal fertilizations from guardian males. Small sneaker males steal fertilizations from guardian males by hovering near the nest margin and darting in and out to release sperm beneath the spawning female and guardian male (Dominey 1980; Gross 1982, 1984, 1991). When sneaker males are about as large as reproducing females, they can switch to the satellite tactic (Gross 1982). Satellite males mimic females in behavior and coloration and, if the guardian male is deceived, which occurs frequently, they can hold a position in the nest between the spawning female and guardian male and steal fertilizations (Dominey 1980; Gross 1982; Fu *et al*. 2001). Sneaker and satellite morphs are documented only in bluegill (Dominey 1980; Gross 1982). Sneaker male morphs occur in populations of longear sunfish (Jennings and Philipp 1992b,c), northern longear sunfish (Keenleyside 1972; Jennings and Philipp 1992c), pumpkinseed (Gross 1979, 1982), and spotted sunfish (DeWoody *et al*. 2000a). Cuckolder male morphs were sought but not detected in North Carolina populations of dollar sunfish, bluegill, and redbreast sunfish (Belk 1995; DeWoody *et al*. 1998; Mackiewicz *et al*. 2002). Even so, observations of the intrusion of ostensibly "small females" between spawning pairs of *Lepomis* suggest that the parasitic strategy may occur in other populations or species (e.g., Hunter 1963; Boyer and Vogele 1971; Lukas and Orth 1993).

The life history of parasitic males differs dramatically from that of guardian males. Parasitic males do not develop breeding colors and are smaller, grow slower, mature earlier, allocate more body mass to testis weight, differ in size-adjusted body shape, and are shorter lived than guardian males (Gross 1982; Jennings and Philipp 1992c; Drake *et al*. 1997; Ehlinger 1997; Ehlinger *et al*. 1997; Stoltz *et al*. 2005). Demographic analyses of bluegill populations indicate that parasitic phenotypes do not become guardian males (Dominey 1980; Gross 1982; Drake *et al*. 1997) and that alternative male phenotypes are determined early in the life history (Ehlinger *et al*. 1997). In other *Lepomis* with alternative strategies, demographic data also are suggestive, although not conclusively, of an early and permanent divergence in life history between guardian and sneaker male phenotypes (Jennings and Philipp 1992c).

Generic characteristics: Deep, compressed body (somewhat elongate in *Lepomis cyanellus* and *Lepomis gulosus*). Opercle rounded or produced into flexible ear flap. Emarginate caudal fin. Dorsal fin shallowly emarginate, spiny portion continuous with soft-rayed portion. Long dorsal fin, usually 10 spines, 10 to 12 rays, usually 20 to 21 total; and short anal fin, 3 spines, 9 to 11 rays, 12 to 14 total. Dorsal fin base about two times longer than anal fin base. Preopercle margin usually entire (weakly crenate in *L. gulosus*). Ctenoid scales. Vertebrae, 29 to 31(12 or 13 + 17 or 18). Branchiostegal rays, 6 (Bailey 1938; Page and Burr 1991; Mabee 1993; Boschung and Mayden 2004).

Similar species: Presence of three anal fin spines separates *Lepomis* from all other centrarchids except *Enneacanthus* and *Micropterus*. *Lepomis* have shallowly emarginate caudal fins (versus rounded in *Enneacanthus*) and deep, laterally compressed bodies with <55 lateral scales (versus elongate body and ≥55 lateral line scales in *Micropterus*).

13.8.1 Lepomis auritus *(Linnaeus)*

13.8.1.1 Redbreast sunfish

Characteristics: See generic account for general characteristics. Body deep, compressed, depth 0.38 to 0.48 of SL. Mouth moderate, terminal, oblique, supramaxilla small (>3 times and ≤4 times into length of maxilla), upper jaw extending to (or almost to) anterior margin of eye. Wavy blue lines apparent on preorbital area, cheek, and usually opercle. Opercular flap long, narrow, flexible, oriented horizontally or pointing upward, black to posterior margin, usually bordered above and below with blue line. Soft dorsal fin acute. Pectoral fin short and rounded, tip usually not reaching past eye when bent forward. Short thick gill rakers, 9 to 12, longest about twice the greatest width in adults. Lateral line complete. Lateral scales, (39)41 to 50(54); rows above lateral line, 7 to 9; rows below lateral line, 14 to 16(17); caudal peduncle scale rows, (21)22 to 23(25); cheek scale rows, 6 to 9; pectoral rays, (13)14(16). Pharyngeal arches narrow with short, pointed teeth. Teeth on palatine bone. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Scott and Crossman 1973; Barlow 1980; Etnier and Starnes 1993; Mabee 1993; Boschung and Mayden 2004).

Size and age: Size at age 1 is highly variable among habitat types and latitudes, ranging from 32 to 102 mm TL (median 59 mm). Large individuals measure 200 to 250 mm TL, weigh 150 to 300 g, and attain age 5+ to 7+ (maximum 305 mm TL, age 8+) (Bass and Hitt 1974; Sandow *et al.* 1975; Carlander 1977; Page and Burr 1991; Marcy *et al.* 2005). World angling record, 0.79 kg, Florida (IGFA 2006). Florida angling record, 0.94 kg (FFWCC 2006). Growth differences between males and females are minimal to nonexistent (Sandow *et al.* 1975; Carlander 1977).

Coloration: Narrow, elongate black ear flap, dark to posterior margin, bordered above and below with blue lines. Wavy, often narrow, blue lines radiate from mouth across sides of snout onto cheek and opercle, broken and often less distinct on opercle. Dark olive above and on sides with yellow flecks and rows of red-brown to orange spots on upper sides, orange spots scattered on lower side. White to orange below. Clear to dusky yellow to orange fins. Breeding male with bright orange breast and belly, orange fins, light powder blue sides with orange spots (Page and Burr 1991; Jenkins and Burkhead 1994; Marcy *et al.* 2005).

Native range: The redbreast sunfish is native to the Atlantic and Gulf Slopes from New Brunswick to central Florida and west to the Apalachicola and possibly the Choctawhatchee River drainages of Georgia and Florida. The native or introduced status in the Tallapoosa and upper Coosa rivers of Alabama and Georgia, where the species is widespread and common, is uncertain (Boschung and Mayden 2004). The species has been widely introduced and is established well outside its native range (e.g., Rio Grande to southeastern Ohio River basin) and in some areas (e.g., upper Tennessee River drainage) may be displacing native *Lepomis* (Page and Burr 1991; Etnier and Starnes 1993; Fuller *et al.* 1999; Miller 2005).

Habitat: The redbreast sunfish inhabits rocky, sandy, or mud-bottomed pools of creeks and small to medium rivers and can also occur in lakes, ponds, or reservoirs (Page and Burr 1991). The species is usually associated with cover (e.g., instream wood, stumps, or undercut banks), and in streams, abundance increases with decreasing water velocity and increasing depth and cover (Meffe and Sheldon 1988). Redbreast sunfish are relatively sedentary (home activity area usually <100 m stream length), but long-distance movements (1–17 km) occur (Hall 1972; Gatz and Adams 1994; Freeman 1995). Peak movements occur in the spring before spawning (Hall 1972; Hudson and Hester 1975; Gatz and Adams 1994).

Food: The redbreast sunfish is an opportunistic invertivore that may feed most heavily during the day or at night (Cooner and Bayne 1982; Bowles and Short 1988; Johnson and Dropkin 1993). Aquatic insects, particularly mayfly, dragonfly, caddisfly, and dipteran larvae, make up the bulk of the diet. Gastropods, aquatic beetles, terrestrial and emerging aquatic insects, crustaceans, and a wide variety of other invertebrate taxa also are consumed frequently, but fish, although eaten, are not important dietary items. As young redbreast sunfish grow, the diet increasingly includes larger aquatic invertebrates and more aerial and terrestrial insects (Sandow *et al.* 1975; Cooner and Bayne 1982; Sheldon and Meffe 1993; Murphy *et al.* 2005). High volumes of vegetation and organic debris in stomachs suggest concentrated foraging among plants and on the bottom (Davis 1972; Bass and Hitt 1974; Sandow *et al.* 1975; Cooner and Bayne 1982). In the summer, diversity of food items in the diet was highest in daylight hours, but feeding occurred throughout a 24-hour period (Cooner and Bayne 1982), and in the fall, feeding peaked between 2000 and 0400 hours (Johnson and Dropkin 1993). In late winter, indirect evidence indicates elective feeding on nocturnally drifting amphipods (Bowles and Short 1988).

Reproduction: Maturity is reached at ages 1+ to 2+ at a minimum size of about 90 to 114 mm TL (Davis 1972; Bass and Hitt 1974; Sandow *et al.* 1975; Lukas and Orth 1993). Nest building and spawning begin as water temperature increases from about 17 to 20°C and continues to 31°C. Spawning is protracted (April–early June to August or even October), depending in part on latitude (Bass and Hitt 1974; Lukas and Orth 1993). Nesting activity decreases over the summer and is related strongly to the number of degree days accumulated after water temperatures reach 20°C, although declines may also be related to renesting by unsuccessful males or declining numbers of spawning-ready females (Sandow *et al.* 1975; Lukas and Orth 1993). Males excavate depressional nests by carrying stones in their mouth and by caudal sweeping. Nests are 47 to 94 cm in diameter, 4 to 15 cm deep, and at water depths of 36 to 200 cm. Nests are usually placed in low-velocity habitats over coarse sand, gravel, or sand–gravel substrates and near cover of logs, stumps, boulders, plants, or bedrock ledges (Breder 1936; Miller 1963; Davis 1972; Sandow *et al.* 1975; Thorp *et al.* 1989; Helfrich *et al.* 1991; Lukas and Orth 1993; Marcy *et al.* 2005). Active nests may be widely spaced (4.5–9.1 m apart) or occur in loose aggregations of >80 nests (about 1.9 m apart) (Lukas and Orth 1993; Fletcher 1993). Nesting and spawning occurs in tidal waters supporting marine faunal elements, beaver ponds, backwaters, coves, and main flowing channels (Davis 1972; Bass and Hitt 1974; Sandow *et al.* 1975; Thorp *et al.* 1989; Helfrich *et al.* 1991; Lukas and Orth 1993; Snodgrass and Meffe 1999; Marcy *et al.* 2005). Nesting males (114–174 mm TL) may actively court females or females may enter nests with no courtship, ultimately spawning with two to six or more nest-guarding males (Lukas and Orth 1993; DeWoody *et al.* 1998). Reported spawning behaviors appear typical of most *Lepomis* (e.g., nest circling, repeated dips), but males use caudal sweeping to mix fertilized eggs into the nest substrate (Miller 1963; Lukas and Orth 1993). Genetic paternity analyses in a North Carolina population indicated that nest-guarding males sired most (>96%) of the young in their nests. Nest takeovers were rare, but 44% of assayed nests contained low percentages of offspring from nonguardian males, even though no sneaker male morphs were detected (DeWoody *et al.* 1998; DeWoody and Avise 2001). Intrusion by an ostensible female between a spawning pair (Lukas and Orth 1993) also suggests the possibility of sneaker males in some populations. Mature ovarian eggs range from 0.90 to 1.64 mm (mean 1.20 mm) (Sandow *et al.* 1975). The relationship between total number of mature ova (Y) and total length (X) is described by the linear function $\log Y = -3.8786 + 3.1628 \log X$ ($n = 79$, $R^2 = 0.71$, equation from Sandow *et al.* 1975). At a median size of 153 mm TL, a female can potentially produce 1074 mature eggs in a single batch (range: 435 at 115 mm TL to 6104 eggs at 265 mm TL). The adhesive, yellow to amber, fertilized eggs hatch in 3 days at 20 to 24°C. Newly hatched larvae are 4.6 to 5.1 mm TL, and most larvae are free swimming at 7.6 to 8.2 mm TL (Hardy 1978; Buynak and Mohr 1978; Yeager 1981). The guardian male vigorously defends the nest, eggs, and larvae from nest predators, may reduce foraging activity, and may cannibalize offspring in his own nest (Thorp *et al.* 1989; Lukas and Orth 1993; DeWoody *et al.* 2001).

Nest associates: Dusky shiner, *Notropis cummingsae* (Fletcher 1993); swallowtail shiner, *Notropis procne* (Buynak and Mohr 1978); golden shiner, *Notemigonus crysoleucas* (Shao 1997).

Freshwater mussel host: Putative host to *Lampsilis teres*, *L. recta*, and *V. constricta* (unpublished sources in OSUDM 2006).

Conservation status: The redbreast sunfish is widespread and often abundant within its native range. It is considered vulnerable in Rhode Island, Massachusetts, and New York (Smith 1985; NatureServe 2006). In Massachusetts, it appears to have declined since the mid-1800s owing to changes in water quality or behavioral interactions with introduced species, especially the bluegill (Hartel *et al.* 2002).

Similar species: Adult longear, northern longear, and dollar sunfishes have a shorter ear flap that is bordered by a white or orange edge, possess blue marbling or spots on the side of the adult, and lack distinct rows of red-brown spots on the upper side (Page and Burr 1991).

Systematic notes: *Lepomis auritus* is sister to a clade inclusive of *L. marginatus*, *L. megalotis*, and *L. peltastes* (Near *et al.* 2004, 2005). Comparative studies of variation across the range of *L. auritus* are lacking.

Importance to humans: The redbreast sunfish is a popular, sought-after sport fish in streams and rivers across most of the Atlantic Slope and eastern Gulf Coast (e.g., Suwannee River). On light tackle, redbreast sunfish offer excellent sport, being somewhat more aggressive, more surface oriented, and more active in cool waters than bluegill. The quality of the flesh is excellent and rated higher than that of *Micropterus* by some (Etnier and Starnes 1993; Jenkins and Burkhead 1994).

13.8.2 Lepomis cyanellus *Rafinesque*

13.8.2.1 Green sunfish

Characteristics: See generic account for general characteristics. Body deep, compressed, but elongate and thick relative to other *Lepomis*, depth 0.37 to 0.45 of SL. Mouth large, terminal, slightly oblique, supramaxilla small (>3 and ≤4 times length of maxilla), upper jaw extends well beyond anterior edge of eye, and in large individuals may extend to posterior edge of eye or beyond. Adult with dark spot at posterior base of soft dorsal and sometimes anal fin. Green to blue wavy lines on sides of snout, cheek, and opercle. Opercular flap stiff, short, black in center, edged in pale or yellow tinge that extends forward to form light borders above and below. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Long slender gill rakers, 11 to 14, longest about six times greatest width, thicker in large adults. Lateral line complete. Scales small. Lateral scales, (41)45 to 50(53); rows above lateral line, 8 to 10; rows below lateral line, 16 to 19; cheek scale rows, 6 to 9; caudal peduncle scale rows, 23 to 25; pectoral rays, 13 to 15. Pharyngeal arches narrow, strong, with small, thin, sharply pointed to conically blunt teeth. Teeth on palatine bone. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue, rarely a few teeth present) bones (Bailey 1938; Childers 1967; Trautman 1981; Becker 1983; Page and Burr 1991; Etnier and Starnes 1993; Mabee 1993).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, ranging from 30 to 165 mm TL (median 51 mm). Large individuals measure 150 to 225 mm TL, weigh 85 to 200 g, and attain age 5+ to 6+ (maximum 310 mm TL, age 10+) (Carlander 1977; Page and Burr 1991; Pflieger 1997; Quist and Guy 2001). World angling record, 0.96 kg, Missouri (IGFA 2006). Growth in mid-western prairie streams, where the species is common, is associated positively with abundance of instream wood, likely reflecting cover or food resources associated with wood (Quist and Guy 2001). Males may grow faster and perhaps live longer than females, but differences can be slight, becoming most apparent in individuals >100 mm TL (Hubbs and Cooper 1935; Carlander 1977).

Coloration: Black, relatively short, ear flap with conspicuous light border. Wavy, often narrow, blue lines radiate from mouth across sides of snout onto cheek and opercle (often broken on opercle). Yellow, orange, or whitish margins on second dorsal fin, caudal fin lobes, anal fin, and pelvic fins, more prominent in breeding males. Blue-green above and on sides; iridescent, narrow, pale blue stripes on body scales interspersed with yellow metallic flecking; the blue stripes often broken into irregular mottling or spotting, especially posteriorly; sometimes with dusky bars on side. White to yellow belly (Hunter 1963; Page and Burr 1991; Etnier and Starnes 1993; Jenkins and Burkhead 1994).

Native range: The green sunfish is native to the east-central United States, west of the Appalachians from the Great Lakes, Hudson Bay, and Mississippi River Basins from New York and Ontario to Minnesota and South Dakota and south to the Gulf Slope drainages from the Escambia River, Florida, and Mobile Basin, Georgia and Alabama, west to the lower Rio Grande basin, Texas, and northern Mexico (Page and Burr 1991; Miller 2005). The species has been widely introduced and is established over much of the United States including Atlantic and Pacific Slope drainages and Hawaii (Page and Burr 1991; Fuller *et al.* 1999). Introduced populations of green sunfish in Atlantic Slope and in western US waters are implicated in suppression and decline of native game and nongame fishes as well as frogs and salamanders (Lemly 1985; Fuller *et al.* 1999; Dudley and Matter 2000; Moyle 2002).

Habitat: The green sunfish is a highly successful, aggressive, competitive species occurring in a variety of habitats including clear to turbid headwaters, sluggish pools of large streams, isolated, dry season–stream pools, and shallow shorelines of lakes, ponds, and reservoirs (Werner and Hall 1977; Werner *et al.* 1977; Capone and Kushlan 1991; Page and Burr 1991; Etnier and Starnes 1993; Taylor and Warren 2001; Smiley *et al.* 2005). In pond experiments, the presence of green sunfish induced dramatic shifts in foraging habitat and prey types in co-occurring congeners (Werner and Hall 1977, 1979). Green sunfish also invoke strong antipredator behaviors in aquatic insects and amphibians (e.g., Sih *et al.* 1992; Krupa and Sih 1998). The species is among the most tolerant of *Lepomis* to adverse conditions of high turbidity (<3500 FTU), low dissolved oxygen (DO) (<1 ppm), high temperatures (average critical thermal maxima 37.9°C, acclimated at 26°C), and high alkalinity (>2000 ppm, pH = 9.5) (McCarraher 1971; Horkel and Pearson 1976; Matthews 1987; Smale and Rabeni 1995a,b; Beitinger *et al.* 2000). Marked individuals in streams may show little movement, being recaptured in home pools over multiple seasons or longer (Gerking 1950, 1953; Smithson and Johnston 1999). Homing ability after short-distance displacement, exploratory pool-to-pool movements (>400 m), and long-distance movements (>16 km) are documented (Funk 1957; Hasler and Wisby 1958; Kudrna 1965; Smithson and Johnston 1999). The green sunfish is also an adept disperser and "pioneer" species, rapidly colonizing streams recovering from seasonal drying or drought, moving into and out of seasonally inundated floodplain habitats, and often invading ponds or small lakes (Ross and Baker 1983; Matthews 1987; Kwak 1988; Capone and Kushlan 1991; Etnier and Starnes 1993; Taylor and Warren 2001; Moyle 2002; Adams and Warren 2005).

Food: The adult green sunfish is a solitary ambush predator whose large mouth allows it to feed on larger food items at a given body size than most congeners (Sadzikowski and Wallace 1976; Werner and Hall 1977). The size-adjusted gape area of the species is the second largest within the genus (see *L. gulosus*; Collar *et al*. 2005a,b). The adult diet consists primarily of aquatic insects, particularly large odonate, mayfly, and beetle larvae; fish; crayfish; and terrestrial invertebrates, but a variety of other taxa are consumed (e.g., snails, and unusually, a bat) (Minckley 1963; Applegate *et al*. 1967; Etnier 1971; Sadzikowski and Wallace 1976; Werner 1977; Carlander 1977; Lemly 1985). Young green sunfish transition from an initial diet of microcrustaceans to larger invertebrates and at 50 to 99 mm TL increase consumption of crayfishes and fishes (Applegate *et al*. 1967; Mittelbach and Persson 1998). High volumes of plant material in stomachs are indicative of considerable foraging for invertebrates, such as odonate larvae, associated with vegetation (Etnier 1971; Sadzikowski and Wallace 1976). In laboratory studies, activity levels are largely diurnal, peaking at dusk and dawn, but the presence in stomachs of prey only available after dark indicates a nocturnal or at least crepuscular component to feeding (Etnier 1971; Beitinger *et al*. 1975; Langley *et al*. 1993). Green sunfish produce a chemical alarm substance that induces antipredatory behaviors in conspecifics, regardless of size. In contrast, chemical alarm cues from sympatric heterospecific fishes induce antipredator responses in juvenile green sunfish and foraging responses in adults (Golub and Brown 2003).

Reproduction: Maturity is reached at age 1+ to 3+ at a minimum size of about 45 to 76 mm TL (Carlander 1977). The combined effects of increased photoperiod (15 hours) and rising temperature in spring control prespawning gonadal development (Kaya and Hasler 1972; Smith 1975). Under controlled photoperiods, temperature, and food availability, 6-month old individuals (60–100 mm TL) can be induced to spawn (Smith 1975). Spawning is protracted (mid-May to early August), with the initiation of spawning depending in part on latitude (Hunter 1963; Kaya and Hasler 1972; Carlander 1977; Pflieger 1997). Nest building and spawning begin as water temperatures increase to 20°C, and peak spawning occurs between about 20 and 28°C (Hunter 1963). Nesting activity decreases and gonadal regression occurs as water temperatures remain over 28°C for extended periods (Hunter 1963; Kaya 1973). Males excavate nests by caudal sweeping. Nests are about 31 cm in diameter and usually placed over gravel in open, shallow areas (4–35 cm water depth, rarely 100 cm). Within a population, small males nest later in the season and in shallower water than large males (Hunter 1963), and at similar latitudes, individuals from stunted populations become ripe 2 to 4 weeks later than nonstunted populations (Childers 1967). Nests may be widely spaced (up to 30 m apart) when population densities are low but can also be placed rim-to-rim in crowded colonies (Hunter 1963; Childers 1967; Pflieger 1997). Colony formation closely parallels that of other colonial-nesting *Lepomis* (e.g., Bietz 1981; Neff *et al*. 2004), but whether colonial nesting occurs in the absence of habitat limitation is not completely clear (Hunter 1963; Childers 1967; Pflieger 1997). Spawning events are synchronous in colonies, occurring at intervals of 8 to 9 days over the spawning season; males may nest five or more times in succession during this period, and females presumably participate in multiple spawning events (three to six) over the season (Hunter 1963). Nest-guarding males produce gruntlike sounds as part of courtship (Gerald 1971); other reported courtship, spawning, and nest defense behaviors appear typical for the genus (Hunter 1963; Childers 1967). During nest building and spawning, males are territorial, aggressive, and even combative toward other males, females, and nest predators; only the most persistent spawning-ready females are allowed into the nest. Activity of spawning males is intensified. For example, in a 10-minute period a guardian male completed five spawning acts, made ten defensive forays outside the nest, threatened his neighbor once, and rim-circled 39 times (Hunter 1963). During a given spawning event, females attempt to mate (and likely do mate) with multiple males, but appear most attracted to males that are already spawning. Occasional intrusions by an ostensible female between a spawning pair (Hunter 1963) suggest the presence of sneaker males in at least some populations, but alternative mating systems in green sunfish are unconfirmed. Mature ovarian eggs are 0.8 to 1.0 mm in diameter, and fertilized eggs are 1.0 to 1.4 mm in diameter (mean 1.23 mm) (Meyer 1970; Kaya and Hasler 1972; Taubert 1977). Depending on their size, females may carry 2000 to 10,000 eggs (Beckman 1952 in Moyle 2002), but little else is apparently known about fecundity. The adhesive, fertilized eggs hatch in 2.1 days at 23.8°C (1.3 days at 27.1°C) (Childers 1967). Newly hatched larvae are 3.6 to 3.7 mm TL, and, depending on temperature, larvae are free swimming for about 3 to 6 days after fertilization at 4.6 to 6.3 mm TL (Childers 1967; Meyer 1970; Taubert

1977). Successful males guard and vigorously defend the nest, eggs, and larvae for 5 to 7 days, but earlier abandonment of nests is common (Hunter 1963).

Nest associates: Red shiner, *Cyprinella lutrensis* (Pflieger 1997); redfin shiner, *Lythrurus umbratilis* (Hunter and Wisby 1961; Hunter and Hasler 1965; Snelson and Pflieger 1975; Trautman 1981; Johnston 1994a,b; Pflieger 1997); golden shiner, *N. crysoleucas* (suspected, Pflieger 1997); Topeka shiner, *Natropis topeka* (Pflieger 1997).

Freshwater mussel host: Confirmed host to *A. ligamentina, Anodonta suborbiculata, Elliptio complanata, Glebula rotundata, Lampsilis altilis, Lampsilis bracteata, Lampsilis cardium, Lampsilis higginsii, Lampsilis hydiana, L. reeveiana, Lasmigona complanata, Ligumia subrostrata, L. recta, Megalonaias nervosa, P. grandis, V. iris, Villosa vibex*, and *U. imbecillis* (Young 1911; Lefevre and Curtis 1912; Tucker 1927, 1928; Stern and Felder 1978; Trdan and Hoeh 1982; Parker *et al.* 1984; Waller and Holland-Bartels 1988; Howells 1997; Barnhart and Roberts 1997; Haag *et al.* 1999; O'Dee and Watters 2000). Putative host to *A. plicata, Lampsilis radiata, Lasmigona compressa, S. undulatus, Toxolasma lividus*, and *Toxolasma parvus*, (unpublished sources in OSUDM 2006).

Conservation status: Although abundant in few natural habitats (e.g., Pflieger 1997; Quist and Guy 2001), the green sunfish is widespread and stable within its native range.

Similar species: Other *Lepomis* lack yellow-orange edges on the fins and the black spot at posterior base of the dorsal fin (except the bluegill) and have a smaller mouth (except the warmouth). The bluegill has long, pointed pectoral fins, and the warmouth has dark red-brown lines radiating posteriorly from the eye, mottling on the side, and a small patch of teeth on the tongue (Page and Burr 1991).

Systematic notes: *Lepomis cyanellus* forms a sister pair with *L. symmetricus*, and the pair represents the second largest and the smallest *Lepomis*, respectively (Near *et al.* 2004, 2005). Comparative studies of variation across the range of *L. cyanellus* are lacking.

Importance to humans: The green sunfish rarely reaches a size of interest to anglers other than children. Because of its propensity to invade, overpopulate, stunt, and compete with other fishes in ponds or small lakes, green sunfish are considered a pest by those attempting to maintain quality bluegill-bass sport fisheries. The species is commonly used by anglers as live bait on trotlines, set hooks, and jugs for catfishes. Hybrids between a female green sunfish and a male bluegill (known as "hybrid bream") are cultured and stocked in ponds to create put-and-take fisheries. The hybrids are aggressive, fast growing, and easy to catch, and if properly managed, produce excellent results (Ross 2001).

13.8.3 Lepomis gibbosus *(Linnaeus)*

13.8.3.1 Pumpkinseed

Characteristics: See generic account for general characteristics. Body, deep, compressed, often almost disk-like, depth about 0.40 to 0.53 of SL. Mouth moderate, terminal, slightly oblique, supramaxilla absent, upper jaw extends almost to, or to, anterior edge of eye. Wavy blue lines on cheek and opercle of adult. Bold dark brown wavy lines or orange spots on soft dorsal, anal, and caudal fins. Opercular flap stiff, short, with black center bordered in white or yellow with a prominent red (males) to yellowish (females) semicircular spot at posterior edge (often pale or yellowish in young). Pectoral fin long, sharply pointed, usually reaching far past eye when laid forward across cheek. Short, thick gill rakers, about 12; scarcely longer than wide. Lateral line complete. Lateral scales, (35)37 to 44(47); rows above lateral line, 6 to 8; rows below lateral line, 12 to 15; cheek scale rows, 3 to 6; caudal peduncle scale rows, 17 to 21; pectoral rays, 11 to 14. Pharyngeal arches extremely broad, heavy with large rounded, molariform teeth. Teeth present or absent on palatine bone. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Scott and Crossman 1973; Trautman 1981; Becker 1983; Page and Burr 1991; Mabee 1993; Jenkins and Burkhead 1994).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, ranging from 15 to 99 mm TL (median 40 mm). Large individuals measure 150 to 225 mm TL, weigh about 150 to 200 g, and attain age 6 to 9+ (maximum 400 mm TL, age 10+) (Carlander 1977; Page and Burr 1991; Fox 1994). World angling record, 0.63 kg, New Mexico (IGFA

2006). Pumpkinseed populations sympatric with bluegill show increased early growth rates, despite reduced resources, relative to populations allopatric with bluegill, providing evidence for counter-gradient evolutionary selection for rapid growth (Arendt and Wilson 1997, 1999). Older males tend to be larger than same-age females, and subtle differences in body form occur between male and female pumpkinseed (Deacon and Keast 1987; Brinsmead and Fox 2002).

Coloration: Ear flap black with light border, marked with bright red or yellow-orange spot on posterior edge. Wavy, usually wide, blue lines radiate from mouth across sides of snout onto cheek and opercle of adult. Many bold dark brown wavy lines or orange spots on second dorsal, caudal, and anal fins. Olive above and on sides with many gold and yellow flecks. Adults blue-green, spotted with orange; dusky chainlike bars mark sides of young and adult female; white to red-orange below (Page and Burr 1991).

Native range: The pumpkinseed is native to Atlantic Slope drainages from New Brunswick south to the Edisto River, South Carolina, and to the Great Lakes, Hudson Bay, and upper Mississippi River Basins from Quebec and New York west to southeast Manitoba and North Dakota and south to northern Kentucky and Missouri. The species has been widely introduced and is established over much of the United States and southern Canada, including some Pacific Slope drainages (Scott and Crossman 1973; Page and Burr 1991; Fuller *et al.* 1999; Moyle 2002).

Habitat: The pumpkinseed inhabits vegetated lakes and ponds and quiet vegetated pools of creeks and small rivers (Page and Burr 1991). Lake- and stream-dwelling populations differ in subtle aspects of body morphology (e.g., pectoral fin length), differences attributed to adaptation to lentic versus lotic environments (Brinsmead and Fox 2002). Juvenile and adult pumpkinseed tend toward lengthy occupancy of home activity areas (about 11 m^2 to 1.12 hectares, respectively) and can home to those areas when displaced (Shoemaker 1952; Hasler *et al.* 1958; Kudrna 1965; Reed 1971; Fish and Savitz 1983; Wilson *et al.* 1993; Coleman and Wilson 1996; McCairns and Fox 2004).

Food: The pumpkinseed is a highly specialized molluscivore, feeding primarily on snails by crushing them between heavy pharyngeal jaw bones that are equipped with molariform teeth, enlarged muscles, and specialized neuromuscular adaptations (Lauder 1983a,b, 1986; Hambright and Hall 1992; Wainwright and Lauder 1992; Huckins 1997). Adults also feed heavily on dipteran, mayfly, and caddisfly larvae and beetles, and also ingest cladocerans, amphipods, isopods, ostracods, larval odonates, and terrestrial invertebrates (Seaburg and Moyle 1964; Sadzikowski and Wallace 1976; Keast 1978; Laughlin and Werner 1980; Deacon and Keast 1987; Huckins 1997; Jastrebski and Robinson 2004). Young age-0 fish (>18 mm TL) consume a diet predominated in biomass by zooplankton and chironomids (Hanson and Qadri 1984), and at least in pond experiments, their combined predatory effects can change zooplankton composition (Hambright and Hall 1992). As they grow from 35 to 100 mm TL, the young transition gradually from a diet of soft-bodied littoral invertebrates to high numbers of snails (Keast 1978; Mittelbach 1984a; Keast and Fox 1990; Osenberg *et al.* 1992; Huckins 1997). Full development of the pharyngeal snail-crushing apparatus of pumpkinseeds depends on repeated, consistent consumption of snails (Bailey 1938). Pharyngeal bones and musculature associated with snail crushing are substantially reduced in individuals in snail-poor lakes relative to individuals from snail-rich lakes (Wainwright *et al.* 1991; Mittelbach *et al.* 1992; Osenberg *et al.* 2004). In the summer, peaks in feeding occur in late afternoon and at dawn with reduced but notable feeding after midnight (Keast and Welsh 1968). In the fall, daylight feeding is low and feeding peaks occur between 2000 and 0400 hours (Johnson and Dropkin 1993). In summer, age-0 pumpkinseed feed from shortly after sunrise until sunset (Hanson and Qadri 1984). Periodic infrared videography of foraging pumpkinseed over 8 months revealed frequent nocturnal foraging, mediated by a switch from benthic picking during daylight to zooplanktivory at night (Collins and Hinch 1993). In support of these field observations, laboratory experiments indicate volumes searched and feeding rates on zooplankton decrease at light intensities ≤10 lux (Hartleb and Haney 1998). Pumpkinseeds produce a chemical alarm substance that induces antipredatory behaviors in conspecific juveniles (<45 mm SL), but depending on the concentration, elicits either antipredatory or foraging responses in conspecific adults (>95 mm SL) (Marcus and Brown 2003; Golub *et al.* 2005). Response of juveniles to alarm cues was diminished under weakly acidic conditions (pH 6.0) (LeDuc *et al.* 2003). Pumpkinseed also respond to chemical alarm cues of largemouth bass (and ostariophysan alarm chemicals), but the response is mediated by size and habitat complexity. Under conditions of low to intermediate habitat complexity, large pumpkinseed (>80 mm SL) exhibit foraging responses and small pumpkinseed antipredator responses to bass chemical alarm cues. In highly complex habitat, both large and small pumpkinseed show antipredator responses to bass chemical alarm cues (Golub *et al.* 2005).

Lake-dwelling pumpkinseeds show subtle intra- or interpopulation differences in body form (e.g., body depth, fin length, gill raker spacing) that are strongly associated with specializations for pelagic or littoral feeding (Robinson *et al*. 1996; Robinson and Schluter 2000; Brinsmead and Fox 2002; Gillespie and Fox 2003; Jastrebski and Robinson 2004; McCairns and Fox 2004). Intermediate forms occur in both habitats but show reduced fitness in growth and body condition (Robinson *et al*. 1996). Evidence from parasite analyses and strong site fidelity in pelagic and littoral zone pumpkinseed morphs suggest that trophic divergence and habitat segregation come into play early in the life history and could potentially affect gene flow (Robinson *et al*. 2000; Jastrebski and Robinson 2004; McCairns and Fox 2004). Intrapopulation morphological divergence between trophic morphs occurs across a relatively broad geographic region (Robinson *et al*. 2000; Gillespie and Fox 2003; Jastrebski and Robinson 2004). Divergence is expressed in the absence of open-water competitors (i.e. bluegill or other *Lepomis*) (Robinson *et al*. 1993), but may also be mediated by complex interactions of a number of ecological factors (Robinson *et al*. 2000).

Reproduction: Maturity is reached at age 1+ to 4+ at 65 to 130 mm TL. Within a population, females may mature earlier and at smaller sizes than males (Carlander 1977; Fox and Keast 1991; Fox 1994; Danylchuk and Fox 1994; Fox *et al*. 1997). Age and size at maturity, onset and duration of spawning, size of eggs, and energy allocated for reproduction are plastic, varying in different, but proximate habitats (e.g., beaver ponds and nearby lakes, adjacent lakes) or regionally. Trade-offs among somatic growth and reproductive timing and allocation are linked to energy limitations, resource uncertainty in highly variable environments, and presence of other *Lepomis* (Deacon and Keast 1987; Fox and Keast 1991; Danylchuk and Fox 1994; Fox 1994; Fox *et al*. 1997). Spawning is protracted (early May to August), the initiation of spawning depending in part on latitude and population size structure (Burns 1976; Carlander 1977; Danylchuk and Fox 1994; Fox and Crivelli 1998). Gonadal development in both sexes accelerates as water temperatures warm to 12.0°C and photoperiod lengthens to 13.5 hours (Burns 1976). A combination of long photoperiod (16 hours) and warm temperature (25°C) induces nest-building behaviors in males (Smith 1970). Nest building and spawning begin as water temperatures increase to 17°C, and peak spawning occurs between about 20 and 22°C, but continues to at least 26°C (Miller 1963; Fox and Crivelli 1998; Cooke *et al*. 2006). Onset of spawning is later and the spawning season is longer in stunted than in nonstunted populations (Danylchuk and Fox 1994). Males excavate nests by caudal sweeping and uprooting and carrying away plants; conspecific or other centrarchid nests are often appropriated or reused (Ingram and Odum 1941; Miller 1963). Nests are 30 to 80 cm in diameter, at water depths of 18 to 50 cm (rarely >1 m), and often near simple cover (e.g., log, stump, boulder). Sand or small rocky substrates are chosen most often for nest sites, but a variety of substrates are used (Breder 1936; Ingram and Odum 1941; Colgan and Ealey 1973; Popiel *et al*. 1996). Nests are usually solitary (>1 m apart), but groups of two or three nests may be rim to rim (Ingram and Odum 1941; Miller 1963; Clark and Keenleyside 1967; Colgan and Ealey 1973). Nest-guarding males produce popping sounds as part of courtship of females and aggression toward conspecific males and other *Lepomis* (Gerald 1971; Ballantyne and Colgan 1978a,b,c). Other reported courtship, spawning, and nest defense behaviors appear typical for the genus (e.g., aggressive displays, courtship circles, rim circling) (Miller 1963; Steele and Keenleyside 1971; Colgan and Gross 1977; Colgan *et al*. 1981; Becker 1983; Clarke *et al*. 1984). Sneaker males are documented for pumpkinseed (Gross 1979), but in one surveyed population, guardian males sired about 85% of the larvae in their nests (range, 43–100%) (Rios-Cardenas and Webster 2005). Mature ovarian eggs average 1.11 mm diameter (Gross and Sargent 1985), but 0.6 to 1.0 mm and 0.8 to 1.2 mm diameters are ranges reported for fertilized or fertilized and water-hardened eggs, respectively (Hardy 1978; Cooke *et al*. 2006). Female batch fecundity increases with weight, but varies significantly among populations (Deacon and Keast 1987). The relationship between batch fecundity (Y) and total weight (X) is described by the linear function, $\log_{10} Y = -0.0592 + 1.9461 \log_{10} X$ ($n = 37$, $R^2 = 0.20$, one of four equations from Deacon and Keast 1987). At 48 g (128 mm TL), a female can potentially produce 5455 mature eggs in a single batch (range: 2451 at 20 g and 98 mm TL to 10,633 eggs at 126 g and 184 mm SL, respectively). The white to transparent, adhesive, fertilized eggs hatch in about 3 days at 18 to 22°C, larvae at hatching are 2.6 to 3.1 mm TL, and larvae reach swim-up at about 5.2 mm TL, some 4 days after hatching (Miller 1963; Colgan and Gross 1977; Hardy 1978). The cycle for the successful guardian male typically takes 10 days (range 6–15 days) with 2 days for territory establishment and nest construction, three for spawning and egg guarding, four for larval guarding, and one for fry dispersal and nest abandonment. Territoriality and aggressiveness in guardian males is highest during egg guarding and early larval stages, diminishing as larvae grow (Colgan and Gross 1977; Colgan and Brown 1988; Cooke *et al*. 2006). Males may lose on average 6.3% of their body weight from spawning to fry dispersal (Rios-Cardenas and Webster 2005). Females can participate in one to six spawning periods (average two to three) over a 7- to 8-week period, during which an estimated

12 to 40% of prespawning body mass is allocated to reproduction (Fox and Crivelli 1998). In lakes, fry apparently initially disperse offshore but return to littoral habitats in late summer (Keast 1978; Brown and Colgan 1984, 1985a; Mittelbach 1984a; Rettig 1998).

Nest associates: Golden shiner, *N. crysoleucas* (Shao 1997).

Freshwater mussel host: Confirmed host to *Alasmidonta varicosa*, *P. grandis*, and *U. imbecillis* (Trdan and Hoeh 1982; Fichtel and Smith 1995). Putative host to *Alasmidonta undulata*, *A. plicata*, *E. complanata*, *L. radiata*, *Lampsilis siliquoidea*, *L. reeviana*, *Lasmigona costata*, *L. recta*, *P. cataracta*, and *S. undulatus* (unpublished sources in OSUDM 2006).

Conservation status: The pumpkinseed is secure across most of its native range but is considered critically imperiled in Manitoba and vulnerable in Illinois (NatureServe 2006), which include the northwestern and southern peripheries of its native distribution, respectively (Page and Burr 1991).

Similar species: All other *Lepomis* have shorter, rounded pectoral fins, except the redear sunfish and bluegill. The redear sunfish and bluegill lack bold spots on the second dorsal fin and wavy blue lines on the gill cover (Page and Burr 1991).

Systematic notes: *Lepomis gibbosus* is basal to a clade consisting of *L. microlophus*, and the sister pair *L. punctatus*–*L. miniatus* (Near *et al.* 2004, 2005). Based on shared behavioral and morphological specializations for snail crushing, *L. gibbosus* was proposed previously as sister to *L. microlophus* (Bailey 1938; Mabee 1993). Frequencies of nuclear-encoded allozyme loci across populations in four east-central Ontario watersheds revealed low genetic variability, but populations were significantly substructured genetically. The patterns in genetic variation are congruent with hypothesized post-Pleistocene recolonization routes (Fox *et al.* 1997). Comparative studies of variation across the entire range of *L. gibbosus* are lacking, but anal and dorsal ray counts and differences in size and age at maturity show east to west differences (Scott and Crossman 1973; Fox *et al.* 1997).

Importance to humans: Although not often reaching a size of interest to many anglers, the pumpkinseed can contribute substantially to the sport fishery catch in northern lakes (e.g., Minnesota, Eddy and Underhill 1974; Wisconsin, Becker 1983), at least historically contributed to the Great Lakes commercial fishery catch (Scott and Crossman 1973), and is an easy and delightful catch for young anglers. The flesh is white, flaky, sweet, and delicious, comparable to that of the bluegill. The species can be taken in late afternoons with light tackle on live bait, small dry flies, poppers, or wet fly trout patterns (Scott and Crossman 1973; Eddy and Underhill 1974; Becker 1983). The pumpkinseed is important ecologically, forming part of the food for many predatory fishes including important game fishes (e.g., black basses, walleye, yellow perch, and muskellunge) (Scott and Crossman 1973). Among northern North American freshwater fishes, the pumpkinseed is among the most striking in beauty and color (Jordan and Evermann 1923; Becker 1983). Because of their color and ease of keeping and breeding, the species is a prized aquarium fish in Europe (Goldstein 2000).

13.8.4 Lepomis gulosus *(Cuvier)*

13.8.4.1 Warmouth

Characteristics: See generic account for general characteristics. Body relatively thick, robust, somewhat elongate, depth 0.4 to 0.5 of SL. Large, terminal oblique mouth, lower jaw projecting slightly, supramaxilla moderately large (>2 to ≤3 times length of maxilla), upper jaw extending well beyond anterior edge of eye to center of eye or beyond in adults. Dark red-brown lines (3–5) radiating posteriorly from snout and red eye. Opercular flap short, stiff, black with paler and often red-tinged border. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Long, thin gill rakers, 9 to 13, longest about four (adults) to six (young) times the greatest width. Lateral line complete. Lateral scales, 36 to 48; rows above lateral line, 6 to 9; rows below lateral line, 12 to 15; cheek scale rows, 5 to 7; caudal peduncle scale rows, 19 to 23; pectoral rays, 12 to 14. Pharyngeal arches narrow with bluntly conical teeth. Teeth on endopterygoid, ectopterygoid, palatine (villiform), and glossohyal (tongue, one patch) bones (Bailey 1938; Birdsong and Yerger 1967; Trautman 1981; Becker 1983; Etnier and Starnes 1993; Mabee 1993; Jenkins and Burkhead 1994; Boschung and Mayden 2004).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, ranging from 25 to 155 mm TL (median 55.5 mm TL). Large individuals measure 150 to 200 mm TL, weigh about 200 g, and attain age 5 to 7+ (maximum 310 mm TL, age 8+) (Carlander 1977; Page and Burr 1991). World angling record, 1.1 kg, Florida (IGFA 2006).

Coloration: Ear flap short, black with yellow edges and posterior red spot (adult). Dark red-brown lines radiating from back of red eye. Olive brown above; dark brown mottling on back and upper side; often 6 to 11 chainlike dark brown bars on sides; cream to light yellow below; dark brown spots (absent on young) and wavy bands on fins. Breeding male boldly patterned on body and fins with a bright red-orange spot at base of second dorsal fin and black pelvic fins (Page and Burr 1991). Young and juveniles usually with a distinctive purplish sheen.

Native range: The warmouth is native to the Great Lakes and Mississippi River Basin from western Pennsylvania to Minnesota and south to the Gulf of Mexico and the Atlantic and Gulf drainages from the Rappahannock River, Virginia, to, but apparently not including, the Rio Grande, Texas, New Mexico, and Mexico (Page and Burr 1991; Miller 2005). The species is an apparent recent (ca. 1966) natural immigrant in the waters of southern Ontario, where it is naturalized (Crossman *et al.* 1996). The warmouth has been introduced widely and is established over much of the United States, including some Pacific Slope drainages (Fuller *et al.* 1999; Moyle 2002).

Habitat: The warmouth inhabits vegetated lakes, ponds, swamps, reservoirs, and quiet waters of slow-flowing streams, being most common, and often abundant, in lowland areas and rare in uplands (Larimore 1957; Holder 1970; Guillory 1978; Page and Burr 1991; Snodgrass and Meffe 1998). Individuals are most often solitary and usually associated with areas of dense vegetation, root wads, stumps, overhanging banks, or rock cavities over silt or mud substrates (Larimore 1957; Loftus and Kushlan 1987). Smaller warmouth (<127 mm TL) tend to remain in dense vegetation in shallow water, but larger individuals occur more often in deeper waters (Larimore 1957). Warmouth appear well adapted to the rigors of coastal plain wetland habitats of the southern United States. The species is tolerant of low DO levels and high turbidity, is adept at locating deep water refuge (e.g., alligator ponds) in response to seasonal drying of wetlands, and tolerates moderately brackish waters (<12.5 ppt) (Larimore 1957; Kushlan 1974; Loftus and Kushlan 1987; Killgore and Hoover 2001; Rutherford *et al.* 2001; Boschung and Mayden 2004). The physiological bases for or limits of these tolerances are unstudied. In a North Carolina swamp system, average movement for 20% of recaptured individuals was 5.0 km over 21 days. Notably, another 31% of recaptures moved 0.6 to 1.8 km (35–75 days at large), and 65% of marked individuals were never recaptured (Whitehurst 1981). Trap catches in the Okefenokee Swamp and Suwannee River suggested highest activity at night and peak movements in spring just before spawning (Holder 1970).

Food: The warmouth is a solitary, opportunistic predator whose large mouth allows it to feed on larger food items at a given body size than congeners. The size-adjusted gape area of the species is the largest among *Lepomis* (Collar *et al.* 2005a,b). The adult (>125 mm TL) diet consists primarily of small fish (e.g., sunfishes, darters, pickerels, killifish, mosquitofish), crayfish, and odonate larvae, but a variety of other taxa are consumed (e.g., freshwater shrimp, isopods, mayflies, caddisflies) (McCormick 1940; Chable 1947; Larimore 1957; Germann *et al.* 1974; Guillory 1978). The largest adults (>200 mm TL) often feed almost exclusively on crayfishes (Guillory 1978). Young warmouth transition from an initial diet of microcrustaceans to invertebrates (e.g., midge and caddisfly larvae) and at about 75 mm TL begin increasing use of the larger prey dominating the adult diet (Larimore 1957; Germann *et al.* 1974; Desselle *et al.* 1978; Guillory 1978). Dawn and dusk samples in the summer suggest that most feeding occurs at or before dawn with little feeding in the afternoon (Larimore 1957).

Reproduction: Maturity is reached at ages 1+ to 2+ at 57 to 152 mm TL (Larimore 1957; Germann *et al.* 1974; Guillory 1978). Spawning is initiated as water temperatures approach 21°C (as low as 15°C) and is protracted (April or May to July or August) with female ovary to body weight ratios peaking in late May to early June as water temperatures reach 27 to 29°C (Larimore 1957; Germann *et al.* 1974; Guillory 1978). Males excavate nests in a few hours by caudal sweeping, and depending on the time spent by the male, the nest may be a rather shapeless oval depression (about 10 cm × 20 cm) with only loose silt swept away or a deep, symmetrical circular depression (45 cm diameter, 13 cm deep). Nests are constructed at water depths of 15 to 152 cm (most <76 cm) and are often near simple cover (e.g., tree base, log, stump, boulder,) or on logs, roots, or mats of submerged plants. If available, small rocky substrates in silt-laden areas are chosen most often for nest sites and sand avoided, but in southern wetlands, nest bottoms often consist of tree leaves and needles swept free of silt. Bottom type appears less important than nearby cover for nest placement (Larimore 1957; Birdsong and Yerger 1967; Fletcher and Burr 1992). Nests are usually solitary (>4 m apart), but if habitat is limiting nests may be closely spaced (Carr 1940; Larimore 1957; Childers 1967). Courtship and spawning behaviors (based primarily on aquarium observations) appear typical for the genus (e.g., male aggressive displays, jaw gapes, opercular flares), but warmouth apparently do not rim circle; other than egg fanning by the male, no detailed observations are available on nest care or nest defense behaviors. During active courtship of a female, the body of a male becomes bright yellow and the eyes blood red in color, the change in colors requiring only 5 to 10 seconds. Only when the female is ready to lay eggs will she allow the male to guide her to the nest. In aquaria, a nest-guarding male will ultimately kill an unresponsive female (Larimore 1957). During paired circling of the nest (female near the center, male outside), the female jaw gapes a few times, violently jerks her body, and releases about 20 eggs while simultaneously thumping the male on the side in an apparent signal for him to release sperm. These behaviors are repeated sequentially for about 1 hour with brief pauses in between bouts, at which time males may use caudal sweeping to mix eggs into the substrate (Larimore 1957). Mature ovarian eggs (water-hardened) average 1.01 mm in diameter (Merriner 1971a). Mature females contain two or more egg class sizes throughout the spawning season (Larimore 1957; Germann *et al.* 1974). Batch fecundity increases with female size. The relationship between batch fecundity (Y) and total length (X) is described by the linear function, $\log_{10} Y = -1.6108 + 2.4859 \log_{10} X$ (data from mean number of mature eggs of nine length classes, $R^2 = 0.85$, Germann *et al.* 1974). At 195 mm TL, a female can potentially produce 12,078 mature eggs in a single batch (range: 6825 eggs at 155 mm TL to 20,238 eggs at 240 mm SL, respectively). Another estimate of batch fecundity is much lower (i.e. $\log_{10} Y = 0.1619 + 1.418 \log_{10} X$; where X is SL, Guillory 1978). The fertilized eggs are pale, amber-colored, and adhesive, hatching in about 1.5 days at 25.0 to 26.4°C (71.1 hours at 22.6°C, 33.9 hours at 26.9°C, and 32.5 hours at 27.3°C). Larvae at hatching are 2.3 to 2.9 mm TL and reach swim-up at about 4.7 to 7.6 mm TL, some 3 to 5 days after hatching (Larimore 1957; Childers 1967). After leaving the nest, young apparently do not form schools, but hide themselves in dense vegetation or other cover. Likewise, juvenile warmouth do not aggregate in large groups (Larimore 1957).

Nest associates: Bluehead shiner, *Pteronotropis hubbsi* (Fletcher and Burr 1992).

Freshwater mussel host: Confirmed host to *A. suborbiculata*, *L. subrostrata*, *Toxolasma texasensis*, and *U. imbecillis* (Stern and Felder 1978; Barnhart and Roberts 1997). Putative host to *T. parvus* (unpublished sources in OSUDM 2006).

Conservation status: The warmouth is currently stable over most of its range (Warren *et al.* 2000; NatureServe 2006). Peripheral populations in Pennsylvania and West Virginia are considered imperiled, and recently naturalized populations in Ontario are listed as critically imperiled (NatureServe 2006), although the necessity for the latter status has been questioned (Crossman *et al.* 1996).

Similar species: The green sunfish lacks dark lines radiating posteriorly from eye, lacks teeth on the tongue, and has a dark spot at the posterior base of the second dorsal fin (Page and Burr 1991).

Systematic notes: *Lepomis gulosus* is basal to the sister pair *L. symmetricus* and *L. cyanellus* (Near *et al.* 2004, 2005). Mitochondrial DNA analyses revealed distinct eastern and western populations of *L. gulosus*, occurring along the Atlantic Slope through Florida to eastern tributaries of Mobile Basin and from the Tombigbee River westward, respectively (Bermingham and Avise 1986). *L. gulosus* has a checkered taxonomic and nomenclatural history (summary in Berra 2001), but comparative studies of variation across the range of the species are lacking.

Importance to humans: Over much of its range, the warmouth is taken most often by bream or crappie anglers but usually not in abundance. Even so, warmouth can comprise a large part of the sport fish catch in habitats like the Okefenokee Swamp, Georgia, or Reelfoot Lake, Tennessee (Larimore 1957; Germann *et al.* 1974). Warmouth are quick to take an artificial lure or live bait. The species is an excellent table fish, the flavor and texture of the flesh being judged as intermediate between the bluegill and the largemouth bass (Larimore 1957).

13.8.5 Lepomis humilis *(Girard)*

13.8.5.1 Orangespotted sunfish

Characteristics: See generic account for general characteristics. Body moderately deep, compressed, slab-sided, depth 0.38 to 0.45 of SL. Mouth moderately large, oblique, supramaxilla absent, upper jaw extends to, or just beyond, anterior edge of eye. Orange or red-brown wavy lines on cheek and opercle in adults. Opercular flap moderate to long (in adults), very flexible, usually angled upward with black center and wide, white to pale green, conspicuous border (flushed with orange in breeding males). Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Moderately thin gill rakers, 10 to 15, longest about five times greatest width. Enlarged, elongate sensory pits on preopercle and head between eyes, pits larger than any other *Lepomis*, width of each pit about equal to distance between pits. Lateral line complete or incomplete. Lateral scales, 32 to 42; cheek scale rows, 5; pectoral rays, 13 to 15. Pharyngeal arches narrow with sharply pointed teeth. Teeth on palatine bone. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Bailey 1938; Trautman 1981; Becker 1983; Mabee 1993; Ross 2001; Boschung and Mayden 2004).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, ranging from 23 to 86 mm TL (median 45 mm TL). Large individuals measure 75 to 125 mm TL, weigh <60 g, and attain age 3+ (maximum 177 mm TL, about 150 g, age 4+) (Barney and Anson 1923; Carlander 1977; Page and Burr 1991; TWRA 2006).

Coloration: Black ear flap, usually angled upward, with conspicuous wide white, pale green, pale lavender, pinkish, or light crimson border. Olive above with bright orange (large male) or red-brown (female) spots on silver-green side. Orange (male) or red-brown (female) wavy lines on cheek and opercle. White to orange below; fins unspotted. Young with chainlike vertical bars and no spots on side. Breeding male brilliantly colored with red-orange spots on side; reddish orange eye, belly, anal fin, and dorsal fin edge; pelvic fins white to orange with black edge (Noltie 1990; Page and Burr 1991; Etnier and Starnes 1993).

Native range: The orange-spotted sunfish is native to southwestern Lake Erie and Lake Michigan, the extreme headwaters of the Red River of the North (Hudson Bay drainage), and the Mississippi River Basin from Ohio to southern North Dakota and south to Louisiana and in Gulf Slope drainages from the Mobile Basin, Alabama, to the Colorado River, Texas (Page and Burr 1991). In historical times, the species expanded its range into southeastern Michigan and adjacent Ontario, northward in Wisconsin, and eastward across Indiana and Ohio, as agricultural activities converted formerly clear prairie-type streams into turbid plains-type streams (Trautman 1981; Holm and Coker 1981; Becker 1983; Noltie 1990; Bailey *et al.* 2004). The species has been introduced sporadically on the periphery of its native range, usually unintentionally as stock contaminant with other centrarchids (Fuller *et al.* 1999).

Habitat: The orangespotted sunfish inhabits quiet pools of creeks and small to large, often turbid, rivers, as well as overflow swamps and backwaters of sluggish streams, natural lakes, and reservoirs (Noltie 1990; Page and Burr 1991; Etnier and Starnes 1993; Miranda and Lucas 2004). The species is rarely abundant but is most common in low-gradient habitats. The orangespotted sunfish is among the most tolerant of *Lepomis* to adverse conditions of low DO (<1 ppm) and high temperatures (average critical thermal maxima 36.4°C, acclimated at 26°C) (Matthews 1987; Smale and Rabeni 1995a; Beitinger *et al.* 2000).

Food: The orangespotted sunfish is an opportunistic invertivore, feeding extensively on midge larvae, caddisfly larvae, hemipterans, and microcrustaceans, rarely consuming small fish (Barney and Anson 1923; Clark 1943; Noltie 1990). These primary diet items, along with aerial insects in stomachs, indicate both bottom and surface feeding (Clark 1943; Etnier and Starnes 1993). When exposed to different diets, orangespotted sunfish show subtle but measurable changes in morphology, primarily in head shape, suggesting diet as a strong determinant of trophic morphology (Hegrenes 2001).

Reproduction: Maturity is reached at ages 1+ to 2+ at 30 to 50 mm TL (Barney and Anson 1923; Noltie 1990). Spawning is initiated as water temperatures approach 18°C and is protracted (April or May–late August) beginning 6 weeks earlier at southern (e.g., Louisiana) than at northern (e.g., Iowa) latitudes. Spawning is reported across a range of water temperatures from 24 to 32°C (Barney and Anson 1923; Cross 1967; Becker 1983; Noltie 1990). Ripe males and females are taken throughout the summer months. Scale growth increments suggest that fish hatched early in the spawning season obtain sexual maturation in August of the second year of life (age 1+) and those hatched latter delay maturation to early summer of the third year of life (age 2+) (Barney and Anson 1923). Males build nests at water depths of 30 to 61 cm, using caudal sweeping, pushing with the head, and fin undulations to remove overlying silt and mud, to ultimately form semicircular depressions about 15 to 18 cm in diameter and 30 to 40 mm deep with firm, exposed bottoms. Nests are colonial (<1.0 m apart) with males defending a territory of 30 to 60 cm (Barney and Anson 1923; Miller 1963; Cross 1967). Males actively court females by repeatedly rushing out to them and rapidly returning to the nest, while producing a series of gruntlike sounds (Gerald 1971). Other courtship, spawning, and nest-guarding behaviors appear typical for the genus (e.g., male aggressive displays, rim circling, egg fanning), but few detailed observations are available (Barney and Anson 1923; Miller 1963). Fecundity increases with female size, but it is unclear if available egg counts were based on total or mature ova in females (Barney and Anson 1923; Becker 1983). The relationship between fecundity (Y) and total length (X) is described by the linear function, $\log_{10} Y = -2.2596 + 2.9785 \log_{10} X$ (data from Barney and Anson 1923, $n = 28$, $R^2 = 0.80$, four likely partially spent females deleted). At 68 mm TL, a female can potentially produce 1580 eggs in a single batch (range: 138 eggs at 30 mm TL to 5776 eggs at 105 mm TL). The nearly transparent, amber to colorless, fertilized eggs are about 0.5 to 1.0 mm in diameter and hatch in about 5 days at 18.0 to 21.0°C (Barney and Anson 1923; Cross 1967; Becker 1983). Yolk-sac larvae and larvae (ages unstated) are 5.3 and 7.0 mm TL, respectively (Tin 1982). A reported hatching size of 10 mm TL (Barney and Anson 1923) seems much too large and needs verification.

Nest associates: Red shiner, *C. lutrensis* (Pflieger 1997) and redfin shiner, *L. umbratilis* (Snelson and Pflieger 1975; Trautman 1981).

Freshwater mussel host: Confirmed host to *A. ligamentina*, *E. complanata*, *L. complanata*, *L. recta*, and *P. grandis* (Young 1911; Arey 1932). Putative host to *L. compressa* and *T. parvus* (unpublished sources in OSUDM 2006).

Conservation status: The orangespotted sunfish is secure throughout much of its native range (e.g., Warren *et al.* 2000), but peripheral populations in Michigan, West Virginia, and southwestern Ontario are considered imperiled (NatureServe 2006).

Similar species: Other *Lepomis* with orange spots on the side have dark (blue or olive brown) sides and lack the wide white edge on the ear flap, the elongated sensory pores on the preopercle, and the enlarged sensory pores on top of the head (Page and Burr 1991).

Systematic notes: *Lepomis humilis* forms a sister pair with *L. macrochirus* (Near *et al.* 2004, 2005). This sister pair represents the second smallest and the largest species, respectively, in the genus and interestingly, display near complete overlap in their geographic ranges (Page and Burr 1991; Near *et al.* 2004). Comparative studies of variation across the range of *L. humilis* are lacking.

Importance to humans: The orangespotted sunfish does not reach a size of interest to most anglers. The species is reportedly a good bioassay animal and aquarium fish (Becker 1983; Schleser 1998), and ecologically, is suggested as a natural biological control for mosquitoes (Barney and Anson 1923).

13.8.6 Lepomis macrochirus *Rafinesque*

13.8.6.1 Bluegill

Characteristics: See generic account for general characteristics. Deep, compressed body, depth 0.43 to 0.56 of SL. Mouth small, strongly oblique, supramaxilla absent, upper jaw rarely reaches anterior edge of eye. Large black spot at posterior of soft dorsal fin. Opercular flap moderate to long, flexible, black at margins, lacks distinct pale or light edges. Pectoral fin long and pointed, tip usually reaches past eye when laid forward across cheek. Long, slender gill rakers, 13 to 16, longest about four to five times the greatest width. Lateral line complete. Lateral scales, (38)41 to 46(50); rows above lateral line 7 to 9; rows below lateral line, 14 to 17; cheek scale rows, 4 to 7; caudal peduncle scale rows, 18 to 21; pectoral rays, 12 to 15. Pharyngeal arches moderately wide with thin, sharply pointed teeth. Teeth present or absent on palatine. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Bailey 1938; Keast and Webb 1966; Trautman 1981; Becker 1983; Mabee 1993; Jenkins and Burkhead 1994; Boschung and Mayden 2004).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, ranging from 18 to 122 mm TL (median 51 mm TL) (Carlander 1977). Interestingly, mean size by fall of age-0 bluegill in lakes is the same across a broad range of latitudes (ca. 55 mm TL), suggesting that northern bluegill grow as rapidly in the first summer as southern bluegill (Garvey *et al.* 2003). Local factors, such as abundance of specific prey types (cladocerans versus invertebrates), proportion of littoral habitat, and exploitation can differentially affect growth in small (ca. 50 mm TL) and large bluegills (Shoup *et al.* 2007). Large individuals can exceed 200 mm TL, 200 g, and attain age 6+ to 7+, although individuals in northern populations tend to live longer than their faster growing southern counterparts (maximum about 410 mm TL, 567 g, and age 11+) (Carlander 1977; Page and Burr 1991). World angling record, 2.15 kg, Alabama (IGFA 2006). Parental males grow faster than females and show subtle, but detectable differences in body shape (deeper bodied, longer paired fins) (Ehlinger 1991). Cuckolder, nest-parasitic males grow slower and mature earlier than parental males (Dominey 1980; Gross 1982; Drake *et al.* 1997; Ehlinger 1997; Ehlinger *et al.* 1997).

Coloration: Ear flap, short to moderately long, black to margin. Large black spot at rear of second dorsal fin. Dark bars (chainlike in young and absent in turbid water) or plain sides on body. Adult with blue sheen overall and two blue streaks from chin to edge of gill cover. Olive back and side with yellow and green flecks; paler on belly to brassy yellow on breast; clear to dusky fins. Breeding male with blue, blue-olive, or blue-green head and back; red-orange breast; black pelvic fins (Page and Burr 1991; Jenkins and Burkhead 1994).

Native range: The bluegill is native to the St. Lawrence-Great Lakes system and Mississippi River Basin from Quebec and New York to Minnesota and south to the Gulf of Mexico and in Atlantic and Gulf Slope drainages from the Cape Fear River, Virginia, to the Rio Grande River, Texas and Mexico (Page and Burr 1991; Miller 2005). The species has been widely introduced and is now established and often exceedingly abundant in suitably warm waters of most of North America (Fuller *et al.* 1999; Moyle 2002; Miller 2005) and other continents (e.g., South Africa, Korea, Japan), where because of stunting and competition with native fishes, the species is often considered a pest (De Moor and Bruton 1988; Jang *et al.* 2002; Kawamura *et al.* 2006). Nonnative bluegills are implicated in the decline of the native Sacramento perch in California and other native fishes in the western United States (Marchetti 1999; Moyle 2002).

Habitat: The bluegill inhabits all types of warmwater lacustrine habitats (e.g., oligohaline estuaries, swamps, lakes, ponds, reservoirs, canals) as well as pools of creeks and small to large rivers. In lacustrine environments, whether natural or man made, the bluegill is often the most abundant centrarchid (Desselle *et al.* 1978; Becker 1983; Page and Burr 1991; Peterson and Ross 1991; Jenkins and Burkhead 1994). The species is among the most tolerant *Lepomis* to adverse conditions of low DO (<1.0 ppm) and high temperatures (average critical thermal maxima 40.4–41.4°C, acclimated at 35°C) (Moss and Scott 1961; Matthews 1987; Smale and Rabeni 1995a,b; Beitinger *et al.* 2000; Miranda *et al.* 2000; Killgore and Hoover 2001). However, RNA–DNA ratios indicate bluegill from hypoxic habitats (1.22–3.04 mg/l DO, always <2 mg/l at night) show reduced growth relative to individuals from normoxic habitats (>3.2 mg/l at night) (Aday *et al.* 2000). Bluegill can survive winter conditions of <1°C and <2 mg/l DO (Magnuson and Karlen 1970; Petrosky and Magnuson 1973; Knights *et al.* 1995), but winter anoxia, often associated with iceover of shallow lakes, limits their distribution in northern lakes (Tonn and Magnuson 1982; Rahel 1984). Bluegill indigenous to fresh or brackish waters showed no preference in salinity over a range of 0 to 10 ppt (Peterson *et al.* 1993). Coastal juvenile bluegill showed no influence on growth or osmoregulatory characteristics (e.g., hematocrit activity) at 10 ppt salinities and fed diets containing up to 4% NaCl (Musselman *et al.* 1995).

Home activity area of bluegills in streams generally extends about 50 to 500 linear meters, and marked individuals are often recaptured in the same stream section throughout the summer or even over multiple seasons or years (Gunning and Shoop 1963; Whitehurst 1981; Gatz and Adams 1994). Although observed in few individuals, bluegills ranged as far as 17 linear km in Tennessee streams. About 20% of successive recaptures were ≥250 m apart over 4 years (Gatz and Adams 1994), and in a North Carolina swamp stream bluegills moved 3.4 km in 33 days (Whitehurst 1981). Home range of radio-tagged bluegill (>160 mm TL) over summer and early fall in an Illinois lake ranged from 0.15 to 0.72 ha (occupied from 12–34 days) with core use areas of 0.11 to 0.60 ha (Fish and Savitz 1983). Large, radio-tagged bluegill (>200 mm TL) tracked from April to September in a shallow Great Plains lake showed no difference in diel activity patterns or habitat use and showed low site fidelity, except during spawning (Paukert and Willis 2002; Paukert *et al.* 2004). Home areas ranged from 0.13 to 172 ha (core areas of 0.01 to 27.2 ha); individuals moved up to 1.1 km/h, but most rates of movement ranged from 30 to 100 m/h. Bluegills (40 to 125 mm TL) shifted from using the mid-depth zone (1.5–6.0 m) in summer to wintering in the shallow (<1.5 m) vegetated littoral zones of a Florida lake (Butler 1989), may move onshore after sunset and offshore after sunrise (Baumann and Kitchell 1974; Helfman 1981), and may emigrate in fall to avoid extreme winter conditions (Knights *et al.* 1995; Parsons and Reed 2005).

Food: The bluegill is a generalist, travel-and-pause predator that can routinely exploit zooplankton in pelagic habitats and larger vegetation-dwelling invertebrates in littoral habitats (Werner *et al.* 1981, 1983; Ehlinger and Wilson 1988; Schramm

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and Jirka 1989; Dewey *et al.* 1997). The adult diet consists of an array of invertebrates including amphipods, cladocerans, larval dipterans, mayflies, and odonates, and terrestrial insects (e.g., McCormick 1940; Chable 1947; Seaburg and Moyle 1964; Applegate *et al.* 1967; Etnier 1971; Sadzikowski and Wallace 1976; Werner 1977; Schramm and Jirka 1989; Dewey *et al.* 1997; VanderKooy *et al.* 2000). Notably, bluegill shift from pelagic zooplanktivory to littoral invertivory at small sizes (12–15 mm SL), and then can shift back to zooplanktivory after a period of growth (>80 mm SL) (Werner 1969; Werner and Hall 1988; Rettig 1998). Surprisingly for a primarily diurnal feeder, laboratory-measured activity in bluegill decreased shortly after dawn, peaked about 1.5 hours after darkness, and remained above daylight levels throughout most of the night (Langley *et al.* 1993; see also Reynolds and Casterlin 1976a; Shoup *et al.* 2003). Diet studies indicate that nighttime feeding can be minimal with peak feeding often occurring after sunrise and at dusk (Sarker 1977; Keast and Fox 1992), but foraging in summer can be nearly continuous over a 24-hour period (Seaburg and Moyle 1964; Keast and Welsh 1968; Sarker 1977; Dewey *et al.* 1997). Peak feeding times are size mediated, occurring latter in the day for smaller (<95 mm) than larger individuals (105–135 mm TL) (Baumann and Kitchell 1974).

The bluegill is an effective, adaptive predator. The species uses a highly stereotyped travel-and-pause foraging tactic, which is combined with a generalist but plastic morphology and an elaborate behavioral flexibility. These traits allow bluegills to switch foraging habitats, quickly learn new foraging behaviors (e.g., increased pause duration, faster pursuit), and successfully exploit new prey in response to changes in prey abundance, intraspecific and interspecific competition, or predation risk (e.g., Werner and Hall 1974, 1977, 1979, 1988; Mittelbach 1981, 1984b; Gotceitas and Colgan 1987, 1988; Ehlinger 1989, 1990; Colgan *et al.* 1981; Gotceitas 1990a,b; Wildhaber and Crowder 1991; Dugatkin and Wilson 1992; Mittelbach and Osenberg 1993; Rettig and Mittelbach 2002; Shoup *et al.* 2003). Intense, often selective, predation by bluegills can directly affect the size, abundance, and composition of zooplankton, which indirectly alters the density and composition of phytoplankton communities (Vanni 1986; Hambright *et al.* 1986; Mittelbach and Osenberg 1993). Similarly, bluegill predation on macroinvertebrates includes reductions in the biomass, abundance, and size of invertebrates and is often influenced by complex interspecific interactions with other centrarchids and size-mediated interactions with conspecifics (Crowder and Cooper 1982; Morin 1984a,b; Mittelbach 1988; McPeek 1990; McPeek *et al.* 2001; Rettig and Mittelbach 2002). The presence of the bluegill also can have dramatic effects on predator avoidance and other behaviors of amphibians (Jackson and Semlitsch 1993; Werner and McPeek 1994).

In a mutualistic feeding role, bluegills serve as facultative cleaners by picking off ectoparasites, loose scales, and necrotic tissue from a host (i.e. other bluegill, *Micropterus* spp., striped mullet, *Mugil cephalus*, manatees, and perhaps large ictalurids) (Spall 1970; Sulak 1975; Powell 1984; Loftus and Kushlan 1987; Moyle 2002). Multiple observations tend to occur in the same locations, suggesting that bluegill establish permanent cleaning stations as documented in marine fishes. In the Everglades, groups of bluegills follow alligators through the water and trail closely behind lake chubsuckers (*Erimyzon sucetta*) as they forage along the bottom, presumably feeding on prey disturbed by these animals (Loftus and Kushlan 1987). Bluegills also join similar-sized Florida bass and together they group hunt for small fishes in clumps of vegetation (Annett 1998).

The bluegill is well equipped visually to detect small or mobile prey (Hairston *et al.* 1982; Williamson and Keast 1988). In ample light (>10^{-6} W/cm^2), bluegill can detect prey items 0.3 to 0.7% brighter than the visual background (Hawryshyn *et al.* 1988) with greatest detection ability in a forward-projecting pie-shaped wedge in the horizontal plane of the fish (Walton *et al.* 1994). Visual acuity increases by about 50% as bluegill increase in size from 35 to 60 mm SL (Hairston *et al.* 1982), but the rate of increase in acuity diminishes in fish >60 mm SL (Breck and Gitter 1983; Li *et al.* 1985; Walton *et al.* 1992, 1994, 1997). Increased acuity with growth confers visual access to increasing volumes of search space, and the ability to see increasing numbers of prey (Vinyard and O'Brien 1976; Gardner 1981; Hairston *et al.* 1982; Breck and Gitter 1983; Walton *et al.* 1994). For example, estimated visual and search volumes of bluegill viewing a 2-mm zooplankter increase by nearly three orders of magnitude from about 0.1 l at 8 mm SL to 90 l at 50 mm SL (Walton *et al.* 1994); the estimated visual volume more than doubles from 200 to >400 l for a 3-mm zooplankton target as fish size increases from 60 to 160 mm TL (Breck and Gitter 1983).

Decreased light or increased turbidity dramatically influences feeding (and predator detection) in bluegills. Below illuminance of 10 lux, reactive distance to small zooplankton prey (1–3 mm) decreases at successively lower light levels, such that regardless of prey size, reactive distances at low light (0.7 lux) are reduced to 3 to 4 cm (Vinyard and O'Brien 1976). Similarly, reactive distances to a larger visual target (largemouth bass, 290 mm TL) decrease from about 175 cm at 3340 lux to <50 cm at 1.5 lux (Howick and O'Brien 1983). In ample light and clear water, bluegills (and perhaps other *Lepomis*) can recognize an object as prey (or predator) at greater distances than do largemouth bass (Howick and

O'Brien 1983; Miner and Stein 1996). As light decreases to twilight levels, bluegills >40 mm TL lose their reactive distance advantage over largemouth bass such that only smaller bluegills can locate largemouth bass first under low light intensities (Howick and O'Brien 1983). Under constant light, detection ability of bluegills decreases as a log or exponential function of increasing turbidity for small zooplankton prey and large predators, respectively, but interactions of light and turbidity with feeding success are complex (Vinyard and O'Brien 1976; Gardner 1981; Miner and Stein 1993).

Bluegills show subtle differences in intrapopulation body morphology. In lakes, differences in body morphology are associated with foraging and predator avoidance in littoral or open-water habitats. Bluegills from littoral habitats have deeper bodies, longer paired fins, and more posteriorly attached pectoral fins than those in open water (Ehlinger and Wilson 1988; Chipps *et al.* 2004). The open-water form also has a modified foraging behavior (decreased pause duration) (Ehlinger 1990). Relative to the littoral form, the open-water form shows increased predator avoidance behaviors (i.e. schooling defense), but in cover, predators take three times longer to capture the littoral form than the open-water form (Chipps *et al.* 2004).

The feeding behavior and ecology of the bluegill are among the most extensively documented of any North American freshwater fish. Only a cursory review of this important body of literature is possible here. The interested reader is encouraged to consult papers cited herein and others, including, for example, Werner (1974), O'Brien *et al.* (1976), Werner *et al.* (1977), Bulow *et al.* (1978, 1981), Keast (1978, 1985a,b,c), Vinyard (1980), Savino and Stein (1982, 1989a,b), Mittelbach (1983), Brown and Colgan (1986), Butler (1988), Johnson *et al.* (1988), Osenberg *et al.* (1988, 1992), DeVries *et al.* (1989), DeVries (1990), Gotceitas and Colgan (1990), Savino *et al.* (1992), Schaefer *et al.* (1999), Harrel and Dibble (2001), Wildhaber (2001), Yonekura *et al.* (2002), McCauley (2005), and Spotte (2007).

Reproduction: Maturity varies with sex, male alternative life history strategy, intraspecific competition, and latitude and can be reached at age 0+ (first summer of life) to age 6+ at a minimum size of about 73 to 172 mm TL and 15 to 82 g (Morgan 1951a,b; Carlander 1977; Gross 1982; Ehlinger *et al.* 1997). Time of maturation between the sexes can vary greatly even among lakes at similar latitudes, and cuckolder males within populations mature at an earlier age and size than parental males (Gross 1982; Ehlinger 1991; Drake *et al.* 1997). In ponds, small male bluegill are inhibited from maturing in the presence of large males, regardless of food availability, and laboratory evidence suggests that large parental males produce a pheromone that inhibits maturation in small males (Aday *et al.* 2003, 2006). Increased photoperiod (12–16 hours) and rising temperature in the spring controls prespawning gonadal development (Banner and Hyatt 1975; Mischke and Morris 1997). Spawning is protracted (mid-May–mid-August) (Morgan 1951a,b; Avila 1976; Gross 1982), particularly in southern Florida where reproduction extends from late February or early March through September with pauses in activity for up to 3 weeks (Clugston 1966). Nest building and spawning begin as water temperatures increase to 20°C, and spawning continues up to about 31°C (Morgan 1951a,b; Banner and Hyatt 1975); males in stunted populations initiate nest building several weeks later than males in nonstunted populations (Jennings *et al.* 1997; Aday *et al.* 2002). Males excavate saucer-shaped depressional nests by caudal sweeping (Morgan 1951a,b; Miller 1963; Avila 1976; Gross 1982), which alters substrate composition by removing small particles (<2 mm) to expose hard substrates or larger coarse gravel and pebble substrates (>8 mm diameter). Coarse nest substrates are associated with increased survival of fry (Bain and Helfrich 1983). Nests are placed in open, shallow areas (10–190 cm water depth, rarely >3.0 m), usually away from cover (Carbine 1939; Morgan 1951b; Clugston 1966; Avila 1976; Ehlinger 1999). Median depths of nest placement suggest that males may be able to sense ultraviolet radiation, and place nests deeper in high underwater ultraviolet radiation environments, which can damage developing embryos (Gutiérrez-Rodriguez and Williamson 1999). Bluegills nest in crowded colonies that can contain hundreds of abutting nests, and these colonies often contain other nesting *Lepomis* spp. (Childers 1967; Avila 1976; Gross 1982; Cargnelli and Gross 1996). In colonies, spawning events (five to eight per spawning season) are synchronous, occurring at intervals of 10 to 14 days; males may nest one or more times in a season (Neff and Gross 2001), and females presumably participate in multiple spawning events. Colony formation is a definite social aggregation because it occurs in the absence of habitat limitation (Gross and MacMillan 1981). Colonial nesting affords decreased predation on offspring through cumulative nest defense (e.g., predator mobbing, Dominey 1981, 1983; Gross and MacMillan 1981) and decreased fungal infection of eggs (Côté and Gross 1993), both of primary benefit to parental males located centrally rather than peripherally in a colony (Neff *et al.* 2004). Nevertheless, a consistent but small proportion of bluegill males within a population nest solitarily (Avila 1976; Ehlinger 1999; Neff *et al.* 2004). These males are in better condition than colonial males but possess smaller ear tabs than centrally located males. Solitary nesters experience decreased cuckoldry relative to colonial males and show a nesting success equivalent to centrally located males, but higher success than peripherally located males (Gross 1991; Neff *et al.* 2004), suggesting that females do not discriminate between solitary and central males. Guardian males produce gruntlike sounds as part of courtship of females and aggression toward conspecific and other *Lepomis* males (Gerald 1971; Ballantyne and Colgan 1978a,b,c). Other male courtship, spawning, and nest defense behaviors are well documented and typical for the genus (e.g., aggressive displays, courtship circles, rim circling, paired nest circling, egg fanning) (e.g., Morgan 1951b; Miller 1963; Avila 1976; Colgan *et al.* 1979; Gross 1982; Clarke *et al.* 1984; Coleman *et al.* 1985; Coleman and Fischer 1991; Stoltz and Neff 2006). On the female entering a nest, a 15- to 90-minute spawning bout ensues in which the female releases small groups of eggs in a series of dips into the nest; females may dip hundreds of times during a bout (Avila 1976; Gross 1991; Fu *et al.* 2001). Males control the rate of dips by biting the female (Gross 1991). Males mate sequentially with several females (rarely with two females simultaneously) during synchronous spawning events (usually <1 day), resulting in accumulations of 4600 to 61,000 eggs/nest (Carbine 1939; Avila 1976; Gross 1982, 1991; Cargnelli and Gross 1996). Although discouraged by the male, spawning females frequently succeed in eating a portion of their predecessor's eggs (Gross and MacMillan 1981). Mature ovarian eggs average from 1.09 to 1.30 mm diameter and fertilized, water-hardened eggs 1.2 to 1.4 mm in diameter (Morgan 1951b; Meyer 1970; Merriner 1971a; Hardy 1978; Gross and Sargent 1985; Cooke *et al.* 2006). Fecundity increases with female size. The relationship between potential batch fecundity (Y) and total length (X) is described by the linear function, $\log_{10} Y = -3.39794 + 3.4512 \log_{10} X$ (mean numbers of 18 length class means for 91 females, $R^2 = 0.83$, data from Morgan 1951b). At 165 mm TL, a female can potentially produce 17,990 mature eggs in a single batch (range: 5021 eggs at 114 mm TL to 45,575 eggs at 216 mm TL, respectively). The adhesive, fertilized eggs hatch in 2.1 days at 23.8°C (1.3 days at 27.1°C) (Childers 1967). Newly hatched larvae are 2.2 to 3.7 mm TL, and depending on temperature, larvae are free swimming about 3 to 4 days after hatching at a size of 4.30 to 5.70 mm TL (Childers 1967; Meyer 1970; Anjard 1974; Taubert 1977). Fry size at dispersal is correlated negatively with spawn date and hence, varies within a single population and spawning season (e.g., 4.3–6.7 mm) (Cargnelli and Gross 1996). Males guard and vigorously defend the nest, eggs, and larvae for about 7 days, but earlier abandonment of nests is common (see subsequent, Neff and Gross 2001; Neff 2003ab). Relatively large decreases in body weight (about 11%) and declines in lipid energy reserves occur in guardian males during the parental care period when feeding is reduced or curtailed (Avila 1976; Coleman *et al.* 1985; Coleman and Fischer 1991). During nest guarding, males with large broods sustain egg fanning for longer periods and more intensively defend the fry than males with small broods (Coleman *et al.* 1985; Coleman and Fischer 1991).

Alternative mating strategies are highly developed in male bluegills. Both sneaker and satellite male morphs are only known in a single well-studied population of bluegill in Lake Opinicon, Ontario (Gross 1982), and presumable satellite equivalents (female mimics) were described from a New York lake (Dominey 1980). However, sneaker male morphs occur widely in populations of bluegill (Ehlinger 1997; Drake *et al.* 1997). Parasitic males can outnumber parental males 6:1, are excellent sperm competitors (80% fertilization rate), and are preferred by females, which release up to three times more eggs with the cuckolder than if alone with the guardian male (Fu *et al.* 2001; Neff 2001; Burness *et al.* 2004). Cuckolders reduce guardian male paternity in colonies by as much as 40% (average 23.1%), but their proportion of successfully fertilized eggs, relative to guardian males, decreases in colonies as their frequency reaches and exceeds numbers optimizing their fertilization success (Gross 1991; Philipp and Gross 1994). In an evolutionary response to intense cuckolding, guardian male bluegill apparently assess perceived paternity during the egg guarding stage through visual cues (presence of sneakers), and if perceived sneaker paternity is high, the guardian male decreases egg care or even abandons and cannibalizes eggs shortly after spawning (Neff and Gross 2001; Neff 2003a,b). Later in the brood-guarding phase, the guardian male apparently assesses actual paternity (combined sneaker and satellite male fertilizations) through olfactory cues released by hatchlings and again adjusts his level of parental care, often resulting in a second wave of filial cannibalism and brood abandonment if actual cuckolding is high (Neff and Gross 2001; Neff and Sherman 2003, 2005; Neff 2003a,b). Given that guardian males can distinguish their fry from unrelated offspring (Neff and Sherman 2003), they may be able to selectively forage on unrelated fry while continuing to provide care to their fry (Neff 2003b).

Nest associates: Golden shiner, *N. crysoleucas* (DeMont 1982).

Freshwater mussel host: Confirmed host to *Amblema neislerii*, *A. plicata*, *Elliptio buckleyi*, *Elliptio fisheriana*, *Elliptio icterina*, *Fusconaia masoni*, *G. rotundata*, *L. bracteata*, *L. cardium*, *L. higginsii*, *L. siliquoidea*, *Lampsilis straminea claibornensis*, *M. nervosa*, *P. grandis*, *S. undulatus*, *U. imbecillis*, *Villosa lienosa*, and *Villosa villosa* (Howard 1914, 1922; Coker *et al.* 1921; Penn 1939; Trdan and Hoeh 1982; Parker *et al.* 1984; Waller and Holland-Bartels 1988; Hove *et al.* 1997; Howells 1997; Keller and Ruessler 1997; O'Dee and Watters 2000; O'Brien and Williams 2002; Rogers and Dimock 2003). Putative host to *Anodontoides ferussacianus*, *E. complanata*, *E. hopetonensis*, *L. reeveiana*, *Lampsilis satura*, *L. teres*, *L. compressa*, *L. costata*, *L. recta*, *Pleurobema sintoxia*, and *T. parvus* (unpublished sources in OSUDM 2006).

Conservation status: The bluegill is secure throughout its range (Warren *et al.* 2000; NatureServe 2006). The morphological and genetic variation across the entire native range of this fish is poorly known, despite its considerable importance in fisheries management and compelling evidence of geographic differentiation (e.g., Avise and Smith 1974, 1977; Felley and Smith 1978; Felley 1980). Further, the species is still widely stocked with little or no concern for brood stock origin or effects on genetic integrity of native bluegill stocks or other native fishes.

Similar species: The redear sunfish lacks a large, dark spot in the second dorsal fin and has a red edge on the ear flap and short gill rakers (Page and Burr 1991).

Systematic notes: *Lepomis macrochirus* forms a sister pair with *L. humilis* (Near *et al.* 2004, 2005). The bluegill is polytypic. Three subspecies are generally recognized, but the geographic ranges and diagnostics of all forms are not well defined (Hubbs and Allen 1943; Hubbs and Lagler 1958; Avise and Smith 1974, 1977; Felley 1980; Page and Burr 1991). Populations on the Florida peninsula, colloquially known as coppernose bluegill (Ross 2001), differ morphologically (broader lateral bars and red fins) and genetically from the nominate subspecies *L. m. macrochirus*. Intergradation between the two occurs from the Ochlockonee River (eastern Gulf Coast drainage) north along the Atlantic Slope drainages to South Carolina (Avise and Smith 1974, 1977; Felley 1980). The name applied to the Florida form is *L. m. mystacalis*. The name *L. m. purpurescens*, although traditionally applied to the Florida form (Hubbs and Allen 1943), is associated with a type locality in North Carolina and is a synonym of *L. m. macrochirus* (Gilbert 1998). The name *L. m. speciosus* is applied to populations in Texas and Mexico (Hubbs and Lagler 1958; Page and Burr 1991). *Lepomis m. macrochirus* occupies the remainder of the native range. A color variant, known locally as the "handpaint brim," occurs in the Apalachicola River valley in Florida (Felley and Smith 1978).

Importance to humans: Because of their fearlessness, inquisitiveness, color, and activity, bluegill are seen, recognized, and enjoyed by more of the fishing and nonfishing public than probably any other species of freshwater fish (Scott and Crossman 1973). To many, nearly any *Lepomis* encountered is dubbed a "bluegill." The bluegill probably accounts for more individual catches than any other gamefish in North America (Etnier and Starnes 1993), and for decades, the largemouth bass and bluegill have formed the core predator–prey species combination in sport fisheries management of warmwater ponds, lakes, and reservoirs (Bennett 1948; Swingle 1949). Historically, the species formed part of the commercial "sunfish" catch in natural lakes such as the Great Lakes and Reelfoot Lake, Tennessee (Schoffman 1945; Scott and Crossman 1973). The bluegill is a scrappy fighter that readily takes an array of small artificial flies, spinners, or natural baits (e.g., crickets, earthworms, or even dough balls). They attack the bait in groups, bite hard, and fight hard, creating a challenging catch for the experienced flyfisher, the cane pole enthusiast, or as a child's first catch. The species is an excellent-tasting table fish, the flesh being white and slightly sweet (Scott and Crossman 1973; Etnier and Starnes 1993; Ross 2001).

13.8.7 Lepomis marginatus *(Holbrook)*

13.8.7.1 Dollar sunfish

Characteristics: See generic account for general characteristics. Deep, compressed body, depth 0.5 of SL. Mouth small, terminal, oblique, supramaxilla small (>3 times and ≤4 times length of maxilla), upper jaw not extending posteriorly past anterior edge of eye. Wavy blue lines on cheek and opercle of adult. Opercular flap long, flexible, usually slanted upward, black in center, but often flecked with silver-green blotches, edged with white or pale green, lower and upper borders of equal width. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Short, thick, knoblike gill rakers, 9 to 10, longest about equal (adults) to two (young) times greatest width. Lateral line complete. Lateral scales, (34)37 to 40(44); rows above lateral line, 5 to 6; rows below lateral line, (12)13 to 14(15); cheek scale rows, 3 to

4(6); caudal peduncle scale rows, (18)19(21); pectoral rays, (11)12 to 13. Pharyngeal arches narrow with sharply pointed teeth. No teeth on endopterygoid, ectopterygoid, palatine, or glossohyal (tongue) bones (Bailey 1938; Barlow 1980; Etnier and Starnes 1993; Mabee 1993).

Size and age: Average 57 mm TL at age 1. Large individuals measure 95 mm TL and attain age 4+ or more (maximum 127 mm TL, age 6+) (Lee and Burr 1985; Page and Burr 1991; Winkelman 1993; Etnier and Starnes 1993). Mean male length is greater than that of same-age females (Winkelman 1993).

Coloration: Similar to longear and northern longear sunfish but lateral line is colored brick red. Breeding male bright red, marbled and spotted with blue-green, and often with large silver-green flecks accenting dark center of ear flap (Page and Burr 1991).

Native range: The dollar sunfish occurs in Atlantic and Gulf Slope drainages (mostly below the Fall Line) from the Tar River, North Carolina, to the Brazos River, Texas, and the Mississippi Embayment from western Kentucky and eastern Arkansas, south to the Gulf of Mexico (Page and Burr 1991). The species is most common in the southeastern United States, becoming increasingly uncommon in the western part of its range (Robison and Buchanan 1984; Loftus and Kushlan 1987; Page and Burr 1991; Wolfe and Prophet 1993; Snodgrass *et al.* 1996; Pflieger 1997; Marcy *et al.* 2005).

Habitat: The dollar sunfish inhabits sand- and mud-bottomed wetlands, oxbows, or other swamplike habitats as well as the brushy pools of lowland creeks and small to medium rivers (Page and Burr 1991). The species is most often associated with small, low-gradient headwater streams, side channels of streams, beaver ponds, and periodically isolated floodplain wetlands (Meffe and Sheldon 1988; Etnier and Starnes 1993; Paller 1994; Snodgrass *et al.* 1996; Snodgrass and Meffe 1998). The dollar sunfish is one of the most abundant, but smallest, species of *Lepomis* in the Florida Everglades, where it is almost always associated with dense vegetation and reaches peak numbers in sawgrass marshes and marsh prairies (Loftus and Kushlan 1987). Removal of aquatic vegetation by grass carp (*Ctenopharyngodon idella*) in a eutrophic Texas reservoir resulted in almost complete elimination of the dollar sunfish (Bettoli *et al.* 1993).

Food: The dollar sunfish is an opportunistic invertivore. The primary dietary items are midge larvae, microcrustaceans, terrestrial insects, snails, and oligochaetes (Chable 1947; McLane 1955; Lee and Burr 1985; Sheldon and Meffe 1993). Large amounts of detritus, filamentous algae, and terrestrial insects in stomachs indicate bottom-to-surface feeding (Etnier and Starnes 1993). Dollar sunfish leave stream channels to presumably forage on floodplains inundated during short-term spring flood events (Ross and Baker 1983).

Reproduction: Maturity is reached at age 1+ at a minimum size of about 60 mm SL (Lee and Burr 1985). Spawning is protracted, occurring from April to September in Florida (McLane 1955) and May to July or August in North and South Carolina (Lee and Burr 1985; Winkelman 1996; Marcy *et al.* 2005). In the Carolinas, peak spawning occurs from mid-May to late June or July (Lee and Burr 1985; Winkelman 1996). Males use caudal sweeping to remove silt and organic debris from a variety of substrates to form small, shallow depressions (30 cm diameter), usually <2 m from shore at depths of 10 to 50 cm (Winkelman 1996). Nests may be solitary (>1 m apart) or in dense colonies of 20 or more closely spaced nests (Lee and Burr 1985; Mackiewicz *et al.* 2002; Marcy *et al.* 2005). The agonistic courtship and other reproductive behaviors of guardian males are apparently typical of other *Lepomis*, but observations are not extensive or detailed (Lee and Burr 1985; Winkelman 1996). Genetic analyses indicate that males spawn on average with 2.5 females (range 1–7) in a given spawning event and that about 95% of offspring in nests are sired by the guardian male. One nest takeover and one instance of cuckoldry by a neighboring nesting male were detected in 23 nests examined, but no evidence of nest parasitism by nonparental males was detected by paternity analysis or gonadal examination (Mackiewicz *et al.* 2002). The entire cycle of egg and larval guarding is about 6 days (Winkelman 1996). Colonial spawning in a North Carolina pond was asynchronous, continuing long after eggs were present in the nest and resulting in some males simultaneously guarding eggs and two previous broods. Nests produced about 150 to 200 larvae, and larvae reached 10 mm TL after 1 month (Lee and Burr 1985). Depending on reproductive stage of the nest, guardian males differentially adjusted retreat times from the nest in response to avian predator models (aerial and wading). Males returned to the nest sooner when offspring were present than when nests were empty, indicating awareness of a threat to their survival but a willingness to accept greater risk to protect their current brood (Winkelman 1996).

Nest associates: Bluenose shiner, *Pteronotropis welaka* (Johnston and Knight 1999).

Freshwater mussel host: None known (but see Stern and Felder 1978).

Conservation status: The dollar sunfish is considered secure throughout most of its range, but is regarded within several states, particularly those on the periphery of the range, as vulnerable (Arkansas, Oklahoma, North Carolina) or critically imperiled (Kentucky) (NatureServe 2006). The species was likely much more widespread and abundant historically than it is now in those lowland areas subjected to stream channelization, wetland drainage, and intensive agricultural use (e.g., eastern Arkansas, western Kentucky, western Tennessee) (Robison and Buchanan 1984; Burr and Warren 1986; Etnier and Starnes 1993).

Similar species: Within the range of the dollar sunfish, any longear-like sunfish occurring in nonflowing, low-gradient, or swamplike habitats is likely a dollar sunfish, although longear sunfish and dollar sunfish are taken together, especially in streams draining the eastern Mississippi Embayment (Burr and Warren 1986; Page and Burr 1991; Etnier and Starnes 1993). The longear sunfish usually has 13 to 14 pectoral rays and 5 to 7 cheek scale rows. The northern longear sunfish does not co-occur with the dollar sunfish and has a red spot on the ear flap. The redbreast sunfish lacks blue spots on the sides and has rows of red-brown spots on the upper sides, a longer narrower ear flap that is black to the edge, and usually 14 pectoral rays (Barlow 1980; Page and Burr 1991).

Systematic notes: *Lepomis marginatus* is included in a clade with *L. peltastes* and *L. megalotis* (Near *et al*. 2004, 2005), but relationships among these species are unresolved. Interestingly, nuclear-encoded allozyme frequency data from a limited number of populations indicated that *L. marginatus* is genetically more similar to *L. megalotis breviceps* and *L. m. aquilensis* than to *L. m. megalotis* or *L. peltastes* (Jennings and Philipp 1992a). In contrast, phenetic analysis of 47 morphological and meristic characters indicated that *L. marginatus* (Louisiana and North Carolina samples) is most similar to its allopatric relative *L. peltastes* (Barlow 1980). Comparative studies across the range of *L. marginatus* are lacking, but polytypy is indicated from phenetic analyses of morphological characters (Barlow 1980), differences in opercular tab pigmentation (Page and Burr 1991; Etnier and Starnes 1993), and differences in breeding color patterns described by hobbyists (Wolff 2005).

Importance to humans: Although not reaching a size of interest to panfish anglers, the dollar sunfish, where it occurs commonly, is an ecological indicator of relatively undisturbed lowland and wetland ecosystems.

13.8.8 Lepomis megalotis *(Rafinesque)*

13.8.8.1 Longear sunfish

Characteristics: See generic account for general characteristics. Deep, compressed body, depth 0.43 to 0.45 of SL. Mouth moderately large, terminal oblique, supramaxilla small (>3 times and ≤4 times length of maxilla), upper jaw reaches posteriorly from beyond anterior of eye to just about center of eye. Wavy blue lines on cheek and opercle of adult. Opercular flap long, flexible (flared at end in large individuals), usually oriented horizontally (adult) or slanting upward (young), black in center with white edges, lower and upper edges of equal width, bordered above and below by blue line. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Short, thick, knoblike gill rakers, 12 to 14, longest about equal (adults) to twice (young) greatest width. Lateral line complete. Lateral scales, (31)36 to 48(50); rows above lateral line, (5)6 to 8(9); rows below lateral line, (11)14 to 15(19); cheek scale rows, (4)5 to 6(8); caudal peduncle scale rows, (16)18 to 23(25); pectoral rays, (11)13 to 14(15). Pharyngeal arches narrow with sharply pointed teeth. No teeth on endopterygoid, ectopterygoid, palatine, or glossohyal (tongue) bones (Bailey 1938; Barlow 1980; Trautman 1981; Mabee 1993; Boschung and Mayden 2004).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, ranging from 21 to 114 mm TL (median 47 mm TL). Individuals rarely exceed 155 mm TL or 100 g, and few live beyond age 6+ (maximum about 240 mm TL, 227 g, and age 9+) (Bacon 1968; Carlander 1977; Page and Burr 1991; Etnier and Starnes 1993; Jennings and Philipp 1992c). World angling record, 0.79 kg, New Mexico (IGFA 2006). Parental males grow faster than females (Carlander 1977; Jennings and Philipp 1992c).

Coloration: Ear flap long, black in adult, edged in white, bordered above and below by blue lines. Numerous, wavy blue lines on sides of snout, cheek, and opercle. Young with olive back and side speckled with yellow flecks, often with chainlike bars on sides, white below. Adult dark red above, bright orange below, marbled and spotted with blue; clear to orange and blue, unspotted fins. Breeding males are among the most brilliantly colored North American fishes, with contrasting bright reddish orange and blue body, red eye, orange to red median fins, and blue-black pelvic fins (Page and Burr 1991). Nape with reddish stripe in upper Arkansas and Missouri River populations, and at least some populations in the upper White River, Missouri, lack the light border on the ear flap (Pflieger 1971; Barlow 1980; Goddard and Mathis 1997).

Native range: The longear sunfish is native to the Mississippi River Basin west of the Appalachian Mountains from Indiana west to eastern Illinois and south to the Gulf of Mexico and to Gulf Slope drainages from the Choctawhatchee River, Florida, west to the Rio Grande, Texas, southern New Mexico, and northeastern Mexico (Page and Burr 1991; Miller 2005). The species is generally common, and often the most abundant *Lepomis* in upland or clear streams throughout its range. The species has expanded its range in recent decades north and westward in the Missouri River, Missouri, as a likely result of clear water conditions imposed on that system by upstream reservoirs (Pflieger 1997). The longear sunfish has been introduced sparingly outside its native range and is established in the upper Ohio River basin (New and Kanawha, above the Falls, rivers), the Atlantic Slope (Potomac River drainage and Maryland Coastal Plain), upper Rio Grande (New Mexico), and perhaps, the Pacific Slope of Mexico (Rio Yaqui) (Fuller *et al.* 1999; Miller 2005).

Habitat: The longear sunfish inhabits rocky and sandy pools of headwaters, creeks, and small to medium rivers (Page and Burr 1991) and can thrive along shorelines of reservoirs (Bacon 1968; Gelwick and Matthews 1990; Bettoli *et al.* 1993; Etnier and Starnes 1993; Pflieger 1997). In some rivers, the longear sunfish can be the most abundant centrarchid (Gunning and Suttkus 1990). The species is tolerant of low DO (e.g., 100% survival at <1 ppm for 3 days) and high water temperatures (critical thermal maxima >34°C) (Matthews 1987; Smale and Rabeni 1995a,b; Beitinger *et al.* 2000). In streams, many individuals use restricted home activity areas (<100 m) over several seasons (or years) and displaced individuals can home over short distances apparently using olfactory cues (Gerking 1953; Gunning 1959, 1965; Gunning and Shoop 1963; Huck and Gunning 1967; Fentress *et al.* 2006). Even so, short (>200 m) interhabitat and long-distance (<15 km) exploratory movements are not uncommon, the species can quickly repopulate drought affected streams or defaunated stream reaches, and large individuals in streams appear to desert home activity areas in fall, presumably to migrate to wintering areas (Funk 1957; Boyer 1969; Berra and Gunning 1972; Matthews 1987; Lonzarich *et al.* 1998, 2000; Warren and Pardew 1998; Smithson and Johnston 1999; Fentress *et al.* 2006). A spring branch along Jacks Fork River, Missouri, serves as a winter thermal refuge for large numbers of longear sunfish. Lowest use of the spring branch occurs from April to October when adjacent river temperatures exceed those of the spring branch (13.5°C) and highest use occurs during cold periods when the spring waters exceed river temperatures. During cold, but not warm, periods, biomass and size of individuals in the spring branch are larger than those of individuals remaining in the river. Mark-recapture results suggest the existence of two populations of longear sunfish, one consisting of permanent spring branch residents and another that migrates to the spring branch during cold periods and back to the river during warm periods (Peterson and Rabeni 1996).

Food: The longear sunfish is an opportunistic invertivore. Adults are principally benthic predators on larval midges, mayflies, and caddisflies but also consume a variety of other aquatic insects and terrestrial invertebrates as well as small fish, fish eggs (e.g., *Micropterus* and *Pomoxis*), isopods, amphipods, crayfishes, and gastropods (Minckley 1963; Applegate *et al.* 1967; Boyer 1969; Cooner and Bayne 1982; Angermeier 1985; Shoup and Hill 1997). Young longear sunfish (<50 TL) transition from an initial diet predominated by microcrustaceans and some aquatic insect larvae to increasing use of aquatic and terrestrial insects (50–100 mm TL). Surface insects can contribute substantially to the diet of the largest longear sunfish (>100 TL) (Applegate *et al.* 1967; Cooner and Bayne 1982; Angermeier 1985), and the species is highly efficient at capturing zooplankton or floating prey in flowing water (up to 18 cm/s; Schaefer *et al.* 1999). Feeding rates are initially high in spring, are relatively stable over much of the summer, and decline in October, a pattern attributed to decreasing availability of aquatic insect prey (Angermeier 1985; Kwak *et al.* 1992). Over a series of diel studies (May to October), feeding peaks occurred near dusk and dawn but some feeding occurred continuously over 24-hour periods (Bowles and Short 1988; Kwak *et al.* 1992). In late winter, stream-dwelling individuals collected well before dawn had apparently electively consumed nocturnally drifting amphipods (Bowles and Short 1988). In a laboratory tank, longear sunfish cleaned external fish parasites from a live, heavily infested flathead catfish, suggesting that, like the bluegill, they may serve in nature as commensal cleaners of other fishes (Spall 1970).

Reproduction: Maturity is reached at age 1+ to 3+ at a minimum size of about 60 mm TL in females and 100 to 140 mm TL for guardian males (Boyer 1969; Carlander 1977; Jennings and Philipp 1992c), but sneaker male phenotypes can mature at age 1+ and 40 to 85 mm TL (Jennings and Philipp 1992c). Spawning is protracted and may include up to six relatively discrete nesting periods occurring from late May to mid-July or August at intervals of about 12 days (Huck and Gunning 1967; Boyer and Vogele 1971; Carlander 1977; Jennings and Philipp 1994). Observations in Missouri reservoirs indicate that spawning temperatures range from 22 to 28°C with nest abandonment occurring if water temperature abruptly decreased below or increased above this range (Witt and Marzolf 1954; Boyer and Vogele 1971), but in a Louisiana stream, nesting occurred at 29 to 31°C (Huck and Gunning 1967). Flood events (and presumably lowered water temperatures) delayed initiation of spawning, resulted in high nest abandonment, and decreased brood survival in an Illinois stream (Jennings and Philipp 1994). Vitellogenesis was suppressed in wild females exposed to unbleached Kraft mill effluents (paper mills) in the Pearl River, Mississippi, and the number of spawning cycles appeared to be lower than in unexposed females. No reproductive suppression effects were detected in males (Fentress *et al.* 2006). Males excavate nests by caudal sweeping. The shallow, roughly circular depressional nests range from about 33 to 89 cm diameter, are 3 to 7 cm deep, and are usually placed in areas free of brush or vegetation over sand or gravel at water depths of 20 to 150 cm (up to 3.4 m in reservoirs, Huck and Gunning 1967; Boyer and Vogele 1971; Mueller 1980). Within a population, nesting males tend to be larger than non-nesting males, even though the smaller non-nesting males are mature. Of males nesting, successful males are on average larger than unsuccessful males, suggesting that females prefer large males (Jennings and Philipp 1992b). If male size is equal, females prefer males with longer ear tabs (Goddard and Mathis 1997). Nests are most often colonial (e.g., 2 to 45 nests, <1 m apart), presumably affording subordinate guardian males more access to females, but solitary nests are not uncommon (Boyer and Vogele 1971; Jennings and Philipp 1992b). In some populations, solitary males tend to be larger than colonial males, and their nesting success is equivalent to that of colonial males (Jennings and Philipp 1992b), but in other populations solitary males tend to be smaller than colonial nesters (Boyer 1969). Spawning events in colonies are asynchronous with spawning females entering nests for 1 or 2 days or even as long as 1 week, resulting in some males simultaneously guarding eggs and larvae (Boyer and Vogele 1971; Jennings and Philipp 1994). Nest-guarding males produce gruntlike sounds as part of courtship (Gerald 1971); other reported courtship, spawning, and brood defense and care behaviors appear typical for the genus (e.g., rim circling, lateral threat displays, paired circling). After spawning, the male may alternate egg fanning with caudal sweeping to mix eggs in the substrate, and both males and females engage in frequent substrate biting during nest defense and before circling, respectively (Witt and Marzolf 1954; Huck and Gunning 1967; Boyer 1969; Boyer and Vogele 1971). During a spawning event, a female spawns with a given male about 20 times for 20 to 29 minutes, depositing 7 to 20 eggs with each dip into the nest; several females may ultimately spawn in a single nest. Females may spawn with one male and then enter another nest to spawn with another male (Boyer and Vogele 1971). Spawning pairs are frequently interrupted by sneaker male morphs, neighboring nesting males, or males of other *Lepomis* spp. attempting to steal fertilizations (Huck and Gunning 1967; Boyer and Vogele 1971; Jennings and Philipp 2002). Although patchily distributed, sneaker male morphs are documented in Illinois stream populations (Jennings and Philipp 1992c, 2002). Observations of two ostensible females spawning simultaneously with a male (Boyer 1969; Boyer and Vogele 1971) suggest that the sneaker tactic may be more widespread than is currently documented. Ovaries of mature females contain several distinct sizes and developmental stages of ova, and the mature ovarian eggs are apparently large for *Lepomis*, averaging 1.55 to 2.00 mm diameter (Boyer 1969; Yeager 1981). Fecundity increases with female size, but relationships are apparently unquantified. Estimates of numbers of spawned ova for three size classes of females in two Missouri reservoirs were 1417 to 3600 eggs (≤100 mm TL), 3440 to 4136 eggs (101–129 mm TL), and 4213 eggs (≥130 mm TL) (Boyer 1969). Most of the adhesive, fertilized eggs in a colony hatch in about a week, but time to hatching may extend for 12 days or more at 25°C (Huck and Gunning 1967; Boyer 1969). Numbers of eggs in 12 nests ranged from 608 to 2756, and numbers of larvae in six successful nests averaged 465 (range 3 to 1132). Larvae at hatching are of 5.0 to 5.2 mm TL, and advanced larvae in a nest ranged from 5.8 to 7.5 mm TL (mean = 6.9 mm TL) (Boyer 1969; Boyer and Vogele 1971; Yeager 1981). Successful males guard and vigorously defend the eggs and larvae for up to 9 days, depending on developmental rate of offspring (Jennings and Philipp 1994). While nest guarding, males feed opportunistically, consuming large numbers of longear sunfish eggs, high volumes of detritus, and nearby aquatic insects (Boyer 1969; Boyer and Vogele 1971). Larval swim-up and dispersal occur at 7.3 to 7.6 mm TL about 6 to 8 days after hatching (22–25°C, presumably) (Huck and Gunning 1967; Boyer and Vogele 1971; Yeager 1981). Larval fin development is apparently more rapid than in most other *Lepomis* (Taber 1969; Yeager 1981). After leaving the nest, fry from several nests initially merge to form large schools in dense cover but later separate into small groups or as single individuals (Boyer and Vogele 1971).

Nest associates: Redfin shiner, *L. umbratilis* (Snelson and Pflieger 1975).

Freshwater mussel host: Confirmed host to *A. suborbiculata, L. siliquoidea, M. nervosa, P. grandis, Strophitus subvexus*, and *V. nebulosa* (Penn 1939; Haag and Warren 1997; Howells 1997; O'Dee and Watters 2000). Putative host to *L. recta, S. undulatus, T. lividus, U. imbecillis*, and *Villosa contricta* (unpublished sources in OSUDM 2006).

Conservation status: The longear sunfish as currently conceived appears secure throughout its range (Warren *et al.* 2000; NatureServe 2006, hut latter includes *L. peltastes*), but the status of evolutionarily significant units or undescribed taxa in northern Mexico is of concern (Miller 2005). Because of evidence of polytypy, a comprehensive characterization of variability across the geographic range is needed to clarify the conservation status of the Rio Grande and other suspected forms of the longear sunfish.

Similar species: See accounts on dollar sunfish and northern longear sunfish. The redbreast sunfish lacks blue spots on the sides and has rows of red-brown spots on upper side and a longer, narrower ear flap that is black to its edge. The pumpkinseed has bold spots on the second dorsal fin and long, pointed pectoral fins, and a stiff posterior edge on the gill cover (Page and Burr 1991).

Systematic notes: *Lepomis megalotis* is included in a clade with *L. peltastes* and *L. marginatus* (Near *et al.* 2004, 2005), but relationships among these species are unresolved (see accounts on these species). *L. megalotis* is polytypic. In a morphological analysis of variation that did not include breeding colors (Barlow 1980), four subspecies (not including *L. peltastes*) were delimited: *L. m. megalotis, L. m. breviceps, L. m. aquilensis* (Rio Grande to Brazos River, Texas), and an undescribed subspecies (Little River, Oklahoma and southwestern Arkansas). *L. m. megalotis* was differentiated into four races: eastern Gulf race, Ozark race, Central and Interior Lowland race, and Coosa River race. The subspecies *L. m. breviceps* was differentiated into two races: Upper Arkansas and Missouri basin race and east Texas race. Differences in breeding colors and opercular tab orientation occur in middle Missouri River and upper White River populations (Pflieger 1971). Analysis of nuclear-encoded allozyme loci confirmed genetic distinctiveness of the southwestern populations (*L. m. aquilensis* and *L. m. breviceps*) from *L. m. megalotis*, suggested intergradation or retained ancestral polymorphisms in the Ozark Highlands between *L.m. breviceps* and *L. m. megalotis*, and indicated considerable divergence within *L. m. megalotis* (Jennings and Philipp 1992a). A fifth subspecies, *L. m. occidentalis*, from the Rio Grande system (Bailey 1938), could not be differentiated meristically or morphometrically from *L. m. aquilensis* (Barlow 1980), but striking differences in breeding colors in Rio Grande populations suggest that additional taxa are present (Miller 2005).

Importance to humans: Despite its relatively small size, the longear sunfish is of considerable importance in stream fisheries where it can comprise a large proportion of the creel (up to 37% by weight) (e.g., Mississippi, Missouri, Tennessee). It vigorously attacks a variety of live baits, small spinners, dry flies, and popping bugs, and is a scrappy fighter when taken on light tackle. Larger specimens also provide a tasty morsel for the table (Etnier and Starnes 1993; Pflieger 1997; Ross 2001). In reservoirs, young-of-the-year longear sunfish are an important forage fish for largemouth bass, particularly for 5 to 20 cm bass during summer and fall (Applegate *et al.* 1967).

13.8.9 Lepomis microlophus *(Günther)*

13.8.9.1 Redear sunfish

Characteristics: See generic account for general characteristics. Body moderately deep, compressed, depth 0.42 to 0.50 of SL. Mouth moderate, terminal, oblique, supramaxilla small (>3 times and ≤4 times length of maxilla), upper jaw extends almost to, or to, anterior edge of eye. No wavy blue or dark lines on cheek and opercle; soft dorsal, anal, and caudal fins not marked with dark brown wavy lines or orange spots. Opercular flap, short, moderately flexible with black center bordered above and below in white or light slate and posteriorly by prominent red (male) to orange (female) crescent (often pale in young). Pectoral fin long and pointed, tip extending far past eye when laid across cheek. Gill rakers short, 9 to 11, longest about two times greatest width. Lateral line complete. Lateral scales, 34 to 47; rows above lateral line, 6 to

8; rows below lateral line, 13 to 16; cheek scale rows, 3 to 6; caudal peduncle scale rows, 16 to 22; pectoral rays, 13 to 16. Pharyngeal arches extremely broad, heavy with large rounded, molariform teeth. Teeth present or absent on palatine. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Bailey 1938; Trautman 1981; Mabee 1993).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, varying from about 30 to 185 mm TL (median 86.5 mm TL). Large individuals measure 200 to 250 mm TL, weigh about 200 to 300 g, and can attain age 6+ to 9+ (maximum 269 mm TL, age 11+) (Schoffman 1939; Carlander 1977; Trautman 1981; Page and Burr 1991; Sammons *et al.* 2006). World angling record, 2.48 kg, South Carolina (IGFA 2006).

Coloration: Bright red or orange spot on light colored edge of ear flap (best developed on large adult). Light gold-green above; dusky gray spots (adults) or bars (young) on sides; white to yellow below. Fins mostly clear, some dark mottling in second dorsal fin of adult. Breeding male brassy gold with dusky pelvic fins (Page and Burr 1991).

Native range: The redear sunfish is native to the Atlantic and Gulf Slope drainages from about the Savannah River, South Carolina, to the Nueces River, Texas, and ranges in the Mississippi River basin north from the Gulf to southern Indiana and Illinois (Page and Burr 1991). The species is now widely introduced and established in the eastern and western United States, usually in reservoirs, including the Colorado River basin and Pacific Slope drainages (Page and Burr 1991; Fuller *et al.* 1999). After the introduction of the nonnative redear sunfish, native pumpkinseed in a southern Michigan lake experienced a 56% decline in abundance (Huckins *et al.* 2000).

Habitat: The redear sunfish inhabits ponds, oxbows, swamps, lakes, and reservoirs and the sluggish pools and backwaters of small to medium size rivers (Page and Burr 1991). The species is much more abundant in clear, vegetated backwaters than in turbid, hypoxic backwaters or flowing main channels of streams and rivers (Beecher *et al.* 1977; Pflieger 1997; Rutherford *et al.* 2001; Miranda and Lucas 2004). Redear sunfish, known from salinities up to 20 ppt, acclimate physiologically more quickly to salinity changes (1 hour, ≤8 ppt) relative to congeners and *Micropterus* (12 hours), and are among the most euryhaline centrarchids. This physiological adaptation may allow redear sunfish to withstand the rapidly changing salinities of tidal rivers (Peterson 1988).

Food: The redear sunfish is highly specialized for crushing hard-bodied prey such as snails, small bivalves, and ostracods, earning it the appellation of "shellcracker" among anglers. Similar to the pumpkinseed, the species possesses heavy pharyngeal jaw bones that are equipped with molariform teeth, enlarged muscles, and specialized neuromuscular adaptations (Lauder 1983a,b, 1986; Wainwright and Lauder 1992; Huckins 1997). In contrast to the pumpkinseed, the redear sunfish uses the crushing apparatus on all prey types as evidenced by muscular activity patterns, but the pumpkinseed displays the crushing pattern only when feeding on snails (Lauder 1983a,b). Redear sunfish also appear better adapted for hard-bodied prey than pumpkinseed. At a given size, redear sunfish have more robust pharyngeal structures and possess about twice the shell crushing capacity of pumpkinseed, and hence, can consume larger (and harder) snails than similar-sized pumpkinseed (Huckins 1997). In laboratory choice experiments, redear sunfish discriminated against thick-shelled snail species and chose thin-shelled snail species (Stein *et al.* 1984). Young redear sunfish undergo a dramatic and rapid shift in diet from soft-bodied invertebrates to high numbers of snails as they grow from 25 to 75 mm TL. As principally benthic feeders, redear sunfish are certainly not limited to feeding on snails but also consume large numbers of larval dipterans and burrowing mayflies, amphipods, larval odonates, and a variety of other invertebrates (McCormick 1940; Chable 1947; Wilbur 1969; Desselle *et al.* 1978; Huckins 1997; VanderKooy *et al.* 2000). Feeding occurs frequently and apparently at random throughout the day (Wilbur 1969).

Reproduction: Maturity is reached at age 0+ or 2+ in females at 100 to 164 mm TL (Schoffman 1939; Wilbur 1969; Carlander 1977; Adams and Kilambi 1979). Spawning in Florida begins in late February or early March as water temperatures reach 21°C, and continues for 6 to 7 months and may involve up to five synchronous spawning peaks (Wilbur 1969). Over the reproductive season, spawning may cease for periods of 1 to 3 weeks. Nests are most abundant at water temperatures of 23.8 to 26.7°C, but nesting may continue up to 32.2°C (Clugston 1966). In less southerly latitudes, spawning occurs from about May to July or August (Adams and Kilambi 1979). Males excavate nests by caudal sweeping, the nests are colonial (<1 m apart), and colonies often contain nests of congeners (Childers 1967). Nests may be placed in shallow water (<0.5 m) (Clugston 1966), although the redear sunfish frequently nests in somewhat deeper water than most *Lepomis* (1 to >2 m, Wilbur 1969). Nests are 25 to 61 cm in diameter and 5 to 10 cm deep and constructed in bottoms of sand, gravel, or mud (Wilbur 1969). Nest-guarding males produce popping sounds (presumably with the jaw and pharyngeal bones) that are directed at the sides and head of females during courtship (Gerald 1971; see account on *L. gibbosus*). Little else is apparently known about nest-building, spawning, or nest-guarding behaviors. In ponds, female bluegills, the males of which have completely black opercular flaps, interbred with redear sunfish males when their red, white, and black opercular flaps were removed, but females did not interbreed when redear male flaps were intact (Childers 1967). Mature ovarian eggs range from 0.60 to 1.30 mm diameter (Adams and Kilambi 1979) and water-hardened, fertilized eggs from 1.3 to 1.6 mm diameter (Meyer 1970). Fecundity increases with female size. The relationships between potential batch fecundity (Y) and total length (X) are described by the functions, $\ln_{10} Y = 5.95424 + 0.01967X$ and $\log Y = 263.75 + 1.7109 \log X$ (formulas from Adams and Kilambi (1979), $n = 15$, $R^2 = 0.90$, and from Wilbur (1969), based on means from eight length classes, 82 females, $R^2 = 0.88$, respectively). At 182 mm TL, a female can potentially produce 13,824 to 17,812 mature eggs in a single batch (range: 7513 to 12,943 eggs at 151 mm TL to 23,316 to 25,437 eggs at 213 mm TL, respectively). Eggs hatch in 50.3 hours at 23.8°C, 26.6 to 28.1 hours at 28.5°C; newly hatched larvae are 3.3 to 3.8 mm TL and reach swim-up in about 3 days at 4.78 to 5.80 mm TL (Childers 1967; Meyer 1970; Yeager 1981).

Nest associates: None known.

Freshwater mussel host: Confirmed host to *A. neislerii* (O'Brien and Williams 2002). Putative host to *L. teres* (unpublished sources in OSUDM 2006).

Conservation status: The redear sunfish is apparently secure throughout its range (but see section on systematic notes), except for peripheral populations in Illinois that are considered imperiled (NatureServe 2006). Historically, abundant, widely distributed redear populations occurred in lakes on the large Yazoo River alluvial floodplain in Mississippi. Now, the species has practically disappeared from these lentic habitats apparently in response to increased turbidity from agricultural activities (Miranda and Lucas 2004).

Similar species: The pumpkinseed has bold spots on the second dorsal fin, wavy blue lines on the cheek and opercle, and a stiff rear edge on the gill cover. The longear, northern longear, and dollar sunfishes have short, rounded pectoral fins, wavy blue lines on the cheek and opercle, and a long ear flap (Page and Burr 1991).

Systematic notes: *Lepomis microlophus* is sister to the species pair, *L. punctatus* and *L. miniatus* (Near *et al.* 2004). On the basis of shared behavioral and morphological specializations for mollusk-crushing, *L. gibbosus* was proposed previously as sister to *L. microlophus* (Bailey 1938; Mabee 1993). Two subspecies of the redear sunfish, *L. m. microlophus* and an undescribed subspecies, are recognized based on essentially nonoverlapping scale counts, pectoral fin length differences, and opercular flap coloration (Bailey 1938). The range of the two subspecies is not entirely clear from the original work (Bailey 1938), but the undescribed subspecies occurs in the Mississippi River Valley westward to the San Marcos River, Texas, and perhaps east in the middle Gulf Slope to southern Mississippi, and *L. m. microlophus* occurs in eastern Gulf and Atlantic Slope drainages of Alabama, Georgia, and Florida (Page and Burr 1991). Phylogeographic analyses using mtDNA haplotypes along the southeastern seaboard of the United States revealed genetic discontinuities that were largely congruent with boundaries identified by morphological differentiation (Bailey 1938; Bermingham and Avise 1986). The widespread practice of moving and stocking redear sunfish in the southern United States may have obscured the boundaries of the two forms, but clarification of their current status awaits thorough genetic and morphological comparisons.

Importance to humans: The redear sunfish, the "shellcracker" to many anglers, is a popular sport fish that is often stocked in combination with largemouth bass and bluegill in ponds and reservoirs. Because of its bottom-feeding habits, the species fills a niche little used by other *Lepomis*, and redear sunfish do not tend to overcrowd and stunt in ponds as do bluegill. The fast growth rate, large size, and mild flavor combine to make them a highly desirable pan fish. The redear sunfish is often one of the primary fish in sunfish sport fisheries and can account for a substantial portion (up to 66%) of the sunfish harvest by weight in southern lakes and reservoirs (Schramm *et al.* 1985; Crawford and Allen 2006; Sammons *et al.* 2006). From 1976 to 1981, 36 to 332 thousand kilograms of redear sunfish were harvested annually by commercial fishing operations in Lake Okeechobee, Florida, constituting about 8% of the total commercial catch over this period (Schramm *et al.* 1985). The species is less likely to be taken on artificial lures than bluegill but readily takes worms and other natural baits fished near the bottom. Nesting males are taken in large number by anglers (Wilbur 1969; Etnier and Starnes 1993; Ross 2001). Nonnative snails and bivalves (e.g., Asian clam, *Corbicula fluminea*) are often exploited as food by redear sunfish (Moyle 2002), and the species is used effectively as a native biological control for snails that serve as intermediate hosts to detrimental parasites of pond-raised channel catfish (Ledford and Kelly 2006).

13.8.10 Lepomis miniatus *Jordan*

13.8.10.1 Redspotted sunfish

Characteristics: See generic account for general characteristics. Body deep, compressed, depth 0.45 to 0.50 of SL. Mouth moderate, terminal, oblique, supramaxilla small (>3 times and ≤ 4 times length of maxilla), upper jaw extending just to or slightly beyond anterior margin of eye. Iridescent turquoise crescent outlining ventral curvature of red or dark eye. No wavy blue lines on head. Two to three diffuse bars often radiate posterior to the eye, and small spots on head, if present, most prominent on the preopercle and subopercle, often diffuse or coalesce to form dark, short streaks. Body in breeding males with horizontal rows of red-orange spots (one per scale) below the lateral line; black specks rarely present. Opercular flap, stiff, short with black center narrowly bordered above and below by pale white, posterior edge with narrow pale white border, often lacking; dorsal edge of flap red-orange in breeding males. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Gill rakers moderate to long, 8 to 11, longest about two to four times greatest width. Lateral line complete. Lateral scales, (33)35 to 41(42); rows above lateral line, (4)6 to 7(8); rows below lateral line, (11)12 to 14(15); cheek scale rows 4 to 6(7); breast scale rows (11)12 to 15(18); caudal peduncle scale rows, (15)18 to 21(22); pectoral rays (12)13 to 14(15). Pharyngeal arches narrow with sharply pointed teeth. Teeth present or absent on palatine bones. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Bailey 1938; Warren 1992; Mabee 1993).

Size and age: Typically reach 30 to 80 mm TL at age 1. Large individuals measure 133 to 153 mm TL and attain age 4+ (maximum about 164 mm TL) (Carlander 1977; Warren 1992; Roberts *et al.* 2004).

Coloration: Ear flap, short, black with narrow dorsal and ventral white edges (suffused in orange in breeding male). Sides with red-orange, horizontal rows of spots, best developed at level of pectoral fin in breeding males. Ventral curvature of dark or red eye outlined with iridescent turquoise crescent (in life), a characteristic unique to *L. miniatus* and *L. punctatus*. Dark olive above; pale to yellow on breast and anterior belly. Breeding males with red-orange on breast, anterior belly, and pale circular to quadrate blotch above ear flap; dusky to dark pelvic fins; distal one-half to one-third of soft dorsal, soft anal, and caudal fins suffused with red-orange to reddish brown and narrowly edged in silvery, creamy, pinkish, or white margins (Page and Burr 1991; Warren 1992).

Native range: The redspotted sunfish is native to the Illinois River, Illinois (relictual population, Burr and Page 1986), and south in the Mississippi River Valley to the Gulf Slope. On the Gulf Slope, the species occurs from the Nueces River, Texas, to, and inclusive of, the Mobile Basin, Alabama (Warren 1992). The introduced or native status of individuals from the Devils River (Rio Grande drainage), Texas, is equivocal (Warren 1990). Populations in drainages of the Florida Panhandle (inclusive of drainages from the Perdido to Apalachicola rivers), upper Coosa River tributaries (Alabama River drainage), and Lookout Creek (Tennessee River drainage) form a zone of contact in which individuals cannot be clearly identified morphologically as redspotted or spotted sunfishes (Warren 1992).

Habitat: The redspotted sunfish inhabits well-vegetated ponds, lakes, and slow-flowing pools of creeks and small to medium rivers, being most abundant in natural floodplain lakes (Page and Burr 1991), where it tolerates periodic hypoxic conditions (<1 mg/l DO, Killgore and Hoover 2001). Removal of aquatic vegetation by grass carp (*C. idella*) in a eutrophic Texas reservoir resulted in almost complete elimination of redspotted sunfish (Bettoli *et al.* 1993). The species also occurs in coastal habitats of low salinity (usually <4 ppt), where it can be one of the most abundant centrarchids (Desselle *et al.* 1978; Peterson and Ross 1991). Length–weight relationships were not different between two populations experiencing annual salinities ranging from 1 to 10 ppt (average = 4) and 0 to 4 ppt annually (average = 0.91), respectively, suggesting that oligohaline conditions produce little or no metabolic consequences for the species (Peterson 1991; Peterson and Ross 1991).

Food: The redspotted sunfish is an invertivore that forages primarily in submerged aquatic vegetation and bottom sediments but can also exploit surface prey. The most comprehensive food studies were conducted in low-salinity coastal environments with marine faunal elements (Lake Pontchartrain, Louisiana, and Davis Bayou, Mississippi). In oligohaline habitats, adult fish (>60 mm SL) feed on mud crabs, isopods, amphipods, and a variety of aquatic insects (dipteran larvae, caddisfly larvae, terrestrial insects) (Desselle *et al.* 1978). In a freshwater stream, food consisted primarily of adult and larval insects (Robison and Buchanan 1984). Small fish (≤60 mm SL) feed initially on copepods, midges, cladocera, mysid shrimp, and mayfly larvae, gradually transitioning to higher consumption of larger crustaceans and insects (Desselle *et al.* 1978; VanderKooy *et al.* 2000).

Reproduction: The reproductive biology of the redspotted sunfish is not well studied but is presumably similar to that of its sister species, the spotted sunfish, *L. punctatus*. Spawning is protracted. Nesting activity was observed from early April to August in Texas, May to early August in Illinois, and in July in Missouri (Forbes and Richardson 1920; Robison and Buchanan 1984; Pflieger 1997; Roberts *et al.* 2004). When transferred from experimental ponds in Illinois to indoor aquaria, males and females spawned in artificial nests in August (Roberts *et al.* 2004). In Missouri streams, nests are placed in a few centimeters of water among stems of water willow over a bottom of sand and gravel. Some males nest solitarily, but two or more males often build adjacent or even confluent nests (Pflieger 1997). Eggs hatch in about 36 hours at 26°C, and larvae reach swim-up about 4 to 5 days after hatching (Roberts *et al.* 2004).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The redspotted sunfish is secure throughout its range (Warren *et al.* 2000), but peripheral northern populations are considered vulnerable (Indiana, Tennessee) or imperiled (Illinois and Kentucky) (NatureServe 2006) because of losses of populations and lowland habitats (Smith 1979; Burr and Warren 1986; Burr *et al.* 1988).

Similar species: The spotted sunfish lacks rows of red or yellow spots on the sides and has discrete black specks, often numerous, on head and body. The bantam sunfish lacks rows of red or yellow spots on the sides, lacks a brassy-red patch above the ear flap, has a black spot in the posterior second dorsal fin (in juveniles), and has an interrupted or incomplete lateral line. The longear, northern longear, dollar, and redbreast sunfishes have wavy blue lines on the cheek, longer ear flaps, and short, thick to knobby gill rakers (Page and Burr 1991).

Systematic notes: *Lepomis miniatus* is the sister species of *L. punctatus* (Near *et al.* 2004, 2005). Although long recognized as distinct (Jordan 1877), *L. miniatus* was considered a subspecies of *L. punctatus* throughout most of the twentieth century (Bailey 1938; Bailey *et al.* 1954). Morphological (meristics, pigmentation, breeding color) and genetic (nuclear-encoded allozyme loci and mitochondrial and nuclear DNA) data support recognition of *L. miniatus* as a distinct species (Warren 1989, 1992; Bermingham and Avise 1986; Near *et al.* 2004, 2005). Populations from the Perdido River, Alabama, east to the Apalachicola river and those in upper Coosa River tributaries (Alabama River drainage) and Lookout Creek (Tennessee River drainage) show scale counts that are intermediate morphologically between the two species. Genetic distance analyses from nuclear-encoded allozyme loci, pigmentation patterns, and breeding colors suggest closer affinity of these contact zone populations to *L. punctatus*, but population sampling was limited for the allozyme analyses (Warren 1989, 1992). Whether these contact zone populations represent past or ongoing introgression and retained ancestral polymorphisms or a distinct evolutionary lineage awaits further analyses.

Importance to humans: The redspotted sunfish, although providing sport, is generally too small to be a significant pan fish. Even so, the species contributes to the bream creel, particularly for bank anglers using cane poles in wetlands, backwaters, and small, lowland streams. The species is most often taken using worms or crickets but may also be taken at the surface on popping bugs. The flesh is firm and mild (Etnier and Starnes 1993).

13.8.11 Lepomis peltastes *Cope*

13.8.11.1 Northern longear sunfish

Characteristics: See generic account for general characteristics. Deep, compressed body, depth 0.42 to 0.53 of SL. Mouth moderately large, oblique, jaws subequal, supramaxilla small (>3 times and ≤4 times length of maxilla), upper jaw extends to about center of eye, always beyond anterior edge of eye. Wavy blue lines on cheek and opercle of adult. Opercular flap long, flexible, pointing upward with black center edged above and below in yellow or white, posterior edge often with red spot; lower border usually wider than upper. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Short, thick, knoblike gill rakers, 12 to 14, longest about equal (adults) to two (young) times greatest width. Lateral line often incomplete or interrupted behind posterior base of dorsal fin. Lateral scales, (31)35 to 37(41); rows above lateral line, 5 to 6(7); rows below lateral line, (11)12 to 13(14); cheek scale rows, 4 to 6(7); caudal peduncle scale rows, (14)17 to 19(21); pectoral rays, (11)12 to 13(14). Pharyngeal arches narrow with pointed teeth. No teeth on endopterygoid, ectopterygoid, palatine, or glossohyal (tongue) bones (Bailey 1938; Gruchy and Scott 1966; Scott and Crossman 1973; Barlow 1980; Trautman 1981; Becker 1983; Mabee 1993; Bailey *et al.* 2004).

Size and age: Typically reach 30 to 48 mm TL at age 1. Large individuals measure 96 to 102 mm TL and attain age 4+ (maximum about 150 mm TL, 9+ years) (Hubbs and Cooper 1935; Scott and Crossman 1973; Becker 1983; Jennings and Philipp 1992c).

Coloration: Similar to *L. megalotis*, but black ear flap edged in yellow (or red), the lower edge often wider than upper (Barlow 1980; Trautman 1981; Page and Burr 1991).

Native range: The northern longear sunfish occurs in the St. Lawrence-Great Lakes drainages from southern Quebec, western New York, northwestern Pennsylvania, northern Ohio and Indiana, the Lower Peninsula of Michigan, eastern Wisconsin, northern Minnesota, and southern Ontario (including Hudson Bay system). The species occurs, or occurred historically, in scattered localities in the Mississippi River basin in northwestern Wisconsin, northeastern Illinois, Minnesota, and Iowa (Smith 1979; Trautman 1981; Becker 1983; Underhill 1986; Jennings and Philipp 1992a; Bailey *et al.* 2004).

Habitat: The northern longear sunfish inhabits pools of clear, shallow streams and moderate sized rivers as well as ponds and lakes (Scott and Crossman 1973; Trautman 1981; Becker 1983). The species avoids densely vegetated littoral habitats and sediment-laden, turbid habitats. In southern Michigan, northern longear sunfish occurred in greatest abundance in lakes containing shoreline benches of exposed marl sediments and was rare or absent in lakes with organic-laden sediments or dense aquatic vegetation covering shallow (<2 m) littoral zones, regardless of sediment type (Laughlin and Werner 1980). Within a lake, most large individuals (>75 mm TL) occur in sparsely to moderately vegetated habitats, and small individuals (<38 mm TL) concentrate in the most densely vegetated areas. The species decreased dramatically in distribution and abundance in tributaries and shallows of Lake Erie as those habitats received increased sediment loads in the twentieth century (Trautman 1981).

Food: The northern longear sunfish is a benthic invertivore. In a summer diet study, lake-dwelling adults (>75 mm TL) primarily consumed dragonfly and mayfly larvae and amphipods. The species uses a sit-and-wait foraging strategy, remaining still and close to the bottom, apparently keying in on the slight movements of cryptic or burrowing prey (Laughlin and Werner 1980).

Reproduction: Maturity is reached at age 2+ at 45 to 75 mm SL, occasional large individuals mature at age 1+ (Hubbs and Cooper 1935; Jennings and Philipp 1992c). In experimental ponds, both males and females matured at age 1+, but sneaker male phenotypes (e.g., drab coloration, large gonads) matured at a smaller size (40–60 mm TL) than parental males (60 mm TL) (Jennings and Philipp 1992c). Spawning is protracted (late May to August) with peaks in July (Hubbs and Cooper 1935; Keenleyside 1972; Dupuis and Keenleyside 1988). Nest building and spawning occur as water temperatures exceed 20°C, but lengthening photoperiod in spring is most strongly associated with initiation of nest-building behaviors in males. Out-of-season nest building occurred under experimental conditions of long photoperiod (16 hours) and warm water temperatures (25°C). Under a long photoperiod and cold temperature (11–13°C), some males began but did not complete nests; no males built nests under a short photoperiod (8 hours) regardless of temperature (Smith 1970). Most nest-guarding males are 73 to 111 mm TL (Keenleyside 1971; Dupuis and Keenleyside 1988). Males excavate small saucer-shaped nests (average 33 cm diameter) with caudal sweeping over areas of mixed sand and gravel or where gravel substrate is covered by silt, which is swept away by the males before spawning. Nests are usually close to shore in shallow water (10–60 cm) with little current and are often near aquatic vegetation or overhanging shrubs (Bietz 1981; Dupuis and Keenleyside 1988). Although a few males nest solitarily (<4%), most males excavate their nest in close proximity to other nesting males to form dense colonial aggregations of rim-to-rim hexagonally shaped nests (<20 to 100+ nests) (Keenleyside 1972; Bietz 1981; Dupuis and Keenleyside 1988). Colonies are formed when new males (peripheral males) excavate nests around those of early nesting males (central males). Colonies are definitely social aggregations because formation occurs in the absence of habitat limitation (Bietz 1981). Breeding is synchronous in colonies, and over the long breeding season five or six distinct spawning periods occur. Males spawning later in the breeding season obtain larger numbers of larvae (average 750) than those breeding earlier (<300) (Dupuis and Keenleyside 1988). Likewise, males spawning first during a given breeding period obtain more larvae than those nesting on the second or third day. Agonistic, courtship, spawning, and nest defense behaviors are well documented (e.g., opercular spreads, tail-beating, bites, nest circling, dipping), and form a large part of the foundation for our knowledge of reproductive biology and behavior in the genus (Keenleyside 1967, 1971, 1972; Steele and Keenleyside 1971). Nest preparation is accomplished in <24 hours, but females arrive on the spawning grounds before all nests are completed. Females are usually courted by several males (e.g., courtship circles with shivers and vibrations) but may also spawn in a male's nest without any overt courtship (Keenleyside 1967; Steele and Keenleyside 1971). Females often spawn with several males during a spawning event and often enter a nest to eat eggs before being chased away by the guardian male (Keenleyside 1972; Dupuis and Keenleyside 1988). Females can visually distinguish conspecific from other *Lepomis* males (Steele and Keenleyside 1971), suggesting an ability to chose mates. Likewise, nesting males can visually distinguish conspecific from other *Lepomis* females, but non-nesting males show weaker discrimination between conspecific and other *Lepomis* females (Keenleyside 1971). Within colonies, females spawn preferentially with males nesting early within a spawning period and those with centrally located nests. Females also appear to choose larger over smaller males. Solitary nesting males are larger than and as successful as colonial males in obtaining eggs and larvae (Dupuis and Keenleyside 1988). These patterns suggest that nesting colonies arise so that males unlikely to attract females (i.e. smaller, peripheral guardian males) increase their exposure to and probability of spawning with females attracted to centrally located males (Bietz 1981; Dupuis and Keenleyside 1988). Up to five or six small sneaker males, which can be numerous around some nests (50+ individuals), frequently interrupt a spawning pair en masse in an attempt to steal fertilizations (Keenleyside 1972; Dupuis and Keenleyside 1988). The frequency of intrusions into nests by neighboring guardian males is also high (average, one per minute) (Keenleyside 1972). Spawning occurs over a 2- to 3-day period, males guard and fan the eggs, which hatch in 2 to 3 days, and continue guarding the larvae until they reach swim-up and disperse about 4 to 6 days after hatching. Males may then abandon the nest or begin cleaning and preparing it for another spawning (Dupuis and Keenleyside 1988).

Nest associates: Redfin shiner, *L. umbratilis* (Noltie and Smith 1988).

Freshwater mussel host: None known (see longear sunfish, *Lepomis megalotis*).

Conservation status: The northern longear sunfish is apparently secure throughout the center of its native range (e.g., Lower Peninsula of Michigan). The species occurs primarily in scattered and isolated populations in the eastern and western parts of its range, where population declines and losses are documented (e.g., Ohio, Trautman 1981; Wisconsin, Becker 1983). The species is rare and considered critically imperiled in New York and Pennsylvania, imperiled in Quebec and Wisconsin, and vulnerable in Ontario (Scott and Crossman 1973; Becker 1983; Smith 1985; NatureServe 2006).

Similar species: See accounts on longear sunfish and dollar sunfish.

Systematic notes: *Lepomis peltastes*, only recently elevated to species status (Bailey *et al.* 2004), is in a clade with *L. megalotis*, and *L. marginatus*, but relationships among the taxa are unresolved (see accounts on *L. megalotis* and *L. marginatus*; Jennings and Philipp 1992a; Near *et al.* 2004, 2005). *L. peltastes* was long considered a dwarf form of *L. megalotis* (e.g., Hubbs and Cooper 1935) even though there is apparently no evidence of intergradation between the two (Smith 1979; Trautman 1981). In a phenetic cluster analysis using 47 meristic and morphological variables, populations of *L. peltastes* formed a basal cluster that was highly distinctive from all populations of *L. megalotis* (Barlow 1980). Interestingly, specimens from the Muskingum River (Ohio River basin) clustered with *L. peltastes*, suggesting that the southern geographic limits of the species are incompletely known. Frequency data from nuclear-encoded allozyme loci did not separate *L. peltastes* from *L. m. megalotis* (Jennings and Philipp 1992c). Nevertheless, the two clearly differ in morphological and life history traits (i.e. growth, maturity, reproductive investment) (Barlow 1980; Jennings and Philipp 1992a,b,c; Bailey *et al.* 2004).

Importance to humans: The northern longear sunfish does not reach a size of interest to anglers; however, the breeding males are among the most stunningly beautiful of all North American freshwater fish. Although extremely aggressive toward conspecifics, it is otherwise easy to keep and breed in the laboratory or hobbyist's aquaria (e.g., Keenleyside 1967;

Bietz 1981). Studies of the northern longear sunfish increased our understanding of the social, agonistic, and reproductive behaviors and ecology for the genus and highlighted the value of freshwater fishes, especially centrarchids, as models for sociobiological research (e.g., Keenleyside 1967, 1971,1972; Smith 1970; Steele and Keenleyside 1971; Bietz 1981; Dupuis and Keenleyside 1988; Jennings and Philipp 1992a,c).

13.8.12 Lepomis punctatus *(Valenciennes)*

13.8.12.1 Spotted sunfish

Characteristics: See generic account for general characteristics. Body deep, compressed, depth 0.45 to 0.50 of SL. Mouth moderate, terminal, oblique, supramaxilla small (>3 times and ≤4 times length of maxilla), upper jaw extending just to or slightly beyond anterior margin of eye. Iridescent turquoise colored crescent outlining ventral curvature of eye. No wavy blue or dark lines on head and no horizontal rows of red-orange spots on sides. Discrete, small dark spots form irregular horizontal rows on sides of body and dorsum, especially prevalent on lower sides. Cheek and opercle often speckled with black spots. Opercular flap, stiff, short with black center outlined above and below by narrow white edges (yellow-orange to pinkish-orange in breeding males), posterior margin edged with narrow pale white border, often lacking. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Gill rakers moderate to long, 8 to 11, longest about three to five times greatest width. Lateral line complete. Lateral scales, (37)38 to 44(47); rows above lateral line, (6)7 to 8(9); rows below lateral line, (12)13 to 15(16); cheek scale rows, (4)5 to 7(8); breast scale rows, (14)15 to 18(20); caudal peduncle scale rows, (7)8 to 10; pectoral rays, (12)13 to 14(15). Pharyngeal arches narrow with sharply pointed teeth. Teeth present or absent on palatine bones. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Bailey 1938; Warren 1992; Etnier and Starnes 1993; Mabee 1993).

Size and age: Typically reach about 30 to 50 mm TL or more at age 1. Large individuals measure 165 to 180 mm TL, weigh 105 to 140 g (maximum 207 mm TL, 376 g), and presumably attain age 4+ to 5+, but estimates of size at age and maximum longevity are problematic (Caldwell *et al.* 1957; Page and Burr 1991; Warren 1992; Marcy *et al.* 2005).

Coloration: Ear flap, short, black with white to yellow edges. Head and sides with many discrete, black specks, most prominent on lower sides. Ventral curvature of dark or red eye outlined with iridescent turquoise crescent, a characteristic unique to *L. punctatus* and *L. miniatus*. Dark olive above; pale to butterscotch yellow on breast and anterior belly; clear to dusky fins; very narrow silvery, creamy, pinkish, or white margins on median fins. Darkly pigmented breeding males with a pale patch above ear flap and dusky to dark pelvic fins (Page and Burr 1991; Warren 1992).

Native range: The spotted sunfish is native to the Coastal Plain from the Cape Fear River, North Carolina, south in Atlantic Slope drainages to the Everglades and north and west in East Gulf Slope drainages to the Ocklockonee River, Georgia and Florida. From the Perdido River, Alabama, east to the Apalachicola River Basin the spotted sunfish forms a contact zone with the redspotted sunfish (see account on *L. miniatus*).

Habitat: The spotted sunfish inhabits pools of small to medium rivers and heavily vegetated ponds, lakes, and swamps (Page and Burr 1991). In streams, the species is most often associated with instream wood, stumps, or undercut banks in slow current and soft substrates (Meffe and Sheldon 1988; Marcy *et al.* 2005). On the North Carolina Coastal Plain, the spotted sunfish is the most common and widely distributed centrarchid in first- to fourth-order streams and is also common, especially the young-of-the-year, in beaver ponds (Snodgrass and Meffe 1999). In Florida, the species occurs in abundance in densely vegetated springs, spring runs, and spring-fed rivers (Hubbs and Allen 1943; Carr 1946; Swift *et al.* 1977). Spotted sunfish are also the most abundant and ubiquitous centrarchid in the Everglades region, where the species accounts for the second highest biomass of all carnivorous fishes within wet-prairie habitats (Clugston 1966; Loftus and Kushlan 1987; Turner *et al.* 1999). In large pool habitats, adults are often observed in open water during the day, moving inshore at night; juveniles tend to stay in dense vegetation (Hubbs and Allen 1943; Loftus and Kushlan 1987). The species can penetrate waters up to at least 12.5 ppt and is a relatively common inhabitant of coastal tidewater and oligohaline habitats (Kilby 1955; Loftus and Kushlan 1987). Genetic analyses of Everglades populations suggest that the species is adept at immigrating en masse into seasonally dry habitats once the habitats are reinundated (McElroy *et al.* 2003).

Food: The spotted sunfish is an opportunistic invertivore, picking invertebrates from the surface, aquatic plants, the bottom, and the stream drift. In North Carolina streams, adults (>45 mm SL) feed primarily on terrestrial invertebrates, midge larvae, mayflies, and decapods and occasionally on snails, bivalves, and fish (Sheldon and Meffe 1993; Marcy *et al.* 2005). Smaller individuals consume more midge larvae, along with aquatic and terrestrial insects, and a few water mites, amphipods, and copepods. Limited stomach analyses in a Florida spring indicated concentrated foraging in aquatic plant beds and associated sediments. Midge larvae, caddisfly larvae, freshwater shrimp, and isopods dominated the diet (Caldwell *et al.* 1957). Stomachs often contain substantial volumes of plant and algal matter (Caldwell *et al.* 1957; Marcy *et al.* 2005), presumably ingested incidentally while gleaning invertebrates from aquatic plants.

Reproduction: Maturity is reached at age 1+ and a size of about 50 to 55 mm TL (Carr 1946; Caldwell *et al.* 1957). Most actively spawning females are 76 to 101 mm TL (maximum >127 mm TL), and nest-guarding males are 84 to 178 mm TL (Carr 1946; DeWoody *et al.* 2000a). In North Carolina, spawning occurs from late May to late July at water temperatures of 24 to 27°C (Marcy *et al.* 2005). The spawning season is prolonged in the Florida Everglades with nesting occurring from March to November (temperatures from 17.7–33.3°C), but lengthy pauses in spawning occur during this period, presumably in association with water temperatures exceeding 30°C (Clugston 1966; Loftus and Kushlan 1987). In near-constant temperature spring-fed streams in Florida (22.8°C), some individuals appear to be spawning year round because ripe males, ripe females, and juveniles are taken in every month of the year. However, gonads of the majority of individuals in these environments are well developed between March and August (Kilby 1955; Caldwell *et al.* 1957). Males use caudal sweeping over sand or sand mixed with pebbles and snail shells to excavate relatively small nests (15–61 cm diameter, 25–50 cm deep). Nests are placed in shallow water (10–38 cm) near or against the bank (Carr 1946; Clugston 1966; Marcy *et al.* 2005) and tend to be solitary in small streams, but males may also aggregate their nests into groups of two or more (Hubbs and Allen 1943; Carr 1946; DeWoody *et al.* 2000a). During courtship, males frequently flash their solid black ventral fins at nearby females and rush toward females, ultimately driving spawning-ready females to the nest. Males mate with multiple females and continue to accept eggs for up to 3 days after spawning begins. During this period males frequently orient head down with the snout thrust into the gravel in an apparent inspection of the eggs. In a North Carolina stream population, conservative estimates from genetic maternity analyses indicated that a male spawns with an average of four females (range, one to six) (DeWoody *et al.* 2000a). Evidence was suggestive, though not conclusive, that larger males received eggs from more females than smaller males. In the same population, paternity analyses revealed the occurrence of nest takeovers by guardian males, and the presence in low frequencies (5–15%) of precociously mature sneaker males (DeWoody *et al.* 2000a). Cuckoldry, however, was estimated at only 1.3% of all offspring examined. Other spawning, nest-guarding, and associated behaviors are typical of the genus (Carr 1946). Female size and fecundity relationships are apparently not quantified. Water-hardened, fertilized eggs are 1.4 to 1.8 mm in diameter, adhesive (often adhering to fine roots along the shoreline side of the nest), demersal, and dark brownish olive to pale transparent amber in color (Carr 1946; Marcy *et al.* 2005). The male constantly fans the eggs until they hatch (2.0–2.2 days; presumed temperature of 20–24°C; hatchling length, 4 mm TL). About 10 days after hatching, swim-up larvae (6.5–7.0 mm TL) begin leaving the nest over a 2-day period and briefly form loose schools in the surrounding area before dispersing (Carr 1946). Anecdotal accounts suggest that guardian males are among the most pugnacious and tenacious defenders of eggs and larvae among centrarchids (Hubbs and Allen 1943; Carr 1946; Clugston 1966).

Nest associates: Golden shiner, *N. crysoleucas* (Carr 1946).

Freshwater mussel host: None known.

Conservation status: The spotted sunfish is currently stable (Warren *et al.* 2000) but is considered vulnerable in North Carolina, the northern periphery of its range (NatureServe 2006).

Similar species: See account on redspotted sunfish. The redspotted sunfish lacks distinct black specks on head and body (Page and Burr 1991; Warren 1992).

Systematic notes: *Lepomis punctatus* is the sister species of *L. miniatus* (Near *et al.* 2004, 2005) (see account on *L. miniatus*).

Importance to humans: Most spotted sunfish are caught incidentally by bluegill and redear sunfish anglers, but the spotted sunfish is a consistent part of the panfish creel in many Florida waters (e.g., Suwannee River). Although of relatively small size, the species aggressively attacks live baits, such as crickets, mealworms, or Catalpa worms, or small popping bugs. When taken on ultralight gear, the species puts up a scrappy fight, and as table fare, the flesh is excellent (FFWCC 2006).

13.8.13 Lepomis symmetricus *Forbes*

13.8.13.1 Bantam sunfish

Characteristics: See generic account for general characteristics. Body deep, compressed, depth 0.48 to 0.53 of SL. Mouth moderately large, supramaxilla small (>3 times and ≤4 times length of maxilla), upper jaw extending beyond anterior edge of eye. Black spot posterior of soft dorsal fin in young, diminishing with growth, absent in large adults. Lacks the bright coloration of other *Lepomis*. Opercular flap short, stiff, and black with pale posterior margin. Very long slender gill rakers, 12 to 15, longest about six to eight times greatest width. Pectoral fin short and rounded, tip usually not reaching eye when laid forward across cheek. Lateral line usually incomplete (1–18 scales unpored) or interrupted (up to 6 times). Lateral scales, (30)32 to 36(40); rows above lateral line, 5 to 7; rows below lateral line, 12 to 14; cheek scale rows, (4)5(6); caudal peduncle scale rows, (17)18 to 21(22); pectoral rays, (11)12 to 13. Pharyngeal arches narrow with small, blunt subconical teeth. Teeth on palatine bones. No teeth on endopterygoid, ectopterygoid, or glossohyal (tongue) bones (Bailey 1938; Burr 1977; Page and Burr 1991; Etnier and Starnes 1993; Mabee 1993).

Size and age: Typically reach 34 to 46 mm SL at age 1. Large individuals measure 55 to 64 mm SL, and few live beyond age 2+ (maximum, 93 mm TL, age 3+) (Burr 1977; Page and Burr 1991). The bantam sunfish is the smallest and has the shortest maximum lifespan of any *Lepomis*. Growth differences between males and females are minimal (Burr 1977).

Coloration: Ear flap, short, black with light edge. Lacks bright coloration of other *Lepomis*. Dusky green above and on sides; yellow flecks and scattered small dark brown spots (adult) or chainlike bars (young) on sides; yellow-brown below. Anal and dorsal fins, red in young, clear to dusky in adults (Burr 1977; Page and Burr 1991)

Native range: The bantam sunfish is native to drainages of the Mississippi Embayment and lower Ohio River Valley from Illinois and western Indiana to the Gulf of Mexico and the Gulf Coastal Plain from Bay St. Louis, Mississippi, to the Colorado River, Texas (Page and Burr 1991). A post-Pleistocene relict population in the Illinois River is now extirpated as are populations in the lower Wabash River (Illinois and Indiana) (Burr 1977; Burr and Page 1986, 1991; NatureServe 2006). The species is most common in Louisiana and east Texas and a few scattered, relatively undisturbed remnant floodplain lakes and wetland systems in the lower Mississippi River alluvial valley (e.g., Wolf and Horseshoe Lakes, Illinois; Mingo Swamp, Missouri; Murphys Pond, Kentucky; Reelfoot Lake, Tennessee) (Burr 1977; Burr and Warren 1986; Burr *et al.* 1988; Etnier and Starnes 1993; Pflieger 1997).

Habitat: The bantam sunfish is a phytophilic species occurring almost exclusively in oxbow lakes, floodplain ponds, overflow swamps, and sloughs that are characterized by standing timber, submerged logs, and dense beds of aquatic plants (Burr 1977; Page and Burr 1991). Substantial populations can also occur in large, shallow eutrophic reservoirs (Bettoli *et al.* 1993) and freshwater coastal marshes (Gelwick *et al.* 2001). The species occupies the shallow (15–120 cm) heavily vegetated margins of lentic habitats over mud, detritus, and decayed plant material (Burr 1977) and is tolerant of hypoxic conditions associated with dense aquatic plants beds (<1 mg/l DO, Gelwick *et al.* 2001; Killgore and Hoover 2001). Removal of aquatic vegetation in Lake Conroe, Texas, by nonnative grass carp (*C. idella*) resulted in a population collapse of the bantam sunfish (Bettoli *et al.* 1993). The species can apparently migrate across flooded lowlands during major flood events (Mississippi River flood, 1993), resulting in establishment of founder populations in formerly unoccupied habitats (Burr *et al.* 1996).

Food: The bantam sunfish is an opportunistic invertivore. Adult (>40 mm SL) diets are predominated by odonate larvae, amphipods, hemipterans, dipteran larvae, mayflies, and gastropods. The diet of juvenile bantam sunfish (<30 mm TL) is similar to that of the adult, but includes higher consumption (to 40 mm TL) of microcrustaceans and midge larvae and lacks gastropods. Terrestrial or surface-dwelling insects (hemipterans) in stomachs indicate that some surface feeding occurs. Seasonally consumed foods include heavy use of gastropods in winter and spring and hemipterans in summer (Burr 1977).

Reproduction: The female bantam sunfish matures at 34 to 45 mm SL at an age of 11 to 13 months; mature males are at least of age 1+ and ≥40 mm SL (Burr 1977). In captivity with optimal feeding, sexual maturity is reached in as little as 5 to 7 months (Wetzel 2007). Few other *Lepomis* (e.g., green and orangespotted sunfishes) consistently mature at such small sizes. The bantam sunfish also differs from congeners, particularly sympatric species, in its earlier and shorter spawning period, relatively small mature ova, and low batch fecundity. Males and females in breeding condition are present from mid-April to early June with peak breeding condition occurring in May at water temperatures of 18 to 22°C. In aquaria, males used caudal sweeping and the anal fin to excavate nests (70–120 mm diameter, 2 cm deep) over both sand and gravel, but in natural settings nests are excavated over fibrous root material in dense aquatic vegetation or over mud and leaf litter (Robison 1975; Zeman and Burr 2004; Wetzel 2007). Nests are closely spaced (about 40 cm apart), and as territorial boundaries are established, neighhoring males are intensely aggressive (e.g., biting attacks) and display frequently (e.g., opercle flaring) toward neighboring nesting males (Wetzel 2007). In aquaria, if females are unresponsive to courtship, the nest-guarding male will nip, nudge, badger, opercle flare, and continuously circle the female, ultimately killing her (Burr 1977; Zeman and Burr 2004; Wetzel 2007). Receptive females rotate and flash the ventral surface toward the male, and in response, he repeatedly rushes to her and back to the nest until she follows. Once over the nest, the pair circles and spawns for about 30 minutes, at which time the male chases the female away. After spawning, males may engage in brief bouts of caudal sweeping and begin interspersing fanning of the eggs with aggressive displays and actions toward neighboring males. Spawning in aquaria occurred at about dawn at water temperatures of 22 to 26°C. The mature ova are translucent orange in color and range from 0.6 to 0.9 mm in diameter; fertilized eggs are adhesive (Burr 1977; Zeman and Burr 2004; Wetzel 2007). Fecundity increases with female size. The relationship between potential batch fecundity (Y) and adjusted body weight (X, total weight minus ovaries and viscera) is described by the linear function, $Y = -50.94 + 210.7X$ ($n = 14$, $R^2 = 0.67$; for SL, $\log_{10} Y = -2.785 + 3.383 \log_{10} X$, $R^2 = 0.44$; formulas from Burr 1977). At 2.44 g (ca. 42 mm SL), a female can potentially produce 463 mature eggs in a single batch (range: 248 eggs at 1.42 g, ca. 34 mm SL, to 1544 eggs at 7.57 g, ca. 52 mm SL). The male defends eggs and larvae for about 6 to 7 days. Eggs hatch in 26 to 36 hours at 22 to 26°C and reach swim-up about 5 days post hatch. Males defend the eggs and young with aggression noticeably increasing as the fry reach swim-up. Larvae begin leaving the nest by ascending in the water column and at dusk take refuge and feed in vegetation beds. Male defense of the young continues to he high until the larvae ascend into the vegetation (Zeman and Burr 2004; Wetzel 2007).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The bantam sunfish is likely much less widespread and abundant in the lowlands of the Mississippi Embayment and Gulf Coastal Plain than historically because of extensive channelization of streams and drainage of wetlands in the last century. Extirpations of northern populations in the Illinois and lower Wabash rivers exemplify effects of wetland habitat loss (Burr 1977; Zeman and Burr 2004). The species is considered critically imperiled in Indiana and Illinois, imperiled in Missouri and Oklahoma, and vulnerable in Texas and Arkansas (NatureServe 2006).

Similar species: Other *Lepomis* lack the dark spot at the rear of the second dorsal fin (diminishing with growth, absent in large adults) (except the bluegill and green sunfish). The green sunfish is more elongate, has a larger mouth, and has yellow-orange edges on its fins. The bluegill is more compressed, has a longer pectoral fin, and has a dark edge on its ear flap (Page and Burr 1991).

Systematic notes: *Lepomis symmetricus* forms a sister pair with *L. cyanellus* (Near *et al*. 2004, 2005). Interestingly, the sister pair comprises the smallest and second largest *Lepomis* and their ranges are sympatric. In a comprehensive study of morphological variation (Burr 1977), *L. symmetricus* showed surprisingly little variability, particularly given its distribution in isolated patches over a large geographic area. Variation in average counts showed a north–south clinal pattern. Populations in the Wabash River drainage were most aberrant, averaging higher scale and lower fin-ray counts.

Importance to humans: The bantam sunfish does not reach a size of interest to anglers. Ecologically, the presence and abundance of the species within its native range is a decided indicator of functioning, relatively intact wetland ecosystems.

13.9 *Micropterus* Lacépède

The genus *Micropterus*, collectively referred to as the black basses, is a monophyletic clade of eight species and is sister to the genus *Lepomis* (Near *et al*. 2004, 2005). The natural range of extant species encompasses most of eastern North America east of the Rocky Mountains, reaching northward to the Great Lakes, St. Lawrence River, and Hudson Bay drainages of Canada and eastward and southward in the Mississippi River basin, Atlantic Slope, and Gulf of Mexico drainages west to the Rio Grande and Rio Sota la Marina in Mexico (Robbins and MacCrimmon 1974; Page and Burr 1991; Miller 2005). A large fossil species, *Micropterus †relictus* Cavender and Smith, is estimated to have weighed over 5.5 kg and is known from Late Pliocene-Early Pleistocene deposits in Lake Chapala, Jalisco, Mexico, a location south of the native range of all other fossil or extant centrarchids (Smith *et al*. 1975; Miller and Smith 1986).

The smallmouth bass, largemouth bass, Florida bass, and to a lesser extent, the spotted bass form a quadtuplet of the most sought-after and valued freshwater sport fishes in North America. Other *Micropterus* are gaining sport fishing acclaim and popularity as unique, range-restricted fishes associated with beautiful, natural stream settings (e.g., Guadalupe bass, Shoal bass, Suwannee bass). No recreational fishery likely exceeds in economic scale the fishery targeting black basses (Ridgway and Philipp 2002). Of all anglers who fished in freshwater in 2001 (excluding the Great Lakes), 38% sought one or more species of black bass (Leonard 2005). The black bass recreational fishery ranked first among freshwater species in the number of anglers (10.7 million) and time spent fishing (nearly 160 million days). In the Great Lakes, black bass are second only to perch in the numbers of anglers (589,000 anglers) and time spent fishing (6.4 million days). Estimated direct expenditures (e.g., travel, lodging, equipment) associated with black bass fishing (excluding the Great Lakes) exceeded $10.1 billion (US) in 2001, and generated additional tens of billions of dollars more in indirect economic output and taxes (USFWS 2002; ASA 2005).

The reproductive behavior and biology of *Micropterus* are typical for the family in many ways but depart in others. The existence of extended parental care (see next paragraph), alternating mating systems (see account on *Micropterus dolomieu*), and biparental care (see account on *Micropterus salmoides*) distinguish the genus from other centrarchids. Unlike their sister genus *Lepomis*, *Micropterus* do not develop bright breeding colors, and obvious sexual dimorphism of any kind is minimal. During spawning, differential darkening or intensification of pigment patterns occurs in breeding males and females (Carr 1942; Breder and Rosen 1966; Heidinger 1975; Miller 1975; Trautman 1981; Williams and Burgess 1999). As in *Lepomis*, changes in pigment pattern in the female likely function as submissive signals to the male. *Micropterus* males are solitary nesters, usually establishing well-spaced territories and using caudal sweeping and other fin movements to excavate a typical, depressional centrarchid nest. Nests are most often constructed at the base of or near simple cover (Carr 1942; Neves 1975; Vogele 1975a, 1981; Winemiller and Taylor 1982; Wiegmann *et al*. 1992; Hunt and Annett 2002; Hunt *et al*. 2002). Nest-site fidelity in *Micropterus* is apparently high. Males may use nesting areas year after year with individual males often returning to within a few meters of their previous year's nest site or reusing the same nest in subsequent years (Carr 1942; Vogele 1975a; Ridgway *et al*. 1991a, 2002; Rejwan *et al*. 1997, 1999; Hunt *et al*. 2002; Ridgway *et al*. 2002; Waters and Noble 2004). In courtship, *Micropterus* males use leading or guiding courtship behaviors to attract females to the nest, often leaving the nest to approach, but not charge, the ripe female (Carr 1942; Ridgway *et al*. 1989).

In contrast to all other centrarchids, *Micropterus* males stay with their brood well after the swim-up stage and continue to guard free-swimming swarms of young, termed fry balls, until the young reach sizes of about 25 to 30 mm TL (e.g., Kramer and Smith 1962; Miller 1975; Vogele 1975a; Elliott 1976; Brown and Colgan 1985a; Friesen and Ridgway 2000). Large *Micropterus* males tenaciously guard their eggs, yolk-sac fry, free-swimming fry, and juveniles (Hubbs and Bailey 1938; Ridgway 1988; Wiegmann *et al*. 1992; Wiegmann and Baylis 1995; Steinhart *et al*. 2005). For example, males excluded from their nests by exclosures stayed nearby for 11 days and immediately began guarding the young on removal of the nest exclosures (Neves 1975). Although poorly documented in some species (e.g., Guadalupe and Shoal basses), the total period of parental care for successful males (spawning through fry dispersal) can last for 2 to 7 or more weeks (Hubbs and Bailey 1938; Kramer and Smith 1962; Pflieger 1966a; Miller 1975; Vogele 1975a; Cooke *et al*. 2006) but is highly variable even within a population in a single spawning season and among years (e.g., 19 to 45 days; Ridgway and Friesen 1992). Variability is largely a function of changes in water temperature, and hence larval developmental rate, but also involves interactive effects of the time of nesting (early versus late), size of male, and energy depletion in males. Large mature males tend to nest earlier at lower water temperatures and invest longer periods in parental care (through swim-up) than do small mature males (Ridgway and Friesen 1992).

The *Micropterus* male must patrol larger and larger areas as the fry balls forage increasing distances away from the nest (Ridgway 1988; Scott *et al*. 1997). Fry balls of *Micropterus* from single broods contain from several hundred to over ten thousand individuals (Kramer and Smith 1962; Friesen and Ridgway 2000). Individual broods often merge to form even larger groups of intermingled multiple broods of one or more black bass species, aggregations that cover extensive areas, and are under constant protection by one or more males (Carr 1942; Kramer and Smith 1962; Allan and Romero 1975; Vogele 1975a). Free-swimming juveniles of largemouth bass and perhaps other black basses are less oriented toward the nest than smallmouth bass; the juveniles leave the area of the nest and become increasingly mobile, feeding constantly during daylight hours and seeking cover at night (Carr 1942; Kramer and Smith 1962; Elliott 1976; Brown 1984, 1985; Brown and Colgan 1984). The increasing mobility of the roaming juveniles places high diurnal energy demands on the guardian males (Cooke *et al*. 2002a).

Generic characteristics: Elongate, slightly compressed body, depth usually <0.28 of TL. Dusky to black blotch at rear of gill cover (no long opercular flap). Dark, diagonal lines radiating from snout and back of eye to edge of opercle. Clear to olive-yellow fins; dusky spots on median fins. Mouth large, extending at least to below center of eye (in adults), supramaxilla large, well developed (≤2 times length of maxilla). Opercle with two flat projections, lower longer than upper. Emarginate caudal fin. Dorsal fin moderately to deeply emarginate, spiny portion continuous with to almost separate from soft-rayed portion. Long dorsal fin, usually 10 spines (9–10), 12 to 15 rays, usually 22 to 25 total; and short anal fin, 3 spines, 10 to 11 rays, 13 to 15 total. Dorsal fin base about two times longer than anal fin base. Pectoral fin rounded, rays 13 to 18. Preopercle margin entire. Gill rakers moderate in length, 5 to 11. Ctenoid scales. Lateral line complete; lateral line scales, ≥55. Vertebrae, usually 32(30–33) (14 or 15 + 17 or 18). Branchiostegal rays, 6. Pyloric caeca single or branched. Teeth present on palatine (villiform) and ectopterygoid. Teeth absent on endopterygoid and present or absent on glossohyal (tongue) bones (Bailey 1938; Hubbs and Bailey 1940, 1942; Bailey and Hubbs 1949; Bryan 1969; Page and Burr 1991; Mabee 1993; Williams and Burgess 1999).

Similar species: Species of *Micropterus* have three anal fin spines that separate them from all other centrarchids except *Lepomis* and *Enneacanthus*. *Micropterus* have emarginate caudal fins (versus rounded in *Enneacanthus*) and elongate, slightly compressed bodies with ≥55 lateral scales (versus deep, compressed body and <55 lateral line scales in *Enneacanthus* and *Lepomis*).

13.9.1 Micropterus cataractae *Williams and Burgess*

13.9.1.1 Shoal bass

Characteristics: See generic account for general characteristics. Elongate, slightly compressed body, depth 0.20 to 0.26 of TL, increasing with size. Mouth large, terminal, lower jaw slightly projecting, upper jaw reaches to posterior edge of eye in adult. Outline of spinous dorsal fin curved. Juncture of soft and spiny dorsal fins slightly emarginate, broadly connected. Shortest dorsal spine at emargination of fin, usually >0.6 times length of longest spine. Dorsal soft rays, usually 12, 10 to 13; anal soft rays, usually 10, 9 to 11. Gill rakers, usually 7, 6 to 9. Lateral scales, (65)72 to 77(81); rows above lateral line 8 to 9(12); rows below lateral line, (15)17 to 20(24); cheek scale rows, (11)13 to 15(18); caudal peduncle scale rows, (27)30 to 33(35); pectoral rays, (14)16 to 17. Small splintlike scales on interradial membranes at anal and second dorsal fin bases (>60 mm SL). Pyloric caeca, single, rarely branched, usually 12, 8 to 14. Tooth patch absent (a few teeth rarely present) on glossohyal (tongue) bone (Wright 1967; Williams and Burgess 1999; Kassler *et al*. 2002).

Size and age: Typically reach 60 to 109 mm TL (average, 66–96 mm) at age 1 (Parsons and Crittenden 1959; Wright 1967; Hurst 1969). Young-of-the-year stocked in ponds in June at 21 to 24 mm TL reached 142 to 169 mm TL by December (Smitherman and Ramsey 1972). Large individuals reach 380 to 450 mm TL, weigh 0.8 to 1.1 kg, and attain age 6+ to 8+ (maximum about 523 mm TL and 10+ years) (Parsons and Crittenden 1959; Wright 1967; Hurst 1969; Smitherman and Ramsey 1972; Page and Burr 1991; Gilbert 1992a; Williams and Burgess 1999). World angling record, 3.99 kg, Florida (IGFA 2006).

Coloration: Body with 10 to 15 midlateral and 6 to 8 dorsolateral, dark vertically elongate blotches, becoming gradually more quadrate posteriorly. Interspaces between midlateral blotches about equal to width of individual blotches, and supralateral blotches extend into interspaces between lateral blotches (may be obscured by dark dorsum). The vertically elongate blotches form a distinctive "tiger stripe" pattern. Large square to rectangular basicaudal blotch is usually present. Dusky to dark spots on ventrolateral scales frequently coalesce to form wavy lines. Iris typically bright red. Ground coloration above and on sides of head and body olive green to dark olive to black; body white to cream colored below (Williams and Burgess 1999).

Native range: The shoal bass is native to the Apalachicola and Chipola rivers in western Florida, the Chattahoochee River in eastern Alabama and western Georgia, and the Flint River in southwestern Georgia (Page and Burr 1991; Williams and Burgess 1999). In the 1970s, the species was introduced intentionally by state fisheries personnel into the Ocmulgee River (Altamaha River drainage), Georgia, where it is now established along 88 km of the main channel and adjacent tributaries (Williams and Burgess 1999).

Habitat: The shoal bass, as the name implies, is a frequent inhabitant of shoal areas of rivers and large streams (Williams and Burgess 1999). Although individuals of all sizes occur in both pools and shoals, as a percentage of the *Micropterus* assemblage, shoal bass are better represented in shoals. In the Chipola River, Florida, the ratio of age-0 and adult shoal bass to largemouth bass was greater in shoals than in pools (Wheeler and Allen 2003), results consistent with observations elsewhere (Wright 1967). The ratio of age-0 shoal bass to age-0 largemouth bass was 6.9:1 in shoals and 1.4:1 in pools, suggesting shoal habitat as important spawning or nursery areas. Age-0 shoal bass were associated with higher than average percentage of rocky substrate in pools, but not shoals, and larger shoal bass were associated with higher than average percentage of rocky substrate in pools and shoals. Neither was associated with lower than average current speeds in either pools or shoals (Wheeler and Allen 2003).

Food: The shoal bass is a top carnivore, exploiting benthic and water column prey (Wright 1967; Hurst 1969; Wheeler and Allen 2003). Adult food consists primarily of fishes (e.g., darters, madtom catfish, minnows, *Lepomis* spp.), crayfishes, and to a much lesser extent, insects. Fish and crayfish comprise >90% of the diet biomass in fish >140 mm TL. At 40 to 140 mm TL, small shoal bass transition from diets dominated by aquatic insect larvae (e.g., mayflies) to increased consumption of fish and crayfish (Wright 1967; Wheeler and Allen 2003).

Reproduction: Females reach maturity at minimum sizes of 152 to 189 mm SL and age 2+, but most mature at age 3+ (Wright 1967; Hurst 1969; Hurst *et al.* 1975). On the basis of occurrence of ripe, partially spent, or recently spent females and observations in ponds, spawning occurs from April to May (perhaps into June) at water temperatures from 18.0 to 26.0°C. Ripe, presumably prespawning, females are taken at temperatures as low as 14.4°C in early April (Wright 1967; Hurst 1969; Smitherman and Ramsey 1972; Williams and Burgess 1999). Nests are circular depressions about 30 to 92 cm in diameter and 5 to 15 cm deep. In streams, nests are located in shallow water (20–45 cm deep) of pools upstream of riffles or in eddies adjacent to shoals, and in culture ponds, nests were excavated at water depths of 76 to 130 cm over clay, soft clay rubble, or plant roots (Wright 1967; Hurst 1969; Williams and Burgess 1999). Males reportedly vigorously guard the nest (Williams and Burgess 1999). Observations of a single spawning pair indicated an apparently typical *Micropterus* spawning sequence that lasted about 45 minutes and resulted in deposition of about 1000 large (2-mm diameter), amber-colored, adhesive eggs. While over the nest, the pair assumed a blotched coloration of dark green vertical bars on a background color of bronze. Other nests contained 500 to 3000 ova (Williams and Burgess 1999). Fecundity increases with female size but is not well quantified. The number of eggs (unclear whether total or mature) in five mature females ranged from 5396 eggs at 314 mm SL and 884 g to 21,799 eggs at 442 mm SL and 2314 g (Wright 1967). Eggs hatch in about 2 days at 21.1°C (Smitherman and Ramsey 1972), and yolk-sac larvae, averaging 4.4 mm TL, form tight aggregations in the nest bottom. The larvae reach swim-up about 7 days after hatching and disperse about 12 to 14 days after hatching (Smitherman and Ramsey 1972; Williams and Burgess 1999).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The shoal bass is vulnerable throughout its native range (Warren *et al.* 2000). The species is considered critically imperiled in Florida, imperiled in Alabama, and vulnerable in Georgia (NatureServe 2006). In the Chattahoochee River, the shoal bass has disappeared from most of the main channel and declined in tributaries because of impoundments eliminating shoal habitats, increased sedimentation, and water quality degradation. Its former distributional extent in the Apalachicola and Flint rivers is also reduced by impoundments and channel dredging (Williams and Burgess 1999; Johnston 2004).

Similar species: Superficially similar to redeye bass and spotted bass. Shoal bass (92% of specimens) lack a tooth patch on the tongue (versus oval to elongate patch in spotted bass and redeye bass). In adult shoal bass, the anterior half to two-thirds of the body has dark, vertically elongated, midlateral blotches that are separated by lighter areas approximately equal to the width of the blotch (versus irregular to more quadrate blotches in redeye bass); blotches usually confluent to form a midlateral stripe in spotted bass. Shoal bass also lack white outer edges on the caudal fin (present in redeye bass) and have higher caudal peduncle scale counts (Page and Burr 1991; Gilbert 1992a; Williams and Burgess 1999).

Systematic notes: *Micropterus cataractae* is a member of a "Gulf of Mexico" clade of *Micropterus*, including all other *Micropterus* except *M. dolomieu* and *Micropterus punctulatus* (Kassler *et al.* 2002; Near *et al.* 2003, 2004). Relationships within the clade are not well resolved with *M. cataractae* placed as basal to the entire clade, sister to *Micropterus coosae*, sister to *Micropterus notius*, or basal to a clade inclusive of *M. notius*, *M. p. henshalli*, *Micropterus treculi*, and *M. salmoides* + *Micropterus floridanus* (Kassler *et al.* 2002; Near *et al.* 2003, 2004).

Importance to humans: Shoal bass are the signature fish of a productive sport fishery in the Flint River, Georgia, particularly in the upper river (Davis 2006). Anglers wade fish the shoals using fly rods and crayfish-like flies or light to medium spinning gear with a variety of spinners, crayfish imitations, popping bugs, or other bass lures. The fast water habits of the shoal bass, a restricted native range, a scrappy fighting ability, and the propensity to take a fly and dive into the rocks, all combine for an exciting and specialty black bass catch. Supplemental stocking of shoal bass is being undertaken to augment the population in the lower Flint River (Davis 2006).

13.9.2 Micropterus coosae *Hubbs and Bailey*

13.9.2.1 Redeye bass

Characteristics: See generic account for general characteristics. Elongate body, depth 0.20 to 0.24 of TL, increasing with size. Mouth large, terminal, lower jaw slightly projecting, upper jaw extends little or not at all beyond posterior edge of eye. Outline of spinous dorsal fin curved. Juncture of soft and spiny dorsal fins slightly emarginate, broadly connected. Shortest dorsal spine at emargination of fin, usually >0.75 times length of longest spine. Dorsal soft rays, usually 12, 11 to 14; anal soft rays, usually 10, 9 to 11. Gill rakers, (6)7 to 8. Lateral scales, (58)67 to 72(77); rows above lateral line, (7)8 to 9(13); rows below lateral line, (11)14 to 17(21); cheek scale rows, (8)12 to 13(16); caudal peduncle scale rows, (24)26 to 30(31); pectoral rays, (13)15 to 16(17). Small splintlike scales on interradial membranes at anal and second dorsal fin bases (>60 mm SL). Pyloric caeca, usually unbranched, 7 to 12. Teeth present or absent on glossohyal (tongue) bone (Hubbs and Bailey 1940; Ramsey and Smitherman 1972; Turner *et al.* 1991; Williams and Burgess 1999; Kassler *et al.* 2002).

Size and age: Averages 49 to 63 mm TL (range, 38–68 mm) at age 1 in streams. Growth in ponds and reservoirs can be much higher (≥125 mm TL at age 1) (Parsons 1954; Gwinner *et al.* 1975; Catchings 1979; Barwick and Moore 1983). Young-of-the-year (22–25 mm TL) stocked in forage-supplemented ponds in June reached 134 mm TL by mid-December (Smitherman and Ramsey 1972; Smitherman 1975) and in some reservoirs individuals average 122 to 125 mm TL at age 1 (Barwick and Moore 1983). Few redeye bass reach 325 mm TL, exceed 225 g, and attain age 5+ to 7+ (maximum about 470 mm TL, 1.44 kg, and age 10+) (Parsons 1954; Smitherman 1975; Carlander 1977; Barwick and Moore 1983; Page and Burr 1991; Etnier and Starnes 1993; Boschung and Mayden 2004; OutdoorAlabama 2006). Redeye bass are perhaps the slowest growing *Micropterus*. The maximum size attained even in the fastest-growing reservoir populations suggests genetically based size limitations (Barwick and Moore 1983; Moyle 2002).

Coloration: Uniquely, among all *Micropterus*, the outer margins of the caudal fin lobes in redeye bass are narrowly depigmented (in life iridescent white or frosted orange in color, may be less obvious in large individuals) (Ramsey 1975). Color above olive to deep bronze. Back to lateral midline marked with dark, vertically elongate, diamond-shaped to irregularly quadrate blotches, most evident in young, fading with age. Rows of dark spots usually evident on lower sides. Yellow-white ventral area. Iris characteristically red. Breeding males with aqua-blue to blue-green cast on lower half of head and ventral area. Young-of-the-year soft dorsal fin, caudal fin, and front of anal fin tinged brick red to orange; caudal fin lacks sharply contrasting tricolored pigmentation (Ramsey and Smitherman 1972; Page and Burr 1991; Turner *et al.* 1991; Etnier and Starnes 1993; Mettee *et al.* 1996; Boschung and Mayden 2004).

Native range: The redeye bass is native above the Fall Line from the Savannah, Altamaha, and Chattahoochee rivers and the upper Mobile Basin (Coosa, Cahaba, Tallapoosa, and Black Warrior rivers) in North Carolina, South Carolina, Georgia, Tennessee, and Alabama (Page and Burr 1991; Williams and Burgess 1999). The native or introduced status of the species in the Santee River drainage, North and South Carolina, is uncertain (Warren *et al.* 2000), but preliminary genetic analyses suggest that the population(s) in the Saluda River is introduced (F. C. Rohde personal communication, Division of Marine Fishes, North Carolina). From about 1940 through the 1960s, the species was introduced outside its native range and is now established in tributaries of the Tennessee and Cumberland rivers, Tennessee and Kentucky, and in several drainages in California (Fuller *et al.* 1999; Moyle 2002). Although often debated as native rather than introduced (e.g., Clay 1975; Koppelman and Garrett 2002), established populations in Martins Fork Cumberland River, Kentucky, were introduced deliberately by state fisheries personnel around 1950 from stock obtained in Georgia (Burr and Warren 1986). In Tennessee and Cumberland river streams, introduced redeye bass have hybridized extensively and likely introgressed with native smallmouth bass (Turner *et al.* 1991; Pipas and Bulow 1998). Some superabundant stream populations of redeye bass developed after introductions in California, where the species is associated with declines of native minnows, suckers, salamanders, and ranid frogs (Fuller *et al.* 1999; Moyle 2002).

Habitat: The redeye bass inhabits rocky, small upland creeks and small to medium upland rivers, where it is associated with pools, boulders, undercut banks, and water willow beds (Parsons 1954; Page and Burr 1991; Pipas and Bulow 1998; Moyle 2002). The species can be common even in the smallest headwater stream where few other fish and no other *Micropterus* occur (Parsons 1954; Ramsey 1975; Pipas and Bulow 1998). The redeye bass has been viewed traditionally as potentially providing a fishery in waters too cool and small for other *Micropterus* but too warm for trout (e.g., Parsons 1954; Carlander 1977). These conditions, however, are not prerequisites for establishment of thriving redeye bass populations in nonnative habitats (Pipas and Bulow 1998; Moyle 2002). Indirect evidence suggests that redeye bass make large upstream migrations to tributaries to spawn in the spring (and conversely downstream fall migrations to winter habitat) (Parsons 1954). Redeye bass are generally intolerant of ponds and most reservoirs (Parsons 1954; Wood *et al.* 1956; Webb and Reeves 1975; Moyle 2002; but see Barwick and Moore 1983).

Food: The redeye bass is an opportunistic carnivore, feeding from the surface to the bottom. The summer diet in streams consists primarily of terrestrial insects and crayfish. To a lesser extent, stream-dwelling redeye bass also consume small fishes (e.g., minnows and darters), aquatic insects, and salamanders (Parsons 1954; Smitherman 1975; Gwinner *et al.* 1975). Large redeye bass (>216 mm TL) in oligotrophic reservoirs in South Carolina are primarily piscivorous (Barwick and Moore 1983).

Reproduction: Maturity is reached at a minimum size of 120 mm TL at age 3+ in females and age 4+ in males in streams, but faster growing pond-cultured individuals matured at age 1+ (Parsons 1954; Smitherman 1975). Spawning extends from April to early July as water temperatures reach 18 to 21°C (Parsons 1954; Smitherman and Ramsey 1972; Gwinner *et al.* 1975). Practically nothing is published on male or female reproductive behaviors, and overall knowledge about the reproductive biology of redeye bass is at best sketchy. Nests are shallow, circular depressions in coarse gravel at the heads of pools (Parsons 1954). Fertilized, water-hardened eggs average 3.5 mm in diameter (Smitherman and Ramsey 1972). Relationships between female size and fecundity are unquantified. Two females of 145 and 205 mm TL contained 2084 and 2334 eggs, respectively (Parsons 1954). Eggs hatch in about 2 days at 22.8°C; yolk-sac larvae are 6.0 mm TL, and larvae are free swimming at 7 to 8 mm TL about 5 days after hatching (Smitherman and Ramsey 1972). An anecdotal account suggests that fry school for a short time relative to most *Micropterus* (Parsons 1954). In a culture pond, complete breakup of schools occurred at 16 to 25 mm TL about 14 days after swim-up, but school breakup began as early as 6 days after swim-up (Smitherman and Ramsey 1972).

Nest associates: None known.

Freshwater mussel host: Confirmed host to *L. altilis*, *Lampsilis perovalis*, *V. nebulosa*, and *V. vibex* (Haag and Warren 1997; Haag *et al.* 1999).

Conservation status: The redeye bass is secure throughout its range (Warren *et al.* 2000), but native populations on the periphery of the range are considered vulnerable (Tennessee) or critically imperiled (North Carolina) (NatureServe

2006). Obversely, the past introduction and establishment of redeye bass outside its native range now threatens the genetic integrity of populations of native *Micropterus* (Turner *et al.* 1991; Pipas and Bulow 1998).

Similar species: See accounts on Suwannee bass and spotted bass. Differs from all other *Micropterus* in having the outer margins of the caudal fin lobes narrowly depigmented (iridescent white or frosted orange in life) (Ramsey 1975; Page and Burr 1991).

Systematic notes: *Micropterus coosae* is a member of a "Gulf of Mexico" clade of *Micropterus,* including all other *Micropterus* except *M. dolomieu* and *M. punctulatus* (Near *et al.* 2003, 2004). Relationships within the clade are not well resolved with *M. coosae* placed as basal to the clade, sister to *M. cataractae*, sister to *M. punctulatus henshalli* (the Alabama spotted bass), or basal to *M. notius, M. treculi,* and *M. salmoides* + *M. floridanus* (Kassler *et al.* 2002; Near *et al.* 2003). Similarities in form, color, behavior, and ecology led most morphological taxonomists to relate *M. coosae* to *M. dolomieu* or *M. punctulatus* (e.g., Hubbs and Bailey 1940; Ramsey 1975). Data from nuclear-encoded allozyme loci and mitochondrial DNA reveal significant genetic substructuring among populations now known as redeye bass and strongly suggest the existence of multiple, and perhaps specifically distinct, evolutionary lineages (Kassler *et al.* 2002; Koppelman and Garrett 2002). The evolutionary relationships among populations of redeye bass, and of redeye bass to other *Micropterus,* particularly the Alabama spotted bass (see account on *M. punctulatus*), await thorough genetic evaluation.

Importance to humans: The attractive redeye bass is regarded as a somewhat wary, but scrappy fighter in small, wadeable streams, where it provides an exciting catch on ultralight gear combined with small lures and spinners, popping bugs and flies, or natural bait (Parsons 1954; Etnier and Starnes 1993). In its small stream habitat, redeye bass populations can provide a minimal catch-and-release fishery, but slow growth rates limit establishment of harvestable stream fisheries (Pipas and Bulow 1998).

13.9.3 Micropterus dolomieu *(Lacépède)*

13.9.3.1 Smallmouth bass

Characteristics: Elongate, slightly compressed body, depth 0.18 to 0.28 of TL, decreasing with size. Mouth large, terminal, lower jaw slightly projecting, upper jaw extends at least to below center of eye but not beyond posterior edge of eye. Outline of spinous dorsal fin curved. Juncture of soft and spiny dorsal fins slightly emarginate, broadly connected. Shortest dorsal spine at emargination of fin, usually >0.5 times the length of the longest spine. Dorsal soft rays, usually 13 or 14, 10 to 15; anal soft rays, usually 11, 9 to 12. Gill rakers, 6 to 8. Lateral scales, (64)69 to 77(81); rows above lateral line, (10)12 to 13(15); rows below lateral line, (16)19 to 23(32); cheek scale rows, (13)15 to 18(20); caudal peduncle scale rows, (26)29 to 31(33); pectoral rays, (13)16 to 17(18). Small splintlike scales on interradial membranes at anal and second dorsal fin bases (>60 mm SL). Pyloric caeca, unbranched, about 10 to 15. Teeth present or absent on glossohyal (tongue) bone (Bailey 1938; Hubbs and Bailey 1938, 1940; Smitherman and Ramsey 1972; Turner *et al.* 1991; Kassler *et al.* 2002).

Size and age: Size at age 1 is highly variable among habitats and across latitudes and ranges from 40 to 188 mm TL (median 92 mm TL) (Beamesderfer and North 1995). Large individuals can exceed 400 mm TL, weigh 1.5 to 2.5 kg, and attain age 6+ to 12+ (maximum 686 mm TL, 5.2 kg, and age 14+) (Scott and Crossman 1973; Carlander 1977; Paragamian 1984; Page and Burr 1991; Weathers and Bain 1992; Beamesderfer and North 1995; MacMillan *et al.* 2002). World angling record, 4.93 kg, Tennessee (IGFA 2006). Growth rates are similar between males and females (Carlander 1977).

Coloration: No dark lateral band. Dark brown with numerous bronze markings on scales, often with 8 to 16 indistinct vertical bars on a yellow-green to brown side. Olive brown with bronze specks above, yellow to white below. Iris usually reddish. Large male is green-brown to bronze with dark mottling on back and dark vertical bars on the side. Young (<50 mm TL) boldly patterned with vertical bars and blotches and distinct, contrasting tricolored caudal fin markings (yellowish base, black middle, whitish distal edge) (Page and Burr 1991; Etnier and Starnes 1993; Ross 2001).

Native range: The smallmouth bass is native to the St. Lawrence-Great Lakes, Hudson Bay (Red River), and Mississippi River basins from southern Quebec to North Dakota and south to northern Alabama and eastern Oklahoma (Hubbs and Bailey 1938; Page and Burr 1991). The species has been introduced widely and is now established throughout southern Canada and the United States, except in Atlantic and Gulf Slope drainages, where it is rare from south of Virginia to eastern Texas (MacCrimmon and Robbins 1975; Page and Burr 1991; Jenkins and Burkhead 1994; Snyder *et al.* 1996; Fuller *et al.* 1999).

Nonnative smallmouth bass can hybridize and introgress with native species of *Micropterus*, ultimately compromising the genetic integrity of the native bass, and as a top predator, smallmouth bass may have profound direct and indirect impacts on native fishes and whole aquatic ecosystems. The most egregious case of introgression involves the near total genetic swamping of the range-restricted Guadalupe bass, *M. treculi* (Whitmore and Butler 1982; Whitmore 1983; Whitmore and Hellier 1988; Morizot *et al.* 1991; Pierce and Van Den Avyle 1997; Koppelman and Garrett 2002). Predation effects by nonnative smallmouth bass in Canadian lakes resulted in dramatic changes in food–web dynamics and shifted the native top predator, the lake trout (*Salvelinus namaycush*), from a primary diet of littoral fishes to zooplankton. The consequences for the affected lake trout populations are potentially severe (Vander Zanden *et al.* 1999, 2004). Established, nonnative populations of smallmouth bass are also implicated in loss in diversity of nongame freshwater fishes, impacts on migrating salmon, and declines in native amphibians (Bennett *et al.* 1991; Tabor *et al.* 1993; Chapleau and Findlay 1997; Findlay *et al.* 2000; MacRae and Jackson 2001; Jackson 2002; Moyle 2002; Fritts and Pearsons 2004, 2006; Weidel *et al.* 2007).

Habitat: The smallmouth bass inhabits clear, cool, runs and pools of small to large rocky rivers and the rocky shorelines of lakes and reservoirs (Page and Burr 1991). Although frequently and justifiably described as inhabiting clearer and cooler waters than other *Micropterus*, co-occurrence with congeners across the large north-to-south range is common (e.g., Funk 1975), but abundances of smallmouth bass among mesohabitats often differ from co-occurring *Micropterus*. For example, in a Kentucky reservoir with three *Micropterus* species, smallmouth bass tended to be most abundant and largemouth bass least abundant in the oligotrophic section, and spotted bass showed highest abundance in both mesotrophic and oligotrophic sections (Buynak *et al.* 1989). Similarly, in Ozark Border streams in Missouri, abundance of smallmouth bass is related inversely to percent pool area and maximum summer water temperature, a pattern opposite to that observed for largemouth bass (Sowa and Rabeni 1995).

Across its broad range, the smallmouth bass occupies a wide variety of habitats depending on life stage, food availability, and habitat conditions, but the most consistent physical habitat association for adults in rivers, lakes, and reservoirs is proximity to submerged cover (e.g., steep drop-offs, ledges, crevices, boulders, stumps, logs, logjams). Juveniles are often associated with large substrates relative to their body size, but can also use a wide range of currents, depths, substrates, and cover types. The habitat, environmental tolerances, bioenergetics, and spatial ecology of the smallmouth bass from hatching to adult in both lake and riverine environments are documented extensively. Here the focus is to briefly introduce aspects of smallmouth bass movement in lake and riverine environments and some effects of temperature, pH, and DO on the species. A wealth of detailed information is available in the references cited in this account and many other original sources, reviews, and syntheses (e.g., Robbins and MacCrimmon 1974; Coble 1975; Coutant 1975; MacCrimmon and Robbins 1981; Rankin 1986; McClendon and Rabeni 1987; Bain *et al.* 1988; Leonard and Orth 1988; Simonson and Swenson 1990; DeAngelis *et al.* 1991, 1993; Lobb and Orth 1991; Lyons 1991; Armour 1993; Jager *et al.* 1993; Barrett and Maughan 1994; Smale and Rabeni 1995b; Walters and Wilson 1996; Peterson and Kwak 1999; Zweifel *et al.* 1999; Cooke *et al.* 2000b, 2002b; Philipp and Ridgway 2002; Whitledge *et al.* 2006; Brewer *et al.* 2007; Dunlop *et al.* 2007).

In lakes and streams, smallmouth bass rather consistently remain in home areas in summer but can make seasonal movements to specific wintering areas and traverse relatively long distances in apparent exploratory movements (e.g., 66 km) or to return to a home area after being displaced (e.g., Funk 1957; Fajen 1962; Reynolds 1965; Carlander 1977; Gerber and Haynes 1988; Kraai *et al.* 1991; Peterson and Rabeni 1996; Ridgway and Shuter 1996; Hayes *et al.* 1997; Lyons and Kanehl 2002; Bunt *et al.* 2002; Ridgway *et al.* 2002; VanArnum *et al.* 2004). In summer, adults in lakes or reservoirs occupy persistent (weeks to months) postspawning home activity areas (0.2–43 ha) that are usually along rocky shorelines (or areas of steep bottom relief), but during this time individuals may frequently shift areas occupied and, in some cases, move extensively and apparently randomly (Hubert and Lackey 1980; Kraai *et al.* 1991; Savitz *et al.* 1993; Demers *et al.* 1996; Cole and Moring 1997). The size of the activity area is related positively to fish size; larger fish tend to include depths >4 m in their activity areas, and at least some individuals occupy distinctive diurnal and nocturnal activity areas (Emery 1973; Savitz *et al.* 1993; Cole and Moring 1997). In Lake Opeongo, Ontario, smallmouth bass use the largest recorded summer home ranges among centrarchids. Average postnesting home range area is 247 ha for males and 409 ha females, but core use areas (50% use) are smaller (38.4 ha) and similar between sexes. Individual male summer home ranges show high coincidence from year to year, indicating that males in the lake return from nesting areas to the same home ranges over multiple years (Ridgway and Shuter 1996; Ridgway *et al.* 2002). Daytime movements within these large home ranges are extensive, averaging 4.8 km over 6- to 16-hour periods (about 483 m/h), but there is little activity at night (Ridgway *et al.* 2002). The differences in home range size estimates among smallmouth bass in different lakes may be attributable to methods used to estimate home range (e.g., Savitz *et al.* 1993; Cole and Moring 1997; Ridgway *et al.* 2002) but may also reflect differences in resource availability (e.g., forage, cover) or in population-specific adaptations.

Riverine smallmouth bass also show high persistence in relatively small areas throughout the summer months, but fall movement to winter habitats varies among populations (review by Lyons and Kanehl 2002). In a Missouri stream, postspawning home ranges and intrapool movement of adults were greater in summer (0.09 to 0.67 ha, up to 980 m/d at 27.5°C) than in winter (0.06 to 0.22 ha, 120 m/d at 4°C), but fish generally used the same stream sections in winter and summer, moving elsewhere only during the spawning season (Todd and Rabeni 1989). In small Ouachita Mountain streams, interpool movement of smallmouth bass in summer was high, with 35% of marked individuals moving among adjacent pools over a 3-day observation period (Lonzarich *et al.* 2000). Similarly, recolonization rates after complete removal were high; pool populations reached pre-removal abundances in 40 days (Lonzarich *et al.* 1998). Some populations of riverine smallmouth bass, particularly those in areas with severe winters, make fall migrations of several to over 100 km to wintering habitats (usually to downstream bodies of water) (e.g., Langhurst and Schoenike 1990; Peterson and Rabeni 1996; Cooke *et al.* 2000a; Lyons and Kanehl 2002; Schreer and Cooke 2002). Movement to wintering areas can involve numerous short movements with rest periods of several days, or long distances may be covered in short periods (Lyons and Kanehl 2002). For example, a smallmouth bass migrating to downstream wintering habitats in Wisconsin moved 19 km in 24 hours (Langhurst and Schoenike 1990).

Latitudinal differences in temperature and regional variation in annual temperatures exert considerable influence on smallmouth bass distribution, abundance, growth, and survival. A model using temperature, food availability, and lake depth to predict young-of-the-year growth and winter mortality accurately delimited the northern distributional limit of the species (Shuter and Post 1990). Average July temperatures $<15^{\circ}$C prevent young-of-the-year from reaching sufficient size to overwinter, precluding long-term viability of populations on the northern edge of the range (Shuter *et al.* 1980). At northern latitudes, a short-growing season and long, cold winters combined with variability in food availability (e.g., low productivity, high competition) and hence energy reserves can dramatically increase overwinter mortality (to 100%) of young-of-the-year smallmouth bass (Oliver *et al.* 1979; Shuter *et al.* 1989; Lyons 1997; Curry *et al.* 2005). In an analysis of data for 409 smallmouth bass populations across North America, age at length was correlated negatively with mean air temperature (and degree days $>10^{\circ}$C) (Beamesderfer and North 1995). In a study of 129 geographically widespread populations, temperature-related climate differences were significantly related to growth and were most influential in the first 4 years of life (Dunlop and Shuter 2006). On a regional scale, population structure of smallmouth bass in the Laurentian Great Lakes closely tracked changes in water temperatures over several decades. Notably, steep declines in growth and year-class strength occurred with minor temperature shifts (mean shifts $<3^{\circ}$C) caused by global climate events (i.e. peak La Niña cooling effects and eruption of Mount Pinatubo, Philippines in 1992; King *et al.* 1999; Casselman *et al.* 2002). In the upper Mississippi River, first-year growth was also influenced strongly by temperature variation over a 14-year period (Swenson *et al.* 2002). When temperature effects were considered independent of water velocity, modeled first-year growth increased an estimated 7 mm for each 100–degree day increase in growing season temperatures. At even smaller spatial scales, rapid water temperature changes associated with sporadic flooding events in streams can dramatically reduce the probability of survival in larval smallmouth bass by affecting their ability to negotiate current and effectively forage (Larimore 2002). Similarly, minor wind-induced increases in temperature (0.6–1.3°C) (and zooplankton abundance) in downwind areas of northern lakes are implicated, although not conclusively so, in nest-site selection by males and in faster growth of young (Kaevats *et al.* 2005).

Smallmouth bass are among the most sensitive of the centrarchids to reduced pH. Field and laboratory studies demonstrate reproductive impairment at pH <6.0 and total curtailment of recruitment at pH <5.5, depending in part on antagonistic effects of Al and Ca concentrations, fish size, and energy reserves (Rahel and Magnuson 1983; Kwain *et al.* 1984; Cunningham and Shuter 1986; Kane and Rabeni 1987; Hill *et al.* 1988; Holtze and Hutchinson 1989; Shuter and Ihssen 1991; Snucins and Shuter 1991). After experimental stocking of adults in small northern lakes, population estimates over three spawning seasons indicated no recruitment at pH 4.9 to 5.2, and population size was low at pH 5.4 (4–12% of number stocked) relative to a lake with pH 5.9 (41–55%) (Snucins and Shuter 1991). Complete mortality of smallmouth bass larvae and post larvae occurred within 3 days at pH 5.1 and 180 μg/l Al and within 5 days at pH 5.5 and 203 μg/l Al (Kane and Rabeni 1987). In post swim-up larvae (3–36 days old), survival (relative to controls at pH 7) declined to 43% at pH 5.7 and to near zero at pH 5.0 (Hill *et al.* 1988). Natural stress of overwinter starvation is significantly augmented even by moderate exposures to nonlethal low pH, but tolerance increases with body size and Ca concentration (Cunningham and Shuter 1986; Shuter *et al.* 1989; Shuter and Ihssen 1991). An exposure to pH 5.5 increases overwinter starvation loss by

16%, a loss rate that could significantly affect viability of smallmouth bass populations by increasing young-of-the-year starvation (Shuter *et al.* 1989).

Smallmouth bass are more sensitive to hypoxia than many other centrarchids. Of five tested centrarchids (three *Lepomis* spp. and largemouth bass), smallmouth bass showed the highest critical DO concentration (average, 1.19 mg/l at 26°C) (Smale and Rabeni 1995a). Across graded levels of hypoxia, blood plasma adrenalines and noradrenalines, which are indicators of stress, dramatically increased in the blood of smallmouth bass but not largemouth bass. Increases in ventilation rate and decreases in cardiac output also were more pronounced in smallmouth bass than in largemouth bass (Furimsky *et al.* 2003). The differential physiological responses of the two species to hypoxia are likely attributable to differences in the ability of their blood to bind DO (Cech *et al.* 1979; Furimsky *et al.* 2003).

Food: The smallmouth bass is an opportunistic, top carnivore, feeding from the surface to the bottom. The biomass of the adult diet is predominately fish, and if available, crayfish, but adult smallmouth bass also consume an occasional terrestrial vertebrate (e.g., frog) and a wide variety of aquatic and terrestrial insects, the latter being most commonly eaten in small lakes and streams. In lakes and reservoirs with few crayfishes, individuals of >100 mm TL almost exclusively eat fish (e.g., clupeids, *Lepomis*, yellow perch), but if crayfish are present, individuals of <300 mm TL consume large volumes of crayfish (Applegate *et al.* 1967; Hubert 1977; Danehy and Ringler 1991; Gilliland *et al.* 1991; Scott and Angermeier 1998; Liao *et al.* 2002; Dunlop *et al.* 2005b). Young smallmouth bass initially consume microcrustaceans and a wide variety of small aquatic insects, especially dipteran and mayfly larvae, and other invertebrates but transition between 20 and 100 mm TL to the adult diet. The breadth and extent of diet and timing of ontogenetic dietary shifts vary considerably in smallmouth bass in response to interactions among habitat quality, competition, and prey availability (e.g., Hubbs and Bailey 1938; Applegate *et al.* 1967; Clady 1974; Carlander 1977; George and Hadley 1979; Probst *et al.* 1984; Angermeier 1985; Livingstone and Rabeni 1991; Easton and Orth 1992; Rabeni 1992; Roell and Orth 1993; Sabo and Orth 1994, 2002; Sabo *et al.* 1996; Easton *et al.* 1996; Pelham *et al.* 2001; Orth and Newcomb 2002; Pert *et al.* 2002; Olson and Young 2003; Dunlop *et al.* 2005b).

In streams, energy from crayfishes may provide over half the total production of smallmouth bass and over 60% of the energy of adult smallmouth bass, the remainder being obtained from fishes, particularly cyprinids such as stonerollers (*Campostoma* sp.) (Rabeni 1992). In these systems, smallmouth bass can remove about a third of crayfish production and nearly two-thirds of the biomass of crayfishes of vulnerable size. Most crayfish eaten are between 14 and 46 mm (carapace length), even though the available size range of crayfish in the streams is much larger and changes seasonally (Rabeni 1992; Roell and Orth 1993). Interestingly, in a Missouri stream, the size of smallmouth bass and the size of crayfishes eaten were not related. Gape limitation or other morphological constraints apparently were not operative, but rather, there was an optimum size range of crayfishes common to all sizes of bass (>100 mm TL) (Probst *et al.* 1984). In a northern lake and associated laboratory research, size of crayfish prey was related positively to smallmouth bass size, but complex interactions of substrate type and crayfish size, sex, and life stage affected bass selectivity (Stein 1977). Smallmouth bass foraging behaviors appear well adapted for benthic prey. Compared to largemouth bass, foraging smallmouth bass keep the body more horizontal in inspecting the bottom, remain closer to the substrate, and use biting actions more often in feeding. The species uses combinations of suction feeding and grasping and jerking to dislodge crayfishes from rock crevices, but largemouth bass rely primarily on suction feeding (Winemiller and Taylor 1987).

Smallmouth bass are primarily diurnal in habit with activity typically greatly diminishing at night. Feeding and activity peaks are often noted at dawn or dusk, but fish can feed opportunistically over a 24-hour period (Munther 1970; Reynolds and Casterlin 1976b; Helfman 1981; Gerber and Haynes 1988; Todd and Rabeni 1989; Kwak *et al.* 1992; Johnson and Dropkin 1993; Demers *et al.* 1996; Ridgway *et al.* 2002). Nighttime samples taken in the fall in a Pennsylvania river revealed food in stomachs (primarily mayfly larvae and crayfish by weight) of over 60% of smallmouth bass examined (65–346 mm TL, n = 60) (Johnson and Dropkin 1993). Nighttime angling in summer in the Tennessee River, Alabama, accounts for a substantial proportion of the smallmouth bass catch (Weathers and Bain 1992), also suggesting nighttime feeding or at least a propensity to feed at night. Prey consumption by smallmouth bass is affected by turbidity. The reactive distance of smallmouth bass (99 mm TL) to 10-mm prey (dipteran larvae) decreased exponentially from about 65 to 10 cm as turbidity increased from <5 to 40 NTU (at 49 lux) in laboratory trials (Sweka and Hartman 2003).

As highly effective top predators, smallmouth bass can cause shifts in fish assemblages, redistribution or elimination of prey, and dramatic changes in prey behavior. In small Ontario lakes, the presence of smallmouth bass was linked to reduced abundance, altered habitat use, and extirpation of a suite of small-bodied fishes, primarily cyprinids and brook stickleback (MacRae and Jackson 2001). Similar direct and indirect interactions of small-bodied fishes and predation by smallmouth bass are documented across lakes in southern Canada and the northeastern United States (e.g., Chapleau and Findlay 1997; Whittier *et al.* 1997; Whittier and Kincaid 1999; Vander Zanden *et al.* 1999, 2004; Findlay *et al.* 2000; Jackson 2002; Morbey *et al.* 2007). In experimental and natural streams, several small-bodied fish species shifted habitat use from deep pools to the refuge of shallow-flowing habitats when smallmouth bass were present (Schlosser 1988a,b, but see Harvey *et al.* 1988). In experimental tanks with smallmouth bass, the benthic-dwelling johnny darter (*Etheostoma nigrum*) reduced activity to 6% of that observed in tanks without bass, spending most of the time under tile shelters. Even after removal of the bass, darters remained inactive and under shelters for about 24 hours, indicative of a strong residual effect of the predator's presence (Rahel and Stein 1988). In field and laboratory trials, predation risk from smallmouth bass induced shifts in microdistribution (e.g., larger substrate use, hiding in burrows) and behavior (e.g., reduced walking, climbing, and feeding) of small lake-dwelling crayfish, and in experimental streams, the presence of smallmouth bass reduced crayfish activity, aggressive behaviors, and pool use (Stein and Magnuson 1976; Stein 1977; Mather and Stein 1993). Interestingly, daytime larval minnow abundance was influenced differentially by the presence of juvenile and adult smallmouth bass in natural and experimentally manipulated stream pools. Minnow larvae were less abundant in pools with juvenile smallmouth bass and more abundant in pools with adult smallmouth bass. The presence of adult smallmouth bass in a pool apparently reduced the risk to larval fish of predation from juvenile bass and other predators (e.g., *Lepomis*) (Harvey 1991b).

Reproduction: Depending in part on latitude, females mature minimally at age 3+ to 7+ (≥220 mm TL) and males at age 2+ to 5+ (≥200 mm TL) (Carlander 1977; Hubert and Mitchell 1979; Vogele 1981; Serns 1984; Raffetto *et al.* 1990; Ridgway and Friesen 1992; Wiegmann *et al.* 1992; Dunlop *et al.* 2005a,b). Male size appears more important than age in attaining maturity (Wiegmann *et al.* 1997; Dunlop *et al.* 2005a).

Many smallmouth bass populations make regular spring migrations to spawning areas and exhibit a high degree of nest-site fidelity. Patterns of spring movements, some involving relatively long distances (5–75 km), from wintering to spawning areas are documented in populations inhabiting streams, rivers, lakes, and reservoirs (e.g., Reynolds 1965; Hubert and Lackey 1980; Todd and Rabeni 1989; Kraai *et al.* 1991). Movement associated with spawning appears to be population or context specific, perhaps reflecting suitability and availability of nesting sites. Individuals may move to spawning areas and stay until fall, move to spawning areas and then return to home areas after spawning, or spawn in the general area where they occur all year (e.g., Pflieger 1975; Todd and Rabeni 1989; Lyons and Kanehl 2002). Some lake-dwelling populations make large, regular spring migrations of >10 km into lake tributaries to spawn, returning to the lake after reproduction (Lyons and Kanehl 2002), and others consistently use nesting areas within a lake that are spatially distinct from nonspawning home areas. Over a multiyear, multigenerational field study in a Canadian lake, >71% of renesting smallmouth bass males returned to within 100-m linear distance of their previous year's nest site, even though nest habitats were not limiting. In subsequent years, about 35% returned to within 20 m of their original nest site, nesting largely in or adjacent to their old nest (Ridgway *et al.* 1991a, 2002). Nest aggregations along lake shorelines are consistently patchy across years (Rejwan *et al.* 1997), indicative of selection of specific nesting areas, and genetic analyses of offspring from individual nests further support high nest-site fidelity in the species (Gross *et al.* 1994).

In natural settings, smallmouth bass spawn from about April to mid-July at southern latitudes and mid-May to mid-June on the northern edge of the range (Pflieger 1966a, 1975; Neves 1975; Hubert and Mitchell 1979; Vogele 1981; Wrenn 1984; Graham and Orth 1986; Ridgway and Friesen 1992). A second spawning period or multiple renestings may occur, especially if early broods are lost because of high flows and temperature decreases (Beeman 1924; Surber 1943; Pflieger 1966a, 1975; Coble 1975; Neves 1975; Lukas and Orth 1995; Cooke *et al.* 2003a, 2006). Spawning activity and active nests span a broad range of temperatures (12.0–26.7°C); however, most spawning is initiated as water temperatures gradually rise and exceed 15°C, and peak spawning continues to 22°C (e.g., Pflieger 1966a; Smitherman and Ramsey 1972; Neves 1975; Carlander 1977; Shuter *et al.* 1980; Vogele 1981; Wrenn 1984; Graham and Orth 1986; Cooke *et al.* 2003a). Large mature males nest earlier (i.e. at lower temperatures and fewer accumulated degree days >10°C before spawning) than small mature males; females show similar size-related timing in spawning (Ridgway *et al.* 1991b; Wiegmann *et al.* 1992; Baylis *et al.* 1993; Lukas and Orth 1995). Smallmouth bass from the Tennessee River exposed to water temperatures of 2.6, 5.2, and 8.0°C above ambient temperature (beginning in December) showed spawning peaks of 9, 16, and 25 days, respectively, before control fish exposed to ambient river water temperatures (Wrenn 1984). Likewise, in a thermally unstable, but heated effluent canal in Lake Erie, spawning of smallmouth bass was advanced about 1 month relative to spawning in the lake (Cooke *et al.* 2003a). Simulated, compressed winter conditions (short photoperiods, temperatures ~ 6°C) followed by

20 to 22 days of exposure to increasing photoperiod (14 hours) and temperature (18°C) induces out-of-season spawning, but increasing temperature alone does not appear to induce spawning (Cantin and Bromage 1991).

Male smallmouth bass establish a territory and use caudal sweeping to excavate a circular depressional nest down to coarse gravel–cobble substrates, bedrock, or even hard clay. Nests average 45 to 93 cm in diameter and are often near (or just downstream of) rocky or woody cover. In lakes and reservoirs, nests are usually placed in water <4.0 m deep (to 6.7 m). In streams, nests are placed in low-velocity habitats, usually in water <0.75 m deep (Surber 1943; Pflieger 1966a; Neves 1975; Vogele and Rainwater 1975; Carlander 1977; Vogele 1981; Winemiller and Taylor 1982; Lukas and Orth 1995; Bozek *et al.* 2002; Orth and Newcomb 2002; Saunders *et al.* 2002; Bozek *et al.* 2002; Steinhart *et al.* 2005). In riverine habitats, smallmouth bass nests generally are spaced widely, rarely exceeding 3/100 m, although average internest distances of 4.2 m are reported (Surber 1943; Pflieger 1966a, 1975; Coble 1975; Lukas and Orth 1995; Knotek and Orth 1998). In lakes, nesting areas are patchily, but nonrandomly, distributed, and highest nest densities occur in areas with > 17.0°C water temperatures and high shoreline complexity (Rejwan *et al.* 1997). Within a nesting area in lakes, densities are usually 1 to 5 nests/100 m of shoreline, but even when highly concentrated, nest density rarely exceeds 7 nests/100 m of shoreline (Vogele 1981; Scott 1996; Rejwan *et al.* 1997, 1999; Saunders *et al.* 2002). Nest spacing in lakes matches the shape and size of the male's territory (≥18 m apart) and the area needed for foraging of the free-swimming brood but is much greater than that predicted for randomly established nests (Scott 1996). Greater internest spacing and presence of cover increases the probability of mating success of male smallmouth bass (Winemiller and Taylor 1982; Wiegmann *et al.* 1992).

Once the nest is prepared, the male engages in long periods of fanning with the pectoral and median fins. The male intersperses bouts of fanning with frequent reorientation of his longitudinal axis by pivoting the body around the center of the nest (45–90°/turn; 0.5–1.2 turns/s), the pivots being an apparent effort to detect rivals or females around the nest (Beeman 1924; Pflieger 1966a; Winemiller and Taylor 1982). Depending in part on availability of females, elapsed time between nest construction and egg deposition is usually 2 days, but ranges from a few hours up to 16 days (Pflieger 1966a; Wrenn 1984; Ridgway *et al.* 1991b). Males periodically leave the nest to locate spawning-ready females and once located, use push–lead behaviors (jaw displays, contact nips) to direct the female to the nest (Ridgway *et al.* 1989). During courtship and spawning, the male's iris becomes bright red, and the female develops a series of dark vertical bars or mottlings against a light background that are lacking in the breeding male (Breder and Rosen 1966; Schneider 1971; Ridgway *et al.* 1989). In response to male courtship, the spawning-ready female assumes a head-down posture and under coaxing from the male slowly moves toward the nest, where the pair begins circling high above the nest (male below, female above), slowly descending toward the nest as they circle. Ultimately, the pair starts circling the nest rim (female inside, male outside). During circling, the male contact nips the female's opercle and ventral area (pelvic fins to vent). Finally, the two settle to the substrate, the female performs a body wave (i.e. a gentle swinging of her head and caudal peduncle from side to side while in an upright position and close beside the male), tilts to the side, places her vent near the male's vent, and quivers while releasing eggs. The male remains upright during milt release. After egg release, the female rises above the nest in a head-down posture. The complete sequence of rim circling, male to female contact nips, and female quivering occurs repeatedly with brief pauses in between sequences (Schneider 1971; Ridgway *et al.* 1989). The complete spawning bout with a female can last >2 hours and involve 103 female shudders at 30- to 60-second intervals with up to 50 eggs released per shudder. On completion of the bout, the male drives the female from the nest (Reighard 1906; Schneider 1971; Neves 1975). Multiple complete spawning observations, female batch fecundity, and egg developmental stages in nests in natural settings indicate that most males mate with one female, but some males may mate sequentially (or simultaneously) with more than one female (Beeman 1924; Hubbs and Bailey 1938; Neves 1975; Vogele 1981; Ridgway *et al.* 1989; Wiegmann *et al.* 1992). Large guardian males are more likely to successfully attract and spawn with females, but in some populations, many males of various sizes build nests but are unsuccessful in attracting mates (Winemiller and Taylor 1982; Wiegmann *et al.* 1992; Baylis *et al.* 1993). Of males spawning with females, large guardian males receive more eggs and defend the brood more tenaciously than small guardian males, ultimately producing larger broods, which may in part explain the apparent female mate preference for larger males (Neves 1975; Ridgway and Friesen 1992; Lukas and Orth 1995; Wiegmann and Baylis 1995; Wiegmann *et al.* 1992, 1997; Knotek and Orth 1998).

Mature ovarian eggs average from 1.60 to 2.75 mm diameter, and fertilized, water-hardened eggs from 2.0 to 3.5 mm diameter (Meyer 1970; Smitherman and Ramsey 1972; Hubert 1976; Vogele 1981; Wrenn 1984; Cooke *et al.* 2006). Fecundity increases with female weight, length, and age (Clady 1975; Hubert 1976; Kilambi *et al.* 1977; Vogele 1981; Serns 1984; Dunlop *et al.* 2005b). Bimodal egg size classes occur in ovaries of spawning-ready females, suggesting that females have the potential to spawn multiple batches of eggs in a single spawning season. However, over the relatively short spawning season secondary stage ova do not appear to mature after the initial batch is spawned, being resorbed in summer (Hubert and Mitchell 1979; Vogele 1981). The relationship between potential batch fecundity (Y) and total weight or length (X) are described by the linear functions, $Y = -1,347 + 13.65X$, where X is weight in grams ($n = 21, R^2 = 0.85$), or $Y = -1225.15 + 59.39X$, where X is TL ($n = 74, R^2 = 0.39$) (formulas from Vogele 1981 and Raffetto *et al.* 1990, respectively; see also, Hubert 1976; Kilambi *et al.* 1977; Dunlop *et al.* 2005b). At 549 g (about 335 mm TL), a female can potentially produce 6147 mature eggs in a single batch (range: 1724 eggs at 221 g to 21,467 eggs at 1471 g). Average number of eggs per nest ranges from 2149 to 7757 (>19, 000 in some nests) (Pflieger 1966a; Clady 1975; Neves 1975; Vogele 1981; Raffetto *et al.* 1990; Wiegmann *et al.* 1992). The adhesive, grayish white to pale yellow fertilized eggs hatch in 6.4 days at 16°C (2.4 days at 22°C, from formula in Shuter *et al.* 1980). Larvae are 4.4 to 6.8 mm TL at hatching, and depending on water temperature, are free swimming at a size of 8.1 to 10.1 mm TL in 4 to 16 days after hatching (Reighard 1906; Beeman 1924; Tester 1930; Hubbs and Bailey 1938; Meyer 1970; Hardy 1978; Shuter *et al.* 1980; Vogele 1981; Wrenn 1984; Ridgway and Friesen 1992).

At swim-up, smallmouth bass fry begin a diel cycle of moving away from the nest at dawn and returning to the nest at dusk, and the guardian male shows parallel behavior (Ridgway 1988). During the swim-up phase, the brood disperses over about 13.4 m^2 relative to the guardian male's nest range of 22.7 m^2. Later, during the juvenile guarding phase, the brood disperses in the day time over 82.4 m^2, and the male over 176.9 m^2. At dusk, fry and male ranges decrease to 3.1 and 20.7 m^2, respectively. The male apparently responds to changes in brood dispersal and not vice versa, because the diurnal contraction and expansion of the brood continues when males are removed (Scott *et al.* 1997). Juvenile smallmouth bass show nest-site fidelity. In an Ontario lake, age-0 smallmouth bass dispersed little beyond 200 m of their nest of origin by fall, a time long after parental males ceased brood guarding (Gross and Kapuscinski 1997; Ridgway *et al.* 2002). Likewise, stream-dwelling age-0 smallmouth bass appear to remain near the spawning areas for the first summer of life (Lyons and Kanehl 2002).

Male smallmouth bass guard and vigorously defend the nest, eggs, and larvae 24 h/d for 2 to 7 or more weeks, depending in part on male size and energy reserves, spawning time, and water temperatures (e.g., Pflieger 1966a; Neves 1975; Vogele 1981; Hinch and Collins 1991; Ridgway and Friesen 1992; Scott *et al.* 1997; Knotek and Orth 1998; Cooke *et al.* 2002a; Cooke *et al.* 2006). Over eight nesting seasons in a northern lake, average duration of male parental care ranged from 9.4 to 16.4 days (up to 21 days) before swim-up and 9.2 to 11.8 days after swim-up (up to 27 days) (Ridgway and Friesen 1992). Male defense behaviors and swimming activity increase as the offspring progress from egg to hatching, peak before swim-up, and begin to decrease after swim-up (Ridgway 1988; Ongarato and Snucins 1993; Cooke *et al.* 2002a). Nevertheless, males shift from active and close defense of a brood confined to the nest before swim-up to more distant but vigilant patrolling of dispersed larvae and juveniles (Scott *et al.* 1997). Guardian male feeding is curtailed or at least dramatically reduced, which in turn reduces and perhaps depletes energy reserves (Hinch and Collins 1991; Gillooly and Baylis 1999; Mackereth *et al.* 1999; Cooke *et al.* 2002a; Steinhart *et al.* 2005). Large males show higher intensity and longer duration of offspring defense; small guardian males can abandon the brood early or may show little or no defense of juveniles, perhaps as a result of reduced or depleted energy reserves (Ridgway and Friesen 1992; Philipp *et al.* 1997; Mackereth *et al.* 1999). Males experiencing brood loss from simulated predation also show less nest defense and are more likely to completely abandon the brood (Philipp *et al.* 1997; Suski *et al.* 2003).

Compelling evidence of an alternating life history strategy is documented for a smallmouth bass population in Nebish Lake, Wisconsin. Unlike the alternative reproductive strategy of cuckoldry seen in some male *Lepomis*, successive generations of male smallmouth bass in this population alternate their age at first reproduction between ages 3 and 4 (Raffetto *et al.* 1990; *et al.*Wiegmann *et al.* 1992, 1997; Baylis *et al.* 1993). *Micropterus* males are typically iteroparous (reproducing in multiple years), but males in this closed population are essentially semelparous (reproducing once in a lifetime). Reproduction can begin at age 3, but the life history decision for time of first reproduction is conditional on male size at age 3, with large age-3 males being likely to reproduce, and small age-3 males being likely to delay reproduction until age 4 or older. In turn, size at age 3 is determined largely in early ontogeny and is likely a function of birth date. Large, older males (age 4 or older) spawn earlier (average about 4–5 days) in the spring than mature, spawning age-3 males. The late spawning, age-3 males are more likely to produce a cohort of small age-3 males that in turn are more likely to delay reproduction until age 4 or older. Conversely, small age-3 males that delay reproduction until age 4 (or older) are more likely to produce a cohort of large, reproductively active age-3 males. Hence, an alternation of time to maturation is sustained over multiple years and appears to be mediated by just a few days difference in birth date (Baylis *et al.* 1993; Wiegmann *et al.* 1997).

Nest associates: Longnose gar, *Lepisosteus osseus* (Goff 1984); common shiner, *Luxilus cornutus* (Hunter and Wisby 1961); orangethroat darter, *Etheostoma spectabile* (Pflieger 1966b).

Freshwater mussel host: Confirmed host to *A. ligamentina, L. cardium, L. fasciola, L. higginsii, L. radiata, L. rafinesqueana, L. reeviana, L. siliquoidea*, and *V. iris* (Coker *et al.* 1921; Zale and Neves 1982; Waller and Holland-Bartels 1988; Barnhart and Roberts 1997; O'Dee and Watters 2000). Putative host to *Lampsilis abrupta* and *Lexingtonia dolabelloides* (unpublished sources in OSUDM 2006).

Conservation status: The smallmouth bass is secure throughout its range, but native populations in Kansas, along the western periphery of the natural range, are considered vulnerable (NatureServe 2006).

Similar species: Spotted bass have a black midlateral stripe (no vertical bars) and rows of black spots along the lower sides; redeye bass have white or orange edges on the caudal fin lobes and rows of black spots along the lower sides; Florida bass and largemouth bass have a dark, midlateral stripe, a deep notch between the soft and spiny dorsal fins, and in adults, the mouth reaches beyond the rear margin of the eye (Page and Burr 1991).

Systematic notes: *Micropterus dolomieu* and *M. punctulatus* form a sister pair, which is basal to all other *Micropterus* (Kassler *et al.* 2002; Near *et al.* 2003, 2004, 2005). Morphological taxonomists traditionally related *M. dolomieu* to *M. coosae* (Hubbs and Bailey 1940; Ramsey 1975). Although only two subspecies of *M. dolomieu* are usually recognized, the species as currently conceived appears to consist of several distinct evolutionary lineages. The subspecies *M. d. velox* was described from tributaries of the Arkansas River in southwestern Missouri, northeastern Oklahoma, and northwestern Arkansas based on color, body shape, and modal differences in dorsal ray counts (Hubbs and Bailey 1940). Intergrade populations between *M. d. dolomieu* and *M. d. velox* were considered tentatively to occupy the remainder of the southern Ozark and Ouachita uplands, exclusive of the lower Missouri River, and *M. d. dolomieu* the remainder of the range. Limited sampling of mitochondrial and nuclear DNA sequences did not detect geographic differences among *M. dolomieu* populations (Kassler *et al.* 2002; Near *et al.* 2003, 2004), but nuclear-encoded allozyme loci provide evidence for significant genetic substructuring in the Ozark and Ouachita uplands (Stark and Echelle 1998). Three different clades of *M. dolomieu* inhabiting the Ozark and Ouachita uplands are evident: (1) the Ouachita smallmouth bass in the Little and Ouachita river drainages; (2) the Neosho smallmouth bass from the southwestern Ozarks in the Neosho and Illinois rivers and smaller tributaries of the middle Arkansas River; and (3) a clade comprising all other populations on the Ozark Plateau (White, Black, St. Francis, Meramec, and Missouri rivers). The latter clade was similar genetically to populations from the upper Mississippi and Ohio River basins (Stark and Echelle 1998).

Importance to humans: The smallmouth bass is rivaled only by the Florida bass and the largemouth bass as the most sought-after and valued species in the black bass recreational fishery. Until at least 1932, tons of smallmouth bass were taken commercially by hook and line and by net in Canada, until the species was restricted as a noncommercial sport fish (Scott and Crossman 1973). The smallmouth bass reaches a relatively large size, is an intense, strong fighter when hooked, and over its broad distribution flourishes in high-quality lakes, reservoirs, and upland rivers and streams, all attractive attributes to recreational anglers. As a primary North American recreational fish, the smallmouth bass is the focus of intense fisheries research and management efforts increasingly aimed at maintaining quality- and trophy-size catches for anglers (e.g., Reed *et al.* 1991; Beamesderfer and North 1995; Kubacki *et al.* 2002; Noble 2002). Not unexpectedly, techniques for catching smallmouth bass are the subject of a continuous stream of media from the recreational fishing industry (e.g., magazine articles, books, videos). Like other black bass the species is taken by a number of methods including dry flies, wet flies, popping bugs, lures, spinners, jigs, and plastic worms. Effective natural baits include leeches, soft crayfish, hellgrammites, minnow-tipped jigs, frogs, and salamanders. Although most often taken in lakes and reservoirs, smallmouth bass anglers, particularly a growing contingent of fly fishers seeking a quality fishing experience, wade or fish from small boats and canoes in scenic upland streams and rivers (Becker 1983; Etnier and Starnes 1993; Pflieger 1997). The flesh is white, firm, and flaky with fine flavor, being regarded by gourmets as superior table fare (Becker 1983).

13.9.4 Micropterus floridanus *Lesueur*

13.9.4.1 Florida bass

Characteristics: See generic account for general characteristics. Elongate, slightly compressed body, depth about 0.24 to 0.29 of TL, increasing with size. Mouth large, terminal, lower jaw slightly projecting, upper jaw extends beyond posterior edge of eye in adults. Outline of spinous dorsal fin sharply angular. Juncture of soft and spiny dorsal fins deeply emarginate, almost separate. Shortest dorsal spine at emargination of fin, usually 0.3 to 0.4 times the length of longest spine, membranes between short spines deeply incised. Dorsal soft rays, usually 13, 12 to 14; anal soft rays, usually 11, 10 to 12. Gill rakers, 6 to 9. Scales average smaller than largemouth bass. Lateral scales, (65)69 to 73(76); rows above lateral line, (7)8 to 9(10); rows below lateral line, (15)17 to 18(21); cheek scale rows, (10)11 to 13(14); caudal peduncle scale rows, (27)28 to 31(33); pectoral rays, 14 to 15(16). No small splintlike scales on interradial membranes at anal and second dorsal fin bases. Pyloric caeca branched at bases, 26 to 43 or more. Tooth patch absent (rarely a few teeth) on glossohyal (tongue) bone (Bailey and Hubbs 1949; Buchanan 1973; Chew 1974; Ramsey 1975; Kassler *et al.* 2002).

Size and age: Size at age 1 ranges from 142 to 310 mm TL for males and 116 to 330 mm TL for females (Allen *et al.* 2002). Age and weights of trophy Florida bass ($n = 810$, ≥ 4.5 kg) obtained from taxidermists across Florida revealed a maximum age of 16 (average 9.7 years), a maximum weight of 7.9 kg (average 5.0 kg), and a maximum length of 762 mm TL (average 661 mm) (Crawford *et al.* 2002). Florida state record, 7.85 kg (FFWCC 2006). Females grow faster and live longer than males; nearly all large individuals of Florida bass (>400 mm TL) are females (Allen *et al.* 2002; Crawford *et al.* 2002; Bonvechio *et al.* 2005; all cited studies include a few likely populations of *M. floridanus* × *M. salmoides* intergrades in northern Florida).

Coloration: Broad dark olive to olive black, midlateral stripe on caudal peduncle becoming disrupted anteriorly into a series of more or less distinct blotches, the midlateral stripe often faint in large adults. Silver to brassy green above (brownish in tea-stained water) with dark olive mottling. Scattered dark specks on lower sides; whitish below. Iris brown. Young (<50 mm TL) with bicolored caudal fin markings (whitish basally, dark distally) (Bailey and Hubbs 1949; Chew 1974; Page and Burr 1991).

Native range: The Florida bass is native to peninsular Florida (Bailey and Hubbs 1949; Philipp *et al.* 1981, 1983; Page and Burr 1991). The Florida bass and largemouth bass have an extensive hybrid zone across the southeastern United States in large part as a result of stocking of Florida bass outside its native range (see account on *M. salmoides*).

Habitat: The Florida bass inhabits clear vegetated lakes, reservoirs, canals, ponds, swamps, and backwaters, as well as pools of creeks and small to large rivers (Page and Burr 1991). Adults often center home activity areas in close association with structure (e.g., logs, piers) or mixed beds of emergent and submergent aquatic macrophytes but also frequent open water without cover (McLane 1948; Mesing and Wicker 1986; Colle *et al.* 1989; Bruno *et al.* 1990). Young Florida bass are usually most abundant in shallow (<2 m) densely vegetated areas (McLane 1948; Chew 1974; Allen and Tugend 2002). Maximal home activity area of radio-tagged adult Florida bass in two lakes was 5.2 ha, averaging about 1.2 ha for fish tracked over multiple months and seasons. Fish size was related positively to home area, and mean daily movements decreased at seasonal high and low temperatures (Mesing and Wicker 1986). Home activity areas were generally narrow and paralleled the shore for distances of 50 to 2364 m. Most activity (70–90%) was <300 m from the geometric center of the home use area. The largest fish (>600 mm TL) occupied the same home areas for over a year. Nevertheless, considerable offshore movement occurred, and many fishes were not located in littoral areas for long periods, suggesting that a significant proportion of Florida bass used open water extensively (Mesing and Wicker 1986). In a lake lacking aquatic macrophytes, some radio-tagged Florida bass consistently used offshore home areas at depths >3.5 m. The offshore home activity areas lacked any natural or artificial structures. The offshore fish had larger home activity areas (mean 21.0 ha, range 0.6–39.5 ha) than similar-sized fish occupying shallow (<2.0 m) inshore home areas associated with standing timber (mean 4.1 ha, range 1.0–9.8 ha). Although much Florida bass activity is associated with dawn and dusk, movement occurs throughout the day. Interestingly, nocturnal movement of Florida bass can be high, extending into the early morning hours, especially when water temperatures exceed 18°C (Mesing and Wicker 1986; Colle *et al.* 1989).

The Florida bass, having evolved in a subtropical climate, is more adapted to high temperatures and apparently less adapted to low temperatures than its temperate climate sister species, the largemouth bass. The Florida bass, along with the bluegill, has the highest reported critical thermal maxima among centrarchids, exceeding 41°C (acclimation temperatures >30°C, Fields *et al.* 1987; Beitinger *et al.* 2000). Hatching success of eggs and early development of larvae in Florida bass require greater thermal input than in largemouth bass (Philipp *et al.* 1985a). When held for 5 days at 2°C, Florida bass showed higher mortality rates (48%) than largemouth bass (0%), and in Illinois ponds, Florida bass showed significantly lower overwinter survival than largemouth bass (Carmichael *et al.* 1988; Philipp and Whitt 1991). The differences in response to temperatures between the two species appear to be linked to divergence in gene regulatory processes (Philipp *et al.* 1983, 1985b; Parker *et al.* 1985).

Florida bass occur and persist in highly acidic lakes (pH 3.7–4.5, ≤2 mg/l Ca) with relatively high total Al concentrations (≤200 μg/l), water quality conditions unfavorable for many fishes. Growth and body condition are reduced in acidic lakes relative to populations in circumneutral lakes, but changes in blood plasma osmolarity and electrolytes, associated with pH-related stress, are not substantial. Young-of-the-year Florida bass, but no small bluegill or redear sunfish, occurred even in the most acidic lakes studied. The physiological basis for the acid tolerance of the Florida bass is unknown (Canfield *et al.* 1985).

Food: The Florida bass is a top carnivore. Adults (>300 mm TL) feed about equally on fish (e.g., other centrarchids, clupeids, anchovies, topminnows, lake chubsuckers, silversides, minnows, darters) and decapods (crayfish and grass shrimp, if available) (McLane 1948, 1950; Chew 1974; Schramm and Maceina 1986; Huskey and Turingan 2001; Crawford *et al.* 2002). Young-of-the-year (13–30 mm TL) feed heavily on cladocerans, copepods, amphipods, and aquatic insects but with growth (31–75 mm TL) cease zooplankton use and begin including higher volumes of grass shrimp and fish (e.g., mosquitofish, silversides, topminnows). By 75 mm TL, fish and decapods constitute most of the diet biomass (Carr 1942; Chew 1974; Huskey and Turingan 2001; Allen and Tugend 2002). Florida bass feed by using combinations of ram (i.e. rapid acceleration of the body) and suction (i.e. rapid expansion of buccal cavity) strike modes on prey (Sass and Motta 2002). Feeding activity appears to occur randomly during the day (Chew 1974), and in captivity, Florida bass digestion rates are rapid (relative to warmouth, *L. gulosus*), and individuals feed voraciously even when considerable food from previous meals remains in the stomach (Hunt 1960). In the St. Johns River, Florida, early naturalists reported groups of hundreds to thousands of Florida bass pursuing and feeding on enormous schools of threadfin shad. Attacks by the bass on the shad resulted in the surface boiling with activity for several minutes at a time (McLane 1948). Focal animal observations on Florida bass (<300 mm TL) in canals revealed that 75% of the individuals occurred in hunting groups. Large individuals (>300 TL) hunted only with groups of other bass, but small individuals (<300 mm TL) hunted in mixed species groups with similar-sized bluegills (Annett 1998). The mixed groups searched, lunged into vegetation, and struck at schools of small fishes together. The bass-only groups typically oriented toward and surrounded a vegetated area, then one bass flushed a prey fish, and the entire group then pursued the prey. The group then moved to another vegetated patch and repeated the sequence of behaviors (Annett 1998), all of which are suggestive of group foraging if not cooperation.

Reproduction: Maturity is reached at age 1+ to 3+ and 254 to 299 mm TL (Chew 1974). In experimental ponds in southern Florida, individuals matured and spawned at 9 months (Clugston 1964). Gonadal development, as evidenced by gonadosomatic changes and sex hormone levels, begins increasing in November and peaks in February and March (Gross *et al.* 2002; Sepúlveda *et al.* 2002). Lake-dwelling Florida bass engage in spawning movements (≤3 km) to nesting areas protected from wind and wave action, then return to prespawning home areas after spawning (Mesing and Wicker 1986; Colle *et al.* 1989; Bruno *et al.* 1990). When low temperatures interrupted spawning activities, fish returned to their home areas in a lake, and then as temperatures rose, returned to the same canal to reinitiate spawning (Mesing and Wicker 1986). Spawning can occur as early as December in southern Florida, as water temperatures cool to about 18.3°C, but peak spawning is generally from February to April at water temperatures between about 18.0 and 21.1°C (as low as 14°C, up to about 27.8°C) (Clugston 1966; Chew 1974). In experimental ponds in Illinois, average duration of the spawning period as estimated from age differences in young was 21 days (range, 13–71 days), but initiation of spawning occurred 7 to 11 days later than largemouth bass occupying the same ponds (Isely *et al.* 1987). Males excavate nests using strong lateral undulations of the body. To further shape the nest, males position their head in the center of the nest and pivot around the nest while rapidly beating the pectoral, soft dorsal, and caudal fins (Carr 1942). Nests are oval (30–60 cm long, 20–55 cm wide), located in water 30 to 75 cm deep (range 10 cm to 2 m), and spaced as close as 1.5 m apart but usually ≥2.5 m apart (Carr 1942; Clugston 1966; Bruno *et al.* 1990). Males usually build nests near simple cover (e.g., log, overhanging tree limb, near cattail roots) over firm substrates if available. In lakes with bottoms of unconsolidated organic matter, males construct nests on spatterdock rhizomes, firm detritus in emergent grasses, and palmetto leaves over submergent vegetation (Carr 1942; Bruno *et al.* 1990). Anecdotal evidence suggests some degree of year-to-year nest site fidelity (Carr 1942). Early in the season, intervals of 4 to 5 days may occur between nest construction and spawning, but as the spawning intensifies, nests are constructed and receive eggs within a few hours (Carr 1942). Most spawning appears to take place in late afternoon (Carr 1942; Chew 1974; Isaac *et al.* 1998). During prespawning, males leave the nest to locate and guide spawning-ready females back to the nest (Carr 1942). Once at the nest, the female, often much larger than the male, circles the nest with the male, during which time he gently nips and butts her head, tail, and sides to push her toward the nest. The male continues to swim actively around and to nip and bump the female; paired female and male circling can last for 10 to 20 or more minutes. The color pattern of both fish becomes more definite and vivid as they circle and enter the nest to spawn. The female then takes a position over the center of the nest, head downward and tilted slightly to the side. Ultimately, the male takes a position along the side of the female with their vents close, both shudder violently for about 10 seconds, including 15 to 20 jerks from side to side, and release eggs and milt. On spawning, the male inspects the nest, and after a 3- to 5-minute pause, the pair repeats the sequence of behaviors for another spawning episode. A pair may spawn for 2 to 4 hours and include 6 to 13 separate spawning acts, after which the female appears exhausted and has difficulty maintaining her position off the bottom (Carr 1942; Chew 1974; Isaac *et al.* 1998). In indoor raceways in which eggs were removed after each completed pairing, males participated in one to four separate spawning events during 8 days of observation (Isaac *et al.* 1998). Of 19 observed spawnings, only one female Florida bass spawned with each male, although females visited nesting sites of several males before spawning with a male (Isaac *et al.* 1998). On completion of spawning the male begins to energetically fan the eggs day and night, reducing or ceasing fanning activity when the eggs hatch. Mature ovarian eggs average 1.5 mm diameter, and fertilized eggs, 1.59 mm diameter (range, 1.49–1.67, Carr 1942; Chew 1974). Fecundity is apparently unquantified but is likely similar to the largemouth bass. The adhesive, orange-colored, fertilized eggs begin hatching in about 1.9 days at 22.2°C (Carr 1942; Chew 1974). Newly hatched, nearly transparent larvae are 3.4 mm TL, and depending on temperature, larvae are free swimming about 5 to 7 days after hatching at 6.5 to 7.2 mm TL. Male parental care from spawning through fry dispersal from the nest is 10 to 11 days (Carr 1942), but the time males spend guarding free-swimming juveniles is unknown. Biparental care is not documented in Florida bass, but observations of two individuals guarding a single nest for several days (Carr 1942; Miller 1975) are suggestive (e.g., DeWoody *et al.* 2000b).

Nest associates: Lake chubsucker, *E. sucetta* (Carr 1942); taillight shiner, *Notropis maculatus* (Chew 1974); golden shiner, *N. crysoleucas* (Chew 1974).

Freshwater mussel host: Confirmed host to *E. buckleyi*, *E. icterina*, *L. straminea claibornensis*, *L. siliquoidea*, *L. teres*, *M. nervosa*, *U. imbecilis*, *V. lienosa*, *V. iris* (reported as *V. nebulosa*) and *V. villosa* (Neves *et al.* 1985; Keller and Ruessler 1997, experimental hosts from hatchery stock were presumably Florida bass, A. E. Keller, U.S. Environmental Protection Agency, personal communication).

Conservation status: The Florida bass is secure throughout its range (Warren *et al.* 2000; NatureServe 2006).

Similar species: All other species of *Micropterus*, except the largemouth bass, have more confluent dorsal fins, upper jaws that reach to, or barely past, the center of the eye, and unbranched pyloric caeca. The largemouth bass, except in a broad area of intergradation in the southern United States, differs in usually having 59 to 66 lateral line scales and 26 to 28 scales around the caudal peduncle (Page and Burr 1991).

Systematic notes: *Micropterus floridanus* forms a sister pair with *M. salmoides* (Kassler *et al.* 2002; Near *et al.* 2003, 2004). Although long regarded as a subspecies of *M. salmoides*, nuclear-encoded allozyme loci, mitochondrial DNA, and nuclear DNA all indicate that *M. floridanus* is a distinct species (Philipp *et al.* 1983; Nedbal and Philipp 1994; Kassler *et al.* 2002; Near *et al.* 2003, 2004).

Importance to humans: The Florida bass and its sister species, the largemouth bass, are the core of the multibillion dollar black bass recreational fishery. The Florida bass is the most popular sport fish in Florida and its value as a sport fish in the state has prompted a movement toward increased management and catch-and-release fishing (FFWCC 2006). The large maximum size obtained by Florida bass in warm waters provides anglers with a real prospect of catching a trophy-sized black bass. In many Florida lakes and reservoirs anglers routinely catch Florida bass fish weighing 8 to 10 or more pounds (3.6 to 4.5 or more kilograms) (Crawford *et al.* 2002; FFWCC 2006). Although several studies suggest that Florida bass are more difficult to catch than the largemouth bass (Zolcynski and Davies 1976; Kleinsasser *et al.* 1990; Garrett 2002), the Florida bass will aggressively and explosively strike most kinds of artificial lures or live baits. Most individuals are taken on plastic worms, surface plugs, spinnerbaits, crankbaits, bass bugs, and minnows. The meat is white, flaky, and low in oil content (FFWCC 2006).

13.9.5 Micropterus notius *Bailey and Hubbs*

13.9.5.1 Suwannee bass

Characteristics: See generic account for general characteristics. Elongate, slightly compressed, but robust body, depth 0.26 to 0.27 of TL. Mouth large, terminal, lower jaw slightly projecting, upper jaw extends to posterior margin of eye in adults. Outline of spinous dorsal fin curved. Juncture of soft and spiny dorsal fins slightly emarginate, broadly connected. Shortest dorsal spine at emargination of fin, usually >0.6 times length of longest spine. Dorsal soft rays, 12 to 13; anal soft rays, 10 to 11. Gill rakers, usually 5. Relatively large scales. Lateral scales, 57 to 65; rows above lateral line, 6 to 9; rows below lateral line, 14 to 19; cheek scale rows, 9 to 15; caudal peduncle scale rows, 27 to 31; pectoral rays, (15)16(17). Small splintlike scales on interradial membranes at anal and second dorsal fin bases (>60 mm SL). Pyloric caeca single, rarely branched, 10 to 13. Tooth patch on glossohyal (tongue) bone (Bailey and Hubbs 1949; Ramsey and Smitherman 1972; Page and Burr 1991; Kassler *et al.* 2002).

Size and age: Size at age 1 ranges from 146 to 206 mm TL. Large individuals are >305 mm TL, weigh 400 g, and reach age 7+ (maximum 402 mm TL and age 9+ for males, age 12+ for females) (Bass and Hitt 1973; Page and Burr 1991; Cailteux *et al.* 2002; Bonvechio *et al.* 2005). World angling record, 1.75 kg, Florida (IGFA 2006). Females grow faster and live longer than males, and in a given population, 60% to 100% of individuals >305 mm TL are females (Bonvechio *et al.* 2005).

Coloration: Color similar to *M. salmoides* but usually brown overall, and sides marked with about 12 vertically elongate, lateral blotches. Blotches anteriorly are much wider than their interspaces, becoming more confluent with age. The blotches fuse on the caudal peduncle to form a relatively uniform, wide lateral band. Ventrolateral longitudinal streaks are weakly developed. Iris red. Young with a series of thin, closely spaced vertical bars along the sides of the body. Cheeks, breast, and lower sides colored brilliant turquoise blue in nesting males, less so in non-nesting individuals (Bailey and Hubbs 1949; Gilbert 1978; Page and Burr 1991).

Native range: The Suwannee bass is native to the Suwannee and Ochlockonee Rivers, Florida and Georgia (MacCrimmon and Robbins 1975; Page and Burr 1991). The provenance of populations in the Wacissa (Aucilla River drainage), Wakulla, and St. Marks rivers of Florida is uncertain (Koppelman and Garrett 2002; Cailteux *et al.* 2002; Bonvechio *et al.* 2005) but, given the lack of historical records, are likely introduced. Electrofishing catch data indicate that the species is most abundant in the Wacissa River (Aucilla River drainage) and Santa Fe River (Suwannee River drainage) (Schramm and Maceina 1986; Cailteux *et al.* 2002; Bonvechio *et al.* 2005).

Habitat: The Suwannee bass occurs in a variety of habitats in cool, clear, spring-fed rivers, which characteristically have limestone substrates (often covered with sand); alkaline, hard water; relatively stable thermal regimes; and dense submersed macrophyte beds (Bass and Hitt 1973; Gilbert 1978; Schramm and Maceina 1986; Cailteux *et al.* 2002). In the Santa Fe River, individuals (>150 mm TL) are associated with fallen trees over sandy substrate; shallow bedrock riffles (0.7–3.0 m deep); vegetated (eelgrass), gravel–sand riffles; deep vertical rock drop-offs (to 3 m); and shallow, sandy, gently sloping vegetated banks (0.5–1.0 m deep). Small individuals are most common around fallen trees but occur in a variety of flowing and nonflowing habitats (Schramm and Maceina 1986). Individuals also occupy spring runs of river tributaries where they seek cover under dense overhanging or floating vegetation (Gilbert 1978).

Food: The Suwannee bass is a top carnivore, extensively exploiting crayfishes for food. Crayfishes are the predominant food of individuals >150 mm TL, and for large fish (>300 mm TL), the diet is almost exclusively crayfishes. Fish rank second and freshwater shrimp third in importance in the diet; other crustacea, such as blue crabs, and a few aquatic insect larvae are also consumed. Juveniles (<150 mm TL) consume crayfish but also eat other invertebrates (grass shrimp, amphipods, aquatic insects) and some small fish (Bass and Hitt 1973; Gilbert 1978; Schramm and Maceina 1986; Cailteux *et al.* 2002). Size-adjusted throat width of the Suwannee bass is larger than that of Florida bass (or Florida × largemouth bass hybrids), allowing Suwannee bass (>167 mm TL) to consume larger prey items at a given size than the sympatric congener. Stomach contents of 142 Suwannee bass sampled in daylight hours from May to August revealed no obvious feeding periodicity (Schramm and Maceina 1986).

Reproduction: Size and age at maturity are not well documented, and little is published on reproductive behavior and biology of this unique, range-restricted *Micropterus*. Gonads of the sexes are distinguishable at minimum sizes of 125 mm SL in males and 142 mm SL in females, but the smallest females reported with mature ova are ≥215 mm SL (Bass and Hitt 1973). On the basis of female reproductive condition and other observations, spawning apparently begins in February or March as water temperatures reach 18 to 20°C and continues into June. Females with ripe ova are taken from February to May, spent females begin to appear in April with the largest numbers occurring in May. Suwannee bass nests in rivers have been noted in April, and spawning occurred in experimental ponds in Alabama in early April (Bailey and Hubbs 1949; Hellier 1967; Smitherman and Ramsey 1972; Bass and Hitt 1973). Young <25 mm TL are taken from April to July (Hellier 1967). Shallow circular depressions are excavated along stream edges "in typical sunfish fashion," and the male "guards the incubating ova" (Hurst *et al.* 1975) for an unspecified time. Fecundity increases with female size but is not well quantified. Estimated total ova of 18 gravid females (215–285 mm SL) ranged from 2520 to over 12,229 per individual and averaged 5397 (Bass and Hitt 1973). Fertilized eggs are 2.0 mm in diameter and hatch in about 3 to 4 days at 20°C. Yolk-sac larvae are 5.5 mm TL and reach 6.5 to 7.5 mm TL about 6 days after hatching (presumably swim-up stage) (Smitherman and Ramsey 1972).

Nest associates: None known.

Freshwater mussel host: Confirmed host to *V. iris* (reported as *V. nebulosa*, Neves *et al.* 1985).

Conservation status: Because of its restricted range, the Suwannee bass is regarded as vulnerable throughout its native range (Warren *et al.* 2000; Koppelman and Garrett 2002) and is considered imperiled in Georgia and vulnerable in Florida (NatureServe 2006). Nevertheless, the species does not appear to have experienced declines in abundance or distribution in historical times (e.g., Santa Fe River, Bass and Hitt 1973; Bass 1974; Schramm and Maceina 1986; Bonvechio *et al.* 2005). Moreover, the present range includes more independent river systems than were known historically, and some of these rivers support high abundances of the species (Cailteux *et al.* 2002; Bonvechio *et al.* 2005).

Similar species: The largemouth bass and the Florida bass have a deep notch between the spiny and soft dorsal fins, and the pyloric caeca are branched (Page and Burr 1991). Young Suwannee bass have closely spaced, elongate vertical bars along the sides of the body (versus solid longitudinal stripe in young largemouth bass and Florida bass) (Gilbert 1978).

Systematic notes: *Micropterus notius* is a member of a "Gulf of Mexico" clade of *Micropterus*, including all other *Micropterus* except *M. dolomieu* and *M. punctulatus* (Kassler *et al.* 2002; Near *et al.* 2003, 2004). Relationships within the clade are not well resolved, with *M. notius* placed as basal to the entire clade, sister to *M. cataractae*, or sister to *M. treculi* and *M. salmoides* × *M. floridanus* (Kassler *et al.* 2002; Near *et al.* 2003, 2004). Similarities in form and color led most morphological taxonomists to relate *M. notius* to *M. punctulatus* (e.g., Bailey and Hubbs 1949; Ramsey 1975).

Importance to humans: Decades before its scientific description, the Suwannee bass was recognized as unique and sought by local Florida anglers, who knew where and how to fish for the species (Swift *et al.* 1977). Even though relatively small, Suwannee bass are regarded as strong fighters when caught on light tackle. Individuals are taken on small crayfish-colored spinnerbaits, crankbaits, plastic worms, and jigs and live baits (e.g., dobsonfly larvae, crayfish). A limited, but specialty, black bass fishery exists in the lower Santa Fe River where Suwannee bass provide a small portion of the sport fish catch (dominated by redbreast sunfish) but constitute over a third of the total catch of *Micropterus* (Bass and Hitt 1973). In the crystal clear, flowing waters of the Wacissa River, float fishers, using light fly fishing gear and wet flies mimicking bait fish, regard the Suwannee bass as a challenging catch in an exceptionally high-quality environment (Ferrin 2006). The meat is reportedly white, flaky, and flavorful (FFWCC 2006).

13.9.6 Micropterus punctulatus *(Rafinesque)*

13.9.6.1 Spotted bass

Characteristics: See generic account for general characteristics. Elongate, slightly compressed body, depth 0.17 to 0.27 of TL, increasing with size. Mouth large, terminal, lower jaw slightly projecting, upper jaw extends little or not at all beyond posterior edge of eye. Outline of spinous dorsal fin curved. Juncture of soft and spiny dorsal fins slightly emarginate, broadly connected. Shortest dorsal spine at emargination of fin, usually 0.4 to 0.9 times the length of longest spine. Dorsal soft rays, usually 12 or 13, 11 to 14; anal soft rays, usually 10, 9 to 11. Gill rakers, 5 to 7. Lateral scales, (55)60 to 75(79); rows above lateral line, (6)7 to 9(11); rows below lateral line, (11)13 to 18(22); cheek scale rows, (10)13 to 18(20); caudal peduncle scale rows, (21)25 to 31(32); pectoral rays, (13)15 to 17(18). Small splintlike scales on interradial membranes at anal and second dorsal fin bases (>60 mm SL). Pyloric caeca, single, rarely branched, 10 to 13. Tooth patch present on glossohyal (tongue) bone (Hubbs 1927; Hubbs and Bailey 1940, 1942; Applegate 1966; Bryan 1969; Ramsey and Smitherman 1972; Williams and Burgess 1999).

Size and age: Size at age 1 averages about 113 mm TL but varies considerably among habitats and across the geographic range (population averages range from 66 to 216 mm TL) (Vogele 1975b; Webb and Reeves 1975; Carlander 1977; Olmsted and Kilambi 1978; DiCenzo *et al.* 1995; Pflieger 1997; Maceina and Bayne 2001). Growth rate trends higher in reservoirs than in streams (Vogele 1975b), and the Alabama spotted bass, *M. p. henshalli*, lives longer and reaches a larger size than the northern subspecies, *M. p. punctulatus* (DiCenzo *et al.* 1995). However, the Alabama spotted bass may represent a distinct taxon and perhaps be only distantly related to *M. punctulatus* (e.g., Kassler *et al.* 2002). Few individuals exceed 425 mm TL, 2.0 kg, and ages 6+ (maximum about 640 mm TL and age 11+) (Gilbert 1973; Webb and Reeves 1975; Carlander 1977; Olmsted and Kilambi 1978; Page and Burr 1991; DiCenzo *et al.* 1995; Wiens *et al.* 1996; Maceina and Bayne 2001). World angling record, 4.65 kg, California (IGFA 2006). Females of the Alabama spotted bass, *M. p. henshalli*, and perhaps other spotted bass populations (e.g., Ryan *et al.* 1970), can live longer than males (age 8+ versus age 5+) and after the third year show faster growth and weigh more than males (Webb and Reeves 1975).

Coloration: Rows of small black spots on yellow-white lower sides form horizontal lines. Dark midlateral stripe or series of partly joined blotches along light olive to yellowish green side. Caudal spot dark, darkest on young. Light green-gold dorsally with dark olive, often diamond-shaped mottlings. Young (<50 mm TL) with distinct tricolored caudal fin markings (yellowish base, dark middle, whitish edge) (Trautman 1981; Page and Burr 1991).

Native range: The spotted bass is native to the Mississippi River basin from southern Ohio and West Virginia to southeastern Kansas and south to the Gulf and in Gulf drainages from the Choctawhatchee River, Alabama and Florida, west to the Guadalupe River, Texas (Robbins and MacCrimmon 1974; Page and Burr 1991; Miller 2005). Populations in the Apalachicola River Basin were likely introduced (Bailey and Hubbs 1949; Williams and Burgess 1999). The spotted bass was widely introduced and is established outside its native range across most of the southern half of the western United States and in some river systems has rapidly expanded its range after introduction (e.g., Missouri River) (Robbins and MacCrimmon 1974; Pflieger 1997; Fuller *et al.* 1999; Moyle 2002). Hybridization and introgression can be extensive when nonnative *M. punctulatus* are introduced into native populations of *M. dolomieu* (Koppelman 1994; Pierce and Van Den Avyle 1997; Avise *et al.* 1997). Data from nuclear-encoded allozymes and mitochondrial DNA haplotypes revealed a remarkable pattern of faunal turnover and introgressive swamping of the native *M. dolomieu* by the nonnative *M. punctulatus* in a northeastern Georgia reservoir (Hiwassee River drainage, Avise *et al.* 1997). In only 10 to 15 years after the introduction of *M. punctulatus*, the *M. dolomieu* population declined dramatically. Even more surprising was the finding that >95% of remaining *M. dolomieu* mtDNA haplotypes (and nuclear alleles) in the lake population were found in fishes of hybrid ancestry between the introduced and native *Micropterus*. Similar patterns indicative of introgressive swamping occurred when *M. punctulatus* was introduced into a native population of *M. dolomieu* in South Moreau Creek (Missouri River drainage), Missouri (Koppelman 1994), and are suggested for introductions of *M. p. henshalli* into a native population of *M. coosae* in Keowee Reservoir (Savannah River drainage), South Carolina (Barwick *et al.* 2006).

Habitat: The spotted bass inhabits gravelly flowing pools and runs of creeks and small to medium rivers and reservoirs (Page and Burr 1991). In streams, spotted bass are commonly associated with low-velocity pools, particularly those with vegetation, log complexes, rootwads, or undercut banks (Lobb and Orth 1991; Scott and Angermeier 1998; Tillma *et al.* 1998; Horton and Guy 2002; Horton *et al.* 2004). The habitat requirements of the species can be broadly characterized as intermediate between those of the smallmouth bass and largemouth bass. The spotted bass is associated with warmer, more turbid water than smallmouth bass, and faster, less productive waters than the largemouth bass (Trautman 1981; Layher *et al.* 1987; Pflieger 1997). Nevertheless, spotted bass frequently co-occur with largemouth bass, smallmouth bass, and redeye bass but generally show some spatial segregation from co-occurring *Micropterus*, in cover type,

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longitudinal distribution, or water depth (e.g., Viosca 1931; Vogele 1975b; Trautman 1981; Buynak *et al.* 1989; Matthews *et al.* 1992; Pflieger 1997; Scott and Angermeier 1998; Sammons and Bettoli 1999; Long and Fisher 2005). For example, spotted bass were widely distributed in a Virginia impoundment, but occurred most commonly in areas with fine substrate and woody debris, undercut banks, and bank vegetation as cover, avoiding the steep drop-offs and rocky shorelines frequented by smallmouth bass (Scott and Angermeier 1998). In southern US reservoirs, spotted bass are most abundant in oligo-mesotrophic reservoirs or oligo-mesotrophic reaches of reservoirs with abundance decreasing as eutrophication increases; an opposite pattern occurs for largemouth bass abundance (Buynak *et al.* 1989; Greene and Maceina 2000; Maceina and Bayne 2001). Although spotted bass may enter relatively high-salinity coastal environments ($\leq$10 ppt), they infrequently occur in coastal marshes with salinities >4 ppt (Peterson 1988, 1991; Peterson and Ross 1991).

Relatively little is known about movements of spotted bass. In some populations, indirect evidence suggests massive upstream movement in spring from reservoirs and rivers into tributaries to spawn, followed by a gradual downstream drift of most adults and young to overwinter in large, lower-gradient habitats (Vogele 1975b; Trautman 1981). The average home activity area of radio-tagged spotted bass tracked over multiple seasons in a Kansas stream was 0.39 ha (range, 0.06–1.2 ha). Activity area was correlated positively with body size, and activity areas of up to six fish showed simultaneous overlap. During summer and winter, fish typically remained in one pool, but during spring and fall, fish crossed riffles and moved among pools (Horton and Guy 2002).

Food: The spotted bass is an opportunistic carnivore, exploiting prey from the bottom to the water's surface. The adult diet is dominated in biomass by crayfish if present, fish (e.g., clupeids, darters, minnows, catfishes), and to a lesser extent, immature aquatic insects (Applegate *et al.* 1967; Gilbert 1973; Vogele 1975b; Scott and Angermeier 1998). Depending on prey availability, consumption of large numbers and volumes of immature aquatic insects may continue up to 150 mm TL or larger. Spotted bass may exploit relatively large numbers and volumes of terrestrial insects (e.g., hymenoptera, beetles, flies, adult odonates) (Smith and Page 1969; Ryan *et al.* 1970; Vogele 1975a; Scott and Angermeier 1998). The young initially depend on zooplankton (cladocerans and copepods) with juveniles transitioning from large immature aquatic (e.g., mayflies, diptera) insects to fish and crayfish at 50 to 100 mm TL (Applegate *et al.* 1967; Clady and Luker 1982; Matthews *et al.* 1992; Scott and Angermeier 1998). Spotted bass are relatively inactive at night, staying close to cover, but move frequently throughout the day (Horton *et al.* 2004). Even so, diet data reveal no clear diel feeding patterns except for an increase in terrestrial insects in the diet during the day (Scott and Angermeier 1998).

Reproduction: Maturity can be reached as early as age 1+ in fast-growing populations, but most individuals do not mature until age 2+ to 3+ (Gilbert 1973; Olmsted 1974; Vogele 1975a,b). Depending in part on latitude and water temperature, spawning occurs over a 1- to 2-month period from March to May or early June, with the most intensive nesting occurring within about 2 weeks of initial spawning activity (Ryan *et al.* 1970; Gilbert 1973; Olmsted 1974; Vogele 1975a; Sammons *et al.* 1999; Greene and Maceina 2000). Active nests have been observed at temperatures as low as 12.8°C, but most spawning occurs between 14°C and 23°C (Howland 1932a; Ryan *et al.* 1970; Smitherman and Ramsey 1972; Gilbert 1973; Olmsted 1974; Vogele 1975a,b; Aasen and Henry 1981; Sammons *et al.* 1999). The male excavates a solitary, depressional, roughly circular nest by caudal sweeping and removing material with his mouth (Breder and Rosen 1966); nests are spaced widely with densities ranging from 0.5 to 11.3/100 m of shoreline. Most but not all nests are located near cover (e.g., rock overhangs, stumps, submerged tree bases) (Vogele 1975a; Vogele and Rainwater 1975). Nests are 38 to 76 cm in diameter, are located at average water depths of 2.3 to 3.7 m (range, 0.9–6.7 m), and are usually swept out over hard substrates (e.g., sand and gravel, solid rock ledges, flat rocks), but compacted soil and exposed root hairs of flooded trees are also used (Vogele 1975a,b; Aasen and Henry 1981). Males may excavate and defend one to four nest sites for up to 3 days before egg deposition. Limited evidence from tagged males suggests year-to-year fidelity to specific nesting areas (Vogele 1975a). Courtship and spawning are generally typical of other *Micropterus*, but published documentation is not extensive (e.g., male guiding of female, paired circling) (Miller 1975; Vogele 1975a,b, citing Howland 1932b). Once a female is attracted to the nest, the male guides her in circles about the nest (female inside, male outside), repeatedly biting at her opercle and vent. During courtship, the midlateral stripe in the female disappears (Miller 1975). Courtship behaviors continue for 20 minutes to 1 hour before egg deposition begins. Ultimately, the female deposits eggs (for 1.5 to 5 seconds) by tilting on her side, and the male releases milt in an upright position as is typical for most centrarchids. Courtship and spawning sequences between pairs may require up to 3.5 hours for completion (Vogele 1975a). Most spawning observations involved a single male and female. After spawning, males immediately begin fanning the eggs and continue defending the eggs from numerous, persistent *Lepomis* and other predators (Vogele 1975a). Mature ovarian eggs range from 1.30 to 2.20 mm diameter (Gilbert

1973; Vogele 1975a) and fertilized, water-hardened eggs range from 1.60 to 2.30 mm diameter (Smitherman and Ramsey 1972; Vogele 1975a). Fecundity increases with female size. The relationship between potential batch fecundity (Y) and total length (X) is described by the function, $\log_{10} Y = -8.222 + 4.779 \log_{10} X (n = 48, R^2 = 0.71$, data from Olmsted 1974 and Vogele 1975a). At 347 mm TL, a female can potentially produce 8284 mature eggs in a single batch (range: 1728 eggs at 250 mm TL to 26,906 eggs at 444 mm TL, respectively). The adhesive, fertilized eggs hatch in 5 days at 14.4°C to 15.6°C (Vogele 1975a). Larvae are free swimming at 6.0 to 7.5 mm TL in 4 days and 8 days after hatching at 25°C and 15 to 18°C, respectively (Vogele 1975a; DiCenzo and Bettoli 1995). Fry emerging from the nest form compact schools that are guarded by the parental male for up to 4 weeks. Schools with fry from different nests may merge into a single large school and be guarded by two parental males. The schools break up as fry reach about 30 mm TL (Vogele 1975a). In hatchery ponds, males apparently exhibited less parental care, abandoning the fry shortly after swim-up (Smitherman and Ramsey 1972; Vogele 1975b).

Nest associates: None known.

Freshwater mussel host: Confirmed host to *L. altilis, L. perovalis, Lampsilis subangulata, V. iris, V. nebulosa*, and *V. vibex* (Neves *et al*. 1985; Haag and Warren 1997; Haag *et al*. 1999; O'Brien and Brim Box 1999). Putative host to *L. abrupta* (unpublished sources in OSUDM 2006).

Conservation status: The spotted bass is secure throughout its range, but peripheral populations in Illinois are considered vulnerable (Warren *et al*. 2000; NatureServe 2006). Lack of resolution of the genetic relationships among populations now regarded as *M. punctulatus* is of primary conservation concern (Kassler *et al*. 2002; see section on systematic notes).

Similar species: Shoal bass has dark vertically elongate bars on sides and lacks patch of teeth on tongue; redeye bass has white to orange upper and lower edges on caudal fin lobes and young has red medial fins; largemouth bass and Florida bass lack rows of black spots on lower sides and have a deep notch between spiny and soft dorsal fins; young of these species have a bicolored caudal fin (white, black edge); smallmouth bass lacks a distinct lateral stripe (Page and Burr 1991).

Systematic notes: *Micropterus punctulatus* and *M. dolomieu* form a sister pair that is basal to all other *Micropterus* (Kassler *et al*. 2002; Near *et al*. 2003, 2004, 2005). As currently conceived, the long-presumed polytypy of *M. punctulatus* (Hubbs and Bailey 1940) appears to subsume two relatively distantly related and divergent species of *Micropterus*. Morphological and genetic data indicate that a small-scaled form, the Alabama spotted bass (nominal *M. p. henshalli*), occurs in Mobile Basin (Hubbs and Bailey 1940; Gilbert 1973; Kassler *et al*. 2002). Although intergrades between *M. p. punctulatus* and *M. p. henshalli* were suggested from limited samples from west of Mobile Basin to the Lake Pontchartrain system (Hubbs and Bailey 1940), more extensive meristic data revealed no evidence of intergradation in that region (Gilbert 1973). However, individuals above the Fall Line in Mobile Basin were assigned to *M. p. henshalli* and those below the Fall Line were interpreted as intergrades between *M. p. henshalli* and *M. p. punctulatus* (Gilbert 1973). The putative intergrades could just as easily represent *in situ* differentiation of quasi-isolated populations of Alabama spotted bass, rather than intergradation. Importantly, mitochondrial DNA analyses from limited population sampling indicate that the form in Mobile Basin is highly divergent from *M. p. punctulatus* (e.g., fixed allelic differences at multiple gene loci, fixed haplotype differences, sequence divergence of 10.3%) and is genetically most similar to *M. coosae* (Kassler *et al*. 2002). Unfortunately, *M. p. henshalli* has been introduced outside the native range in Mobile Basin and has introgressed with native *Micropterus* (Pierce and Van Den Avyle 1997). The resolution of the relationships of the Alabama spotted bass to other *Micropterus* awaits a thorough genetic analysis across populations in the Mobile Basin. The subspecies *M. p. wichitae*, ostensibly restricted to a single stream in the Red River drainage, Oklahoma (Hubbs and Bailey 1940), was based on *M. punctulatus* × *M. dolomieu* hybrids and is not valid (Cofer 1995). The subspecies *M. p. punctulatus* occupies the remainder of the range (Gilbert 1973).

Importance to humans: Ecologically, the spotted bass can function as the only top carnivore in small, even intermittent, headwater streams and is often the dominant top predator in large rivers and reservoirs (Cross 1967; Trautman 1981; Pflieger 1997). The spotted bass is also a popular sport fish in streams and reservoirs throughout the southeastern United States. The species is sought in streams by anglers favoring fly fishing or ultralight tackle (Cross 1967; Ross 2001). The largest spotted bass are taken in reservoirs and spillways where food availability is higher than in most streams (Ross

2001). In southern US reservoirs, spotted bass can be the dominant or co-dominant *Micropterus* and constitutes a sizable proportion of the black bass catch (e.g., 60%) and harvest (e.g., 50%) (Webb and Reeves 1975; Novinger 1987; Buynak *et al.* 1989, 1991; DiCenzo *et al.* 1995; Pflieger 1997; Sammons *et al.* 1999; Sammons and Bettoli 1999; Long and Fisher 2005). The spotted bass often co-occurs with the largemouth bass or smallmouth bass in reservoirs, where most management effort is usually focused on the latter two species (e.g., Maceina and Bayne 2001; Long and Fisher 2005). Because of its slower growth and high abundance in some reservoirs, fishery managers combine liberalized harvest of spotted bass with increased length limits for largemouth bass (or smallmouth bass) to reduce exploitation and to increase the size of the latter (e.g., Buynak *et al.* 1991; Long and Fisher 2005). The spotted bass takes the same lures (e.g., spinner baits, plastic worms, jigs, crank baits) and live baits (e.g., minnows, crayfishes, salamanders) as other black bass. Anglers consider their strike more aggressive and their fight more spirited than that of the largemouth bass (Ross 2001).

13.9.7 Micropterus salmoides *Lacépède*

13.9.7.1 Largemouth bass

Characteristics: See generic account for general characteristics. Elongate, slightly compressed body, depth 0.24 to 0.29 of TL, increasing with size. Mouth large, terminal, lower jaw slightly projecting, upper jaw extends beyond posterior edge of eye in adults. Outline of spiny dorsal fin sharply angular. Juncture of soft and spiny dorsal fins deeply emarginate, almost separate. Shortest dorsal spine at emargination of fin, usually 0.3 to 0.4 times length of longest spine, membranes between short spines deeply incised. Dorsal soft rays, usually 13 or 14, 11 to 15; anal soft rays, usually 11 or 12, 10 to 14. Gill rakers, 7 to 9. Lateral scales, (55)58 to 67(72); rows above lateral line, 7 to 8(9); rows below lateral line, 13 to 17; cheek scale rows, 9 to 11(13); caudal peduncle scale rows, (24)26 to 28(30); pectoral rays, (13)14 to 15(17). No small splintlike scales on interradial membranes at anal and second dorsal fin bases. Pyloric caeca branched at base, 12 to 45. Tooth patch usually absent on glossohyal (tongue) bone, but tooth patch present or absent in San Antonio and Nueces rivers, southwest Texas, and present in ≥50% of specimens in the Rio Grande system, Mexico and Texas (Hubbs and Bailey 1940; Bailey and Hubbs 1949; Applegate 1966; Keast and Webb 1966; Buchanan 1973; Chew 1974; Edwards 1980; Kassler *et al.* 2002).

Size and age: Size at age 1 is highly variable among habitats and across latitudes, ranging from 33 to 271 mm TL (median 102 mm TL) (Carlander 1977; McCauley and Kilgour 1990; Beamesderfer and North 1995; Garvey *et al.* 2003). Critical periods causing differential size, growth, and survival for age-0 cohorts include time of hatching, onset of piscivory, accumulation of lipids in the fall, and the ability to survive predation, starvation, or both over the first winter (DeAngelis and Coutant 1982; Gutreuter and Anderson 1985; Miranda and Hubbard 1994a,b; Ludsin and DeVries 1997; Maceina and Bettoli 1998; Garvey *et al.* 1998; Post *et al.* 1998; Fullerton *et al.* 2000; Garvey *et al.* 2000, 2002; see section on habitat). Large individuals can exceed 550 mm TL, weigh >3.5 kg, and attain age 8+ to 15+ (Carlander 1977; Beamesderfer and North 1995). The oldest largemouth bass and longest-lived *Micropterus* is a 23- or 24-year-old individual (584 mm TL) from New York (Green and Heidinger 1994). The world angling record for all *Micropterus* (and all centrarchids) is a largemouth bass weighing 10.1 kg (~ 787 mm TL) that was caught in Georgia in 1932 (IGFA 2006). At least in some populations, older females (age 4+) are longer than males, and most older individuals are females (Webb and Reeves 1975; Carlander 1977).

Coloration: Broad olive or olive black midlateral stripe formed of confluent or nearly confluent blotches. Silver to brassy green (brownish in tea-stained water) above with dark olive mottling. Scattered dark specks on lower sides; whitish below. Iris brown. Young (<50 mm TL) with bicolored caudal fin markings (whitish base, dark distally) (Bailey and Hubbs 1949; Page and Burr 1991; Etnier and Starnes 1993; Jenkins and Burkhead 1994).

Native range: The largemouth bass is native to the St. Lawrence-Great Lakes, Hudson Bay (Red River), and Mississippi River basins from southern Quebec to Minnesota and south to the Gulf of Mexico and in Gulf drainages from about Mississippi or Alabama west to the Rio Grande and Soto la Marina in northeastern Mexico (Page and Burr 1991; Miller 2005). On the Atlantic Slope, early introductions of "largemouth bass" in many drainages obscured the northern limit of the native range (Jenkins and Burkhead 1994). Critical evaluation of early records and reports and evaluation of nuclear-encoded allozyme data across Virginia suggests that the species occurred historically on the Atlantic Slope to the Tar

River of North Carolina but not beyond (Jenkins and Burkhead 1994; Dutton *et al.* 2005). A broad area of hybridization between the largemouth bass and the Florida bass occurs across the southeastern United States. Before extensive stocking of Florida bass into the range of the largemouth bass, meristic variation indicated a relatively narrow hybrid zone between the two species from the Savannah River south to the St. Mary's River on the Atlantic Slope and from the Choctawhatchee and St. Andrews bays east to the Suwannee River on the Gulf Slope (Bailey and Hubbs 1949). Genetic data incorporating many reservoir and a few riverine populations prescribe a broader area of hybridization, extending from at least central Texas eastward across parts of Louisiana and Arkansas, and most of Mississippi, Alabama, northern Florida, Georgia, and well northward on the Atlantic Slope to Virginia and Maryland. The large extent of the hybrid zone is primarily the result of repeated, deliberate introductions of Florida bass into the range of the largemouth bass, but the extent of natural, isolated populations of pure *M. salmoides* within this broad hybrid zone is uncertain (Philipp *et al.* 1981, 1983; Maceina *et al.* 1988; Morizot *et al.* 1991; Philipp 1991; Dunham *et al.* 1992; Brown and Murphy 1994; Bulak *et al.* 1995; *et al.*Gelwick *et al.* 1995; Whitmore and Craft 1996; Dutton *et al.* 2005; Lutz-Carillo *et al.* 2006). The largemouth bass, its sister species, the Florida bass, or genetic admixtures of the two species have been introduced and are established in much of North America from southern Canada to Mexico. The species is also established in the Caribbean, Oceania, Asia, Africa, Europe, and South America (Robbins and MacCrimmon 1974; Holčík 1991; Fuller *et al.* 1999). The largemouth bass is one of eight fishes included in the top 100 of the world's worst invasive alien species (Cambray 2003) because of its negative effects on native fishes and ability to literally change ecosystem function (e.g., Whittier *et al.* 1997; Rahel 2000; Skelton 2000; Findlay *et al.* 2000; Gratwicke and Marshall 2001; Jackson 2002; Moyle 2002).

Habitat: The largemouth bass inhabits lakes, ponds, swamps, marshes, and backwaters and pools of creeks, and small to large rivers as well as impoundments (Page and Burr 1991). Generally, the largemouth bass is adapted to warmer, more eutrophic waters than other *Micropterus*, except the Florida bass. Even so, the largemouth bass frequently co-occurs with other black basses, but in those cases the *Micropterus* assemblage often shows shifts in species-relative abundances among mesohabitats (e.g., Rutherford *et al.* 2001, see accounts on *M. dolomieu* and *M. punctulatus*). The species occurs and often thrives in an array of lacustrine habitats including saline marshes along the Gulf of Mexico and Atlantic Coast (Peterson and Meador 1994); bottomland hardwood swamps and associated floodplain lakes (Rutherford *et al.* 2001); and vegetated glacial lakes (Werner *et al.* 1977). Over its broad range, the species tends toward highest abundance in warm eutrophic, vegetated reservoirs or the most eutrophic sections within a reservoir (Robbins and MacCrimmon 1974; Durocher *et al.* 1984; Buynak *et al.* 1989; Maceina and Bettoli 1998; Allen 1999; Allen *et al.* 1999; Greene and Maceina 2000; Maceina and Bayne 2001; Brown and Maceina 2002). In swamps, lakes, and reservoirs, young and adult largemouth bass are associated with shallow shorelines (usually <3 m deep) around aquatic macrophyte beds, logs, or other cover, but the young use gravel substrates and steep shoreline slopes if vegetation or other cover is not present (e.g., Werner *et al.* 1977; Schlagenhaft and Murphy 1985; Matthews *et al.* 1992; Annett *et al.* 1996; Demers *et al.* 1996; Hayse and Wissing 1996; Irwin *et al.* 1997, 2002; Miranda and Pugh 1997; Essington and Kitchell 1999; Sammons and Bettoli 1999; Irwin and Noble 2000; Rutherford *et al.* 2001; Olson *et al.* 2003). Young largemouth bass in lakes and reservoirs move inshore at night and offshore during the day; such diel movement is lessened if inshore cover is present (Werner *et al.* 1977; Irwin and Noble 2000). In riverine habits, both young and adult largemouth bass occupy a variety of habitats but are most common in deep pools or low-velocity habitats near undercut banks, instream wood, overhanging and aquatic vegetation, or other cover (e.g., Killgore *et al.* 1989; Sowa and Rabeni 1995; LaPointe *et al.* 2007).

The physical habitat needs, environmental tolerances, and spatial ecology of nearly all life stages of the largemouth bass, particularly for populations in reservoirs, are one of the most well studied of any fish species in North America, being rivaled only by some salmonids (e.g., rainbow trout) and the bluegill. Here, the focus is to briefly introduce aspects of largemouth bass movement in lakes and rivers, relate some broad effects of temperature, and highlight tolerances to salinity, hypoxia, and pH. These and other habitat-associated topics on largemouth bass are available in the references cited in this account and many other sources (e.g., Dahlberg *et al.* 1968; Glass 1968; Beamish 1970; Aggus and Elliot 1975; Coutant 1975; Heidinger 1975; Siler and Clugston 1975; Farlinger and Beamish 1977; Bennett 1979; McCormick and Wegner 1981; Lemons and Cranshaw 1985; Fields *et al.* 1987; Johnson *et al.* 1988; Koppelman *et al.* 1988; Kolok 1991, 1992; Smale and Rabeni 1995b; Raibley *et al.* 1997b; Miranda and Dibble 2002; Parkos and Wahl 2002).

The largemouth bass exhibits directed movement (homing) over relatively long distances, movement to and from wintering (and spawning) areas, and persistent association with home activity areas over long periods. Movement is related to water temperature with activity generally being lowest at temperature extremes of midsummer and midwinter (Warden and Lorio 1975; Carlson 1992; Nack *et al.* 1993; Richardson-Heft *et al.* 2000; Karchesky and Bennett 2004; Hasler *et al.* 2007). During winter in an iced-over northern lake, acoustically tagged largemouth bass stayed in a deep basin in the lake, but moved in spring to a shallow basin (Hasler *et al.* 2007). In both seasons bass formed multi-individual aggregations (individuals <2 m apart) during the day. Aggregations, especially in winter, lasted for several hours a day, and male–female associations were greater than expected by chance (Hasler *et al.* 2007). Tracking studies suggest that largemouth bass, when moving from one activity area to another, travel along the deepest bottom contours (e.g., submerged creek channels) in shallow lacustrine habitats or in the low-velocity currents along shorelines in flowing rivers (Warden and Lorio 1975; Karchesky and Bennett 2004). In displacement studies, about 26% to 43% of individuals return to their original place of capture; some individuals require months to return and others a few days even if displacement distances are similar (Parker and Hasler 1959; Stang *et al.* 1996; Richardson-Heft *et al.* 2000; Ridgway 2002; Wilde 2003). Many individuals displaced in the upper Chesapeake Bay traveled at least 15 to 21 km across the bay to return to their original place of capture, although return times tended to take longer in fall (228 days) than in spring (65 days) (Richardson-Heft *et al.* 2000). In the same study, mean daily movement of 78 displaced radio-tagged largemouth bass was up to 1.45 km/d and maximal movement was 8.37 km/d. Other studies of the species document even longer distance movements (16–64 km) to consistently used winter refuges (or spawning areas) to avoid extreme flows, wave action, and temperature conditions (Funk 1957; Raibley *et al.* 1997a; Nack *et al.* 1993; Gent *et al.* 1995; Irwin *et al.* 2002; Karchesky and Bennett 2004). Postspawning summer and fall home range areas of largemouth bass in an Ontario lake averaged 16.7 to 17.6 ha (Ridgway 2002). Studies of riverine or other lake-dwelling populations generally reveal high persistence (8–110 days) in even smaller areas (150 linear stream meters, 0.18–3.0 ha). However, movements out of these high-use areas for extended periods, movements among high-use areas, and extensive ostensibly random movements without establishment of apparent activity areas are also common (e.g., Lewis and Flickinger 1967; Warden and Lorio 1975; Winter 1977; Savitz *et al.* 1983, 1993; Meador and Kelso 1989; Bain and Boltz 1992; Gatz and Adams 1994; Rogers and Bergersen 1995; Demers *et al.* 1996; Essington and Kitchell 1999; Karchesky and Bennett 2004).

Temperature exerts considerable influence on largemouth bass populations across the broad band of latitude comprising the total range of the species. The species has a relatively high critical thermal maxima of 38.5 to 40.9°C (acclimated at >30°C, Smith and Scott 1975; Fields *et al.* 1987; Beitinger *et al.* 2000; Currie *et al.* 1998, 2004), so that high temperatures are not particularly limiting. In contrast, the summer thermal regime or, alternatively, the duration and severity of winters profoundly affect the distribution, growth, and survival of largemouth bass. In a synthesis of growth data across North America (from Carlander 1977), over half the latitudinal variation in growth (size at age) for largemouth bass (including Florida bass) was accounted for by differences in monthly mean air temperatures (degree days >10°C) across a north–south latitudinal gradient (McCauley and Kilgour 1990). The northern distributional limit for the largemouth bass was estimated as a thermal unit isocline of 550 degree days above 10°C in extreme southern Canada. In a model incorporating data for largemouth bass populations across North America (again including a few Florida bass), age to reach 300 mm TL was correlated negatively with mean air temperature (also degree days >10°C and latitude), and instantaneous natural mortality rate was correlated positively with mean air temperature (Beamesderfer and North 1995). Likewise, average length by fall of age-0 largemouth bass is related positively to latitude and presumably temperature (Garvey *et al.* 2003). Temperature effects are directly or indirectly related to several critical events in the first year of life including hatch date, length of growing season, transition to piscivory, fall lipid accumulation, winter food availability, and the duration and severity of winter (Kramer and Smith 1960a, 1962; Adams *et al.* 1982a,b; Isely *et al.* 1987; Miranda and Hubbard 1994a,b; Ludsin and DeVries 1997; Post *et al.* 1998; Wright *et al.* 1999; Fullerton *et al.* 2000; Jackson and Noble 2000; Fuhr *et al.* 2002; Philipp *et al.* 2002). For age-0 fish, winter is often a huge survival bottleneck because of complex interactions of winter severity, food availability, and predation. When water temperatures are <6°C for extended periods, feeding is stopped or is infrequent and small individuals experience greater proportional energy loss and increased mortality relative to large individuals (Garvey *et al.* 1998). If low temperature conditions are prolonged, energy reserves built up in summer and fall can be depleted in small individuals regardless of winter food availability (Wright *et al.* 1999). Under less severe winter conditions, warm or fluctuating winter temperatures may exacerbate metabolic costs of young fish during a period of reduced food availability (e.g., fish prey too large) and increased predation risk (Ludsin and DeVries 1997). Common garden and winter simulation experiments measuring differential growth and survival among largemouth bass from different latitudes provide compelling evidence of genetic adaptation to local temperature regimes (and other local environmental factors). When stocks of largemouth bass from Wisconsin, Illinois, and Texas were compared in common garden experiments, the local native stock consistently had higher growth, survival, and reproductive fitness than transplanted nonnative stocks (Philipp *et al.* 2002). In laboratory experiments, 92% to 100% of age-0 largemouth bass from Alabama died when subjected to simulated temperatures, lengths, and photoperiods of an intermediate (Ohio) and long (Wisconsin) winter, but similar-sized Ohio and Wisconsin stocks survived a simulated Alabama winter. Energy depletion measured as weight loss showed a gradient with fed individuals from all three sources maintaining or gaining weight under the Alabama winter, maintaining weight under the Ohio winter, and losing weight under the Wisconsin winter. Winter survival was also size mediated with small fish suffering higher mortality than large fish under both the Alabama and Wisconsin winters (Wright *et al.* 1999; Fullerton *et al.* 2000), results consistent with experimental studies in ponds and empirical observations in reservoirs (Miranda and Hubbard 1994a; Ludsin and DeVries 1997).

Coastal populations of largemouth bass frequent oligohaline marsh systems along the Atlantic and Gulf coasts. These populations are at least moderately tolerant of prolonged saline conditions (usually <8 ppt) and show differences in salinity selection, physiology, and growth relative to freshwater populations (Meador and Kelso 1990a,b; Peterson 1991; Peterson and Ross 1991; Peterson and Meador 1994; Krause 2002; Peer *et al.* 2006). Effects of <4 ppt salinity on blood plasma level concentrations in adult coastal marsh and freshwater largemouth bass populations in Louisiana are minimal, and acclimation does not affect salinity preferences (to 5 ppt), suggesting efficient osmoregulation in low salinities (Meador and Kelso 1990b). Young-of-the-year of freshwater and coastal marsh largemouth bass preferred 0-ppt salinity over a gradient (0, 3, 6, 9, 12 ppt). Adult marsh largemouth bass had significantly more observations at 3 ppt, and freshwater bass had significantly more observations at 0 ppt, although both selected 3 ppt most often (Meador and Kelso 1989). Relative to freshwater populations, coastal marsh largemouth bass can reduce osmoregulatory stress at 8 ppt salinity by conserving adenosine triphosphate (ATP), reducing active ion transport, and tolerating elevated plasma ion levels (Meador and Kelso 1990b). Young-of-the-year coastal marsh largemouth bass appear even better able to maintain osmoregulatory function than adults up to 12-ppt salinity, but mortality is severe with 48-hour exposures to 16 ppt (Susanto and Peterson 1996). Exposure to 12-ppt salinity in laboratory trials caused adults from coastal marsh and freshwater populations to cease feeding and die within 7 days (Meador and Kelso 1990b). Coastal marsh largemouth bass also exhibit small size and reduced length at age, but maintain excellent condition (relative weight) year round, indicating that they are not stressed physicochemically by marsh environments (Meador and Kelso 1990a). Marsh-dwelling largemouth bass also exhibit a decided growth response to increasing salinities. In Louisiana coastal populations, growth in length is reduced at 0-ppt salinity and increased at 8 ppt relative to freshwater largemouth bass (Meador and Kelso 1990a). In Mobile Bay, Alabama, first-year growth of largemouth bass along a freshwater to mesohaline gradient of sites was higher in individuals within or adjacent to brackish waters (Peer *et al.* 2006). A short, rotund body is characteristic of coastal largemouth bass (Hallerman *et al.* 1986; Meador and Kelso 1990a), reflecting a redistribution of somatic growth relative to freshwater populations. The body form may be related to being shifted from a position as a cruising top predator in freshwaters to a secondary predator restricted to highly structured edges to avoid larger predators in these piscivore-rich habitats (Meador and Kelso 1990a). Osmoregulatory adaptations, differential growth responses, and body form suggest genetic differences between coastal and freshwater largemouth bass, but no profound biochemical genetic differences emerged in populations examined thus far (Hallerman *et al.* 1986). Oligohaline marsh populations in Mobile Bay possess higher genetic heterozygosities relative to upstream freshwater populations (Hallerman *et al.* 1986), possibly reflecting adaptation to a more dynamic physicochemical environment (Peterson and Meador 1994; Peer *et al.* 2006).

The largemouth bass is tolerant of low DO levels, avoiding only extreme hypoxia and its associated physiological costs. In natural settings, individuals apparently move to streams or other oxygenated refugia to avoid winter-associated low oxygen levels in northern lakes and bogs, reinvading these habitats when DO levels increase in summer (Tonn and Magnuson 1982; Rahel 1984). Likewise, the species appears to avoid hypoxic conditions in densely vegetated southern reservoirs and wetlands during summer temperature extremes (Rutherford *et al.* 2001; Killgore and Hoover 2001). Hypoxia tolerance in the species is size mediated such that small individuals can use more hypoxic waters than large individuals (Moss and Scott 1961; Cech *et al.* 1979; Burleson *et al.* 2001). This is a potentially important factor for young largemouth bass forced by competition or predation to occupy marginal habitats (Burleson *et al.* 2001). Nevertheless, largemouth bass across a range of sizes (23–3000 g at 24°C) avoid extreme hypoxic conditions, seeking water with >27% air saturation (ca. >2.4 mg/l DO) (Burleson *et al.* 2001) but show little or no avoidance to DO concentrations as low as 3.0 mg/l (19–20°C) (Whitmore *et al.* 1960). In laboratory trials largemouth bass show relatively low average critical DO levels (24-hr survival or cessation of ventilation) of 0.70 to 1.2 mg/l (Moss and Scott 1961; Smale and Rabeni 1995a). Embryos develop and hatch at DO levels as low as 1.0, 1.1, and 1.3 mg/l at 15, 20, 25°C but concentrations below 2.0, 2.1, and 2.8 at these respective temperatures significantly lowered survival; most mortality occurred during hatching when oxygen demand is presumably higher (Dudley and Eipper 1975). At 20 and 23°C, DO concentrations as low as 35% saturation are adequate for larvae, but growth is reduced at $\leq$70% saturation, and at $\leq$50% saturation hatching of eggs is premature and first feeding delayed (Carlson and Siefert 1974). Hypoxic conditions impose other physiological costs and constraints on largemouth bass. Diurnal low oxygen levels (2.5 to 4.1 mg/l at about 20°C), simulating early morning reductions in DO concentration, produce measurable, stress-related changes in serum proteins, reduce food consumption, cause digestive interference, and increase ventilation rates in largemouth bass (Bouck and Ball 1965). Hypoxic conditions (<5 mg/l at 26°C) reduce growth rate and food consumption of small largemouth bass (62–85 mm TL), but food conversion efficiencies are not affected except at extremely low DO concentrations ($\ll$4 mg/l; Stewart *et al.* 1967). Swimming ability of small largemouth bass decreases with decreasing temperature under hypoxic conditions (Katz *et al.* 1959; Dahlberg *et al.* 1968). For example, juveniles (93–100 TL) were able to swim against a current of 3.8 cm/s for 1 day at DO levels of 2.05 mg/l at 25°C, but were unable to swim against the same current at 2.8 mg/l at 20°C or at 5 mg/l at 17°C. Maximum sustained swimming speed of juveniles was reduced at oxygen concentrations <5 to 6 mg/l (at 25°C) (Dahlberg *et al.* 1968). Intraspecific differences in tolerances of geographically disparate populations of largemouth bass to low DO are notable. For example, largemouth bass from Wisconsin showed lower hypoxia tolerance than largemouth bass from Missouri streams (critical levels of 1.01 versus 0.70 mg/l DO, respectively) (Smale and Rabeni 1995a). In another example, swimming performance and routine oxygen consumption differed between largemouth bass stocks from Illinois and Wisconsin in trials at different temperatures. Notably, hybrid individuals between the stocks showed reduced performance relative to locally adapted stocks, particularly at higher temperatures. In essence, the hybrid stocks displayed performance impairment rather than hybrid vigor, which emphasizes the importance of adaptation to local environmental conditions in largemouth bass (Cooke *et al.* 2001a; Cooke and Philipp 2005, 2006).

Adult largemouth bass are generally more tolerant of lowered pH than egg, larval, and juvenile stages. For example, adults nested and spawned each year as pH in an experimental lake was decreased gradually from 6.1 to 4.7 over several years (Little Rock Lake, WI), but the percentage of nests producing swim-up fry declined significantly with decreasing pH. At pH 5.1, percentage of nests producing swim-up fry fell below that observed in the reference basin and overwinter survival decreased, and no swim-up fry were observed at pH 4.7, a lower limit consistent with laboratory and additional *in situ* tests (Eaton *et al.* 1992; Brezonik *et al.* 1993). In a related laboratory study, juvenile largemouth bass (6.7 g) osmoregulated and survived up to 30 days at pH $\geq$4.5 but lost osmoregulatory control at pH 4.0 and died within a few days (McCormick *et al.* 1989). Young-of-the-year (2.5–4.5 g) were subjected (at 3.8°C with a simulated spring increase to 18°C) to a graded series of pH (4.5–8.0), two Ca concentrations (1.5 and 13.4 mg/l), and two monomeric Al concentrations (6 and 30 μg/l) for 113 days (McCormick and Jensen 1992; Leino and McCormick 1993). Survival probabilities were most affected at low Ca and high Al levels and were correlated with decreased osmoregulatory function and gill damage. For example, fish at pH 5.0 and high Al levels had a 56% chance of survival to day 84 compared to a 99% chance for fish at the same pH with no Al. Laboratory analyses of behavioral repertoires of young-of-the-year largemouth bass acclimated to decreasing pH suggest that values <6.1 may increase energy demands. At low pH extremes, feeding and swimming activity of young-of-the-year is reduced (Orsatti and Colgan 1987), ultimately increasing risk of starvation.

Food: The largemouth bass is an opportunistic top carnivore, exploiting prey from the bottom to the surface. Adults feed primarily on fishes (e.g., clupeids, yellow perch, *Lepomis* spp., silversides, minnows, topminnows, darters); crayfish and grass shrimp (if available); and large aquatic insects (e.g., odonate and mayfly larvae), including winged adults (Applegate *et al.* 1967; Olmsted 1974; Carlander 1977; Hubert 1977; Cochran and Adelman 1982; Huskey and Turingan 2001; Pope *et al.* 2001; Sammons and Maceina 2006). In their first summer of life, largemouth bass young-of-the-year shift from an initial diet of microcrustaceans to begin exploiting a variety of aquatic insect larvae, especially diptera larvae and pupae and some fish at about 30 to 70 mm TL. Between about 30 and 100 mm TL, individuals begin a usually rapid transition to a diet predominated by small fishes and if available, amphipods, crayfish, or grass shrimp (Keast 1965; Applegate *et al.* 1967; Miller and Kramer 1971; Timmons *et al.* 1980; Keast 1985b,c; Keast and Eadie 1985; Matthews *et al.* 1992; Olson *et al.* 1995; Olson 1996; Miranda and Pugh 1997; Huskey and Turingan 2001; Pelham *et al.* 2001). In fast-growing individuals or cohorts spawned early, the shift to piscivory occurs in the first summer of life, but if food availability or prey size is limiting the shift can be delayed (Kramer and Smith 1960a; Timmons *et al.* 1980; Miller and Storck 1984; Keast and Eadie 1985; Phillipps *et al.* 1995; Olson 1996; Ludsin and DeVries 1997). For example, in a densely vegetated southern reservoir, most juvenile largemouth bass delayed the shift to piscivory until 140 mm TL, relative to $\geq$60 mm TL after vegetation removal, a delay presumably associated with limited availability of fish prey in the dense vegetation (Bettoli *et al.* 1992). Similarly, late-hatched individuals may not find enough fish prey of suitable size and exploit insect or even zooplankton prey for much of the first year of life (e.g., Phillips *et al.* 1995). Regardless of age, the largemouth bass is adept at exploiting available food resources, feeding almost solely on invertebrates if fish are unavailable or opportunistically preying on vertebrates of terrestrial origin to augment the diet (i.e. salamanders, frogs, snakes, shrews, voles, mice, and birds; Clady 1974; Carlander 1977; Cochran and Adelman 1982; Becker 1983; Hodgson *et al.* 1997; Schindler *et al.* 1997; Ernst and Ernst 2003). In some populations, terrestrial vertebrates contribute substantially to the diet (Clady 1974; Hodgson *et al.* 1997). If large size differences exist among young, or alternate fish prey are unavailable, cannibalism also can contribute a major portion of the juvenile or adult diet, most often involving consumption of young-of-the-year or age-1 bass (e.g., Kramer and Smith 1962; Applegate *et al.* 1967; Clady 1974; Timmons *et al.* 1980; Cochran and Adelman 1982; Hodgson and Kitchell 1987; Olson *et al.* 1995; Hodgson *et al.* 1997; Schindler *et al.* 1997; Post *et al.* 1998; Pothoven *et al.* 1999; Pine *et al.* 2000).

Activity and feeding patterns of largemouth bass are characterized by peaks at or just before dawn, midday, and dusk (Olmsted 1974; Reynolds and Casterlin 1976b; Demers *et al.* 1996). Young-of-the-year, still under the protection of guardian males, and recently dispersed young forage continuously throughout the day, resting at night in cover in shallow water (Elliott 1976; Helfman 1981). Intermediate-size largemouth bass (ca. 6–20 cm) often forage during the day in groups (up to 50) and simultaneously attack schools of prey fishes (Helfman 1981; Becker 1983; Sowa and Rabeni 1995). In adults, feeding tends to show crepuscular peaks, but nocturnal activity, movement, and presumably foraging can be high and extend well after dusk into the early morning hours, especially at high summer water temperatures (>27°C) (Olmsted 1974; Warden and Lorio 1975; Helfman 1981; Demers *et al.* 1996). Although feeding and movement decline as water temperature decreases, largemouth bass actively feed and can grow during the winter at temperatures ≥6°C (Bennett and Gibbons 1972; Olmsted 1974; Warden and Lorio 1975; Hubert 1977; Etnier and Starnes 1993; Garvey *et al.* 1998; Fullerton *et al.* 2000).

The behavior, functional morphology, bioenergetics, and other aspects of the trophic biology and ecology of the largemouth bass are among the most extensively documented of any North American freshwater fish. Aspects of learning and foraging adaptability; prey detection; chemical alarm cues; and predator effects are introduced here. The interested reader is encouraged to consult papers cited in this account on these and other feeding-related topics, including for example, Lewis *et al.* 1961, 1974; Laurence 1969, 1972; Beamish 1972; Niimi 1972a,b; Niimi and Beamish 1974; Heidinger and Crawford 1977; Rice *et al.* 1983; Brown and Colgan 1984; Rice and Cochran 1984; Webb 1986; Hoyle and Keast 1987, 1988; Wahl and Stein 1989; Hambright 1991; Hambright *et al.* 1991; Hodgson *et al.* 1991; Trebitz 1991; Wainwright and Lauder 1992; He *et al.* 1994; Richard and Wainwright 1995; Wainwright and Richard 1995; Wainwright and Shaw 1999; Zweifel *et al.* 1999; Essington *et al.* 2000; and Garvey and Marschall 2003.

Largemouth bass quickly learn to locate, capture, and handle novel prey items, even when shifted from simple to structurally complex habitats. The species can switch among modes of ram strike feeding for water column prey (Norton and Brainerd 1993), suction feeding for benthic prey in crevices, and biting for exposed benthic prey (Nyberg 1971; Winemiller and Taylor 1987). In experimental settings, largemouth bass shifted from a cruising–searching–foraging strategy to an ambush strategy for fish prey as vegetation density was increased (Savino and Stein 1989a,b). Young largemouth bass, often forced into structurally complex habitats to avoid predation, rapidly learned to change foraging tactics in experimental settings. When switched from intermediate to highly structured habitats, the young bass initially used tactics from the previous habitat in the new habitat to capture damselfly nymphs, but individuals modified search and prey selection strategies in a few days to increase capture efficiency in the most structurally complex habitat (Anderson 1984). Learning also plays a role in foraging success of postlarval largemouth bass. Hatchlings raised on natural food (live zooplankton) for 9 weeks were significantly more efficient predators when exposed to live fish than were fry raised on artificial diets. Apparently the fry fed natural foods learned critical aspects of a behavioral repertoire necessary to efficiently capture live fishes. Even so, with exposures to natural diets the artificial diet group improved prey capture efficiency with experience (Colgan *et al.* 1986). In natural settings, the survival to age-1 of stocked pellet-fed largemouth bass is lower than that of individuals fed minnows before stocking (Heidinger and Brooks 2002), providing indirect support for the laboratory findings.

The largemouth bass is a highly vigilant, visual predator but responses to prey or potential predators vary with size, type, and movement of the visual target, light intensity, and water clarity. In choice experiments between close and distant stationary prey, largemouth bass (290 mm TL) chose the closer of two prey of equal size, suggesting that they can judge distances and the absolute size of their prey (or potential predator) (Howick and O'Brien 1983). Largemouth bass also can

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visually assess the differential risk posed by different aerial predators. Cardiac responses of largemouth bass exposed to a blue heron, a predator with size-restricted predation ability on bass, were greater in smaller more vulnerable largemouth bass than in less vulnerable larger largemouth bass. Bass response to an osprey predator with ability to consume larger fish than a blue heron was also size mediated, but the responses were more extreme than in the heron exposures, and individuals of all sizes required more time for recovery (Cooke *et al.* 2003b). Largemouth bass can see effectively even at relatively low light levels. As light level decreases, adults (290 mm TL) show no obvious decline in reactive distance (>120 cm) to motionless bluegill (60 mm TL) prey until light is <5 lux (Howick and O'Brien 1983); then reactive distances decrease steeply to about 33 cm at 0.195 lux. At low light intensity, differences in reactive distances to prey from 30 to 90 mm TL are minimal. Reactive distances increase when largemouth bass are exposed to moving versus stationary prey of similar size. For example, reactive distances of individual bass of 280 to 300 mm TL to crayfish (at 200 lux) increases linearly with crayfish size (17–29 cm carapace length) but reactive distances to moving crayfish is nearly double that of stationary crayfish (Crowl 1989). As prey size increases to about 65 mm TL, reactive distances to moving and stationary prey types converge (Howick and O'Brien 1983). As turbidity increases reactive distance to crayfish prey (17–29 cm carapace length, at 200 lux) decreases from >150 cm at 3 JTU to about 30 cm at 17 JTU; at the higher turbidity, crayfish size or movement does not increase reactive distances. In turbid water, largemouth bass attacked rectangular stones used to assess prey recognition, a behavior never observed under clear water conditions (Crowl 1989). In another water clarity experiment, largemouth bass (83–130 mm FL) showed a trend of decreased capture rates of fathead minnows as turbidities increased from 1 to 70 NTU (at 430 to 538 lux), the trend driven primarily by a decrease in vulnerability of the smallest size class of prey (26–30 mm FL). Even so, only the most extreme turbidity tested showed a significant reduction in minnow capture rates (Reid *et al.* 1999).

Experimental studies indicate that largemouth bass are not totally dependent on vision for feeding but can integrate nonvisual senses with vision to capture and assess palatability of prey. The pharyngeal teeth of largemouth bass are in close association with numerous taste buds, and this association is linked closely with whether a potential food item is ultimately rejected or swallowed (Linser *et al.* 1998). At light intensities ranging from full moonlight (0.003 lux) to low-intensity daylight (312 lux), adult largemouth bass located and ate 95 to 100% of offered live fish prey in 15-minute trials in large tanks. Foraging success declined to 62% and was highly variable under starlight (0.00026 lux) and further declined to 0% in total darkness (0 lux), but when the total darkness trial was extended to 1 hour, capture success increased to 2.5%. From these results, the threshold for visual feeding by largemouth bass (light intensity at 50% prey capture success) is estimated at 0.00016 lux (McMahon and Holanov 1995), much less than that implied by reactive distance studies (e.g., 1.49 lux, Howick and O'Brien 1983), and suggests that nonvisual senses, such as the lateral line, play a role in prey detection and capture. In an experiment testing the role of the lateral line in feeding, largemouth bass were subjected to a visual stimulus (food) and a lateral line stimulus (water jet) directed at various regions of the head. The water jet, with or without the visual stimulus, always elicited an orientation movement and bite toward the stimulus. In individuals with the lateral line pharmacologically ablated, there was no response to the water jet. The orientation and bite were interpreted as unconditioned responses to lateral line stimulation by the water jet with potential importance to prey location (Janssen and Corcoran 1993). In another feeding experiment, largemouth bass were lateral line ablated, bilaterally blinded, or both, and the distances of first orientation to live fish prey and strike measured. Relative to controls, the lateral line–ablated individuals showed decreased distance of first orientation and strike (i.e. both positions closer to prey). Blinded individuals showed even further decreases in first orientation and strike positions. Strike success (prey capture) decreased along a gradient from 79% in controls, 70% in lateral line–ablated individuals, 59% in blinded individuals, and near 0% in blinded, lateral line–ablated individuals. Without input from the lateral line the threshold at which the bass responds to prey apparently is raised (distance to orientation and strike positions reduced), and the lateral line alone provides sufficient information at the closest ranges to successfully capture prey (New and Kang 2000; New 2002).

Largemouth bass respond to chemical alarm cues, which are released from damaged individuals of heterospecifics (e.g., cyprinids). Juvenile bass undergo an ontogenetic shift in response to heterospecific chemical cues, which coincides with shifts in diet and habitat use. Antipredator responses are supplanted by foraging responses at the time juvenile fish switch from invertivory to piscivory and are large enough to avoid predation from large piscivores. In laboratory and field trials, invertivorous young-of-the-year largemouth bass exhibited significant antipredator responses (e.g., freezing, dropping to substrate) to chemical alarm cues of finescale dace and green sunfish, but larger piscivorous individuals exhibited foraging responses to the same cues. In field trials, small largemouth bass (30–60 mm SL) actively avoided areas injected with dace extract, but slightly larger individuals (61–81 mm SL) were attracted to these areas (Brown *et al.* 2001, 2002).

Even though largemouth bass are highly adaptable foragers, the degree of structural complexity of the habitat affects their foraging success. In a variety of experiments, very dense aquatic vegetation (e.g., >270 stems/m^2) decreases feeding success of largemouth bass (e.g., increased search times, reduced attack rate), but foraging success in intermediate densities is comparable to success rates in low-density or open-water habitats (Savino and Stein 1982, 1989a,b; Anderson 1984; Schramm and Zale 1985; Gotceitas and Colgan 1987, 1989; Hayse and Wissing 1996; Valley and Bremigan 2002). Aspects of growth form, architecture, and spatial heterogeneity of vegetation (or other cover) also affect foraging success of the species (Dibble and Harrel 1997; Valley and Bremigan 2002). Juvenile and adult bass showed dramatic shifts in use of macroinvertebrates and fishes in enclosures of Eurasian milfoil compared to pondweed, the shifts being attributed to differences in the fine architecture of the plant growth forms (Dibble and Harrel 1997). Likewise, attack and consumption rates of largemouth bass on bluegill prey were decreased in monoculture aquatic macrophyte beds forming surface canopies relative to diverse beds with growth dispersed throughout the water column (Valley and Bremigan 2002). In field settings, changes in prey vulnerabilities and prey assemblages with sudden shifts in density and composition of aquatic plant communities can lead to large changes in the diet and in the most densely vegetated habitats can even reduce growth (e.g., delay shift to piscivory) and condition in largemouth bass populations (Wiley *et al.* 1984; Bettoli *et al.* 1991, 1992; Dibble *et al.* 1996; Wrenn *et al.* 1996; Miranda and Pugh 1997; Pothoven *et al.* 1999; Unmuth *et al.* 1999; Brown and Maceina 2002; Sammons and Maceina 2006).

The largemouth bass is considered a keystone species in many streams and lakes because of their profound effects as predators on prey habitat use, community structure, and trophic-level biomasses (e.g., Carpenter *et al.* 1987; Harvey 1991a; Mittelbach *et al.* 1995; Power *et al.* 1996; Schindler *et al.* 1997; Jackson 2002; Miranda and Dibble 2002). The striking patterns of complementary distribution of adult largemouth bass and small-bodied fishes and their interaction as predator and prey formed the foundation for much of our understanding of the importance of biotic interactions in structuring fish assemblages in streams and lakes (e.g., Werner 1977; Werner *et al.* 1977, 1983; Power and Matthews 1983; Mittelbach 1983, 1984a, 1986; Power *et al.* 1985; Werner and Hall 1988; Mittelbach *et al.* 1995). The direct and indirect effects of largemouth bass on aquatic communities have been demonstrated in laboratory experiments, in artificial streams, and in manipulations and empirical studies in streams and lakes.

Largemouth bass elicit strong predator avoidance behaviors from many fishes and other aquatic organisms, behaviors that can produce indirect effects on other components of the community. Laboratory and field studies, most often involving *Lepomis*, document dramatic changes in foraging behavior and habitat use of prey fishes faced with predation risk from largemouth bass (e.g., Savino and Stein 1982, 1989a,b; Morgan and Colgan 1987; Morgan 1988; DeVries 1990; Gotceitas 1990b; Gotceitas and Colgan 1990; Harvey 1991a; Matthews *et al.* 1994; Hayse and Wissing 1996). The foraging strategy of prey fish in the presence of bass may shift from an optimal foraging pattern to one minimizing the ratio of mortality rate to foraging rate (e.g., form more compact shoals, increased time in cover or shallow water, increased swimming rate, decreased foraging rate). Experiments in artificial streams using two grazers, a minnow (*Campostoma anomalum*), and a crayfish (*Orconectes virilis*), with and without largemouth bass, exemplify the potential direct and indirect effects of the species. In the presence of largemouth bass, the minnows formed tighter schools, used shallower habitats, and avoided grazing in pools with bass. Crayfish reduced risk from bass predation by foraging at night, hiding in burrows in the daytime, or avoiding pools used most by the bass (Gelwick 2000); similar reductions in activity and habitat use is documented in other studies of crayfish response to largemouth bass (Hill and Lodge 1994; Garvey *et al.* 1994). Algal growth in the experimental stream was also greater in treatments with largemouth bass and grazers than with grazers alone, suggesting that the bass indirectly affected algal productivity by reducing activity levels and locations of grazers (Gelwick 2000) and supporting results in mesocosm experiments on macrophyte–crayfish–bass interactions (Hill and Lodge 1995).

Empirical and manipulative studies in natural stream settings closely parallel laboratory and artificial stream findings of the effects of largemouth bass on stream communities. In stream pools, the distribution of adult largemouth bass is correlated negatively with many small-bodied stream fishes, providing indirect evidence of a bass effect on potential prey species (Power and Matthews 1983; Power *et al.* 1985; Harvey *et al.* 1988; Matthews *et al.* 1994). When adult largemouth bass were added to or removed from stream pools, prey fishes responded with changes in abundance and habitat use, but the response was size mediated. With addition of bass to pools, juvenile *Lepomis* (16–80 mm TL) rapidly moved to shallow water, but larger *Lepomis* did not appreciably alter their depth distributions. Within a stream pool, the abundance of small stream fishes (16–80 mm TL) decreased with increased bass abundance, and abundance of large fish (>80 mm TL) increased with increased bass abundance. Small fishes remaining in bass-containing pools occupied shallow pool margins, but those in pools without bass used the entire pool. Larval minnows and larval *Lepomis* were only found in pools that contained, or had contained, largemouth bass. Experimental manipulation of bass and *Lepomis* larvae in stream pools indicated that bass presence enhanced short-term survival of the larvae, likely an indirect effect of the shift in small fishes that prey on the larvae (Harvey 1991a). A particularly strong seasonal interaction can occur between largemouth bass, an algae-grazing minnow (*Campostoma anomalum*), and attached algae in stream pools. Large schools of *Campostoma* grazing in stream pools can dramatically reduce algal biomass and composition on stream substrates (Power and Matthews 1983; Matthews *et al.* 1987; Power *et al.* 1988) and influence the life histories of other invertebrates as well (Vaughn *et al.* 1993). In a small prairie-margin stream in Oklahoma, largemouth bass (>70 mm SL) and *Campostoma* showed complementary distributions among stream pools with differential crops of periphyton during summer low flow (Power and Matthews 1983; Power *et al.* 1985). Pools with bass had lush standing crops of epiphyton covering rocky substrates, but in the *Campostoma* pools, epiphyton was confined to pool margins, and most rocky substrates were bare. Experimental addition of bass to pools caused *Campostoma* to immediately emigrate from the pool or move to shallow water margins of the pool. Those that did remain in bass pools spent significantly less time in feeding and more time in cover than they did before bass were added. After bass addition, the standing crop of algae in pools increased significantly within 10 to 13 days (Power *et al.* 1985).

The pattern of abundance of adult largemouth bass and small fishes in streams is congruent with that observed in lake communities. Several studies demonstrate the shift of juvenile bluegill to vegetated or shallow littoral zones as a refuge from predation by *Micropterus* (e.g., Savino and Stein 1982, 1989a,b; DeVries 1990; Gotceitas 1990b; Gotceitas and Colgan 1990) and others demonstrate the indirect effects of largemouth bass on the zooplankton prey of bluegills or other *Lepomis* (e.g., Hambright *et al.* 1986; Werner and Hall 1988; Turner and Mittelhach 1990; Hambright 1994). For example, in pond experiments using largemouth bass and small bluegills, the bass induced a habitat shift in small bluegill, resulting in size distributions skewed toward larger bluegill, a direct predation effect of bass. In turn, the shift to larger bluegill produced pronounced differences in zooplankton abundance and size structure (e.g., three cladocerans and the phantom midge became more abundant in the bass treatment), an indirect effect of bass on the aquatic community (Turner and Mittelbach 1990).

A long-term lake study in which largemouth bass were eliminated by a natural event (1978) and then reintroduced (1986) is further illustration of their role as keystone species in some lakes (Mittelbach *et al.* 1995; see also Carpenter *et al.* 1987; Hall and Ehlinger 1989; Drenner *et al.* 2002). Elimination of bass was followed by a dramatic increase in planktivorous fish (e.g., golden shiner, 400,000/lake), the disappearance of large zooplankton, and the appearance of many small-bodied cladocerans, states which were maintained throughout the period of absence of the bass. On reintroduction of largemouth bass, the lake steadily returned to its previous state. Planktivore numbers decreased by two orders of magnitude (golden shiners being practically eliminated), large-bodied zooplankton reappeared and dominated the zooplankton, and the suite of small-bodied cladocerans disappeared. Total zooplankton biomass increased 10-fold and water clarity increased significantly.

Reproduction: Maturity is usually reached by age 2+ to 4+ at minimum sizes of about 250 to 300 mm TL but can occur at age 1+ in fast-growing populations or be delayed until age 5+ in cool north temperate waters (Bryant and Houser 1971; Webb and Reeves 1975; Carlander 1977; Becker 1983). Spawning activity can begin in early spring at a water temperature as low as 12°C, but most individuals initiate spawning after the water temperature reaches and exceeds 15°C. The spawning season extends over 2 to 10 weeks, peaks between water temperatures of 15 and 21°C, and winds down as waters warm to and consistently exceed 24°C. Spawning occurs from mid-May to mid-June or even early July at north temperate latitudes and shifts to earlier dates at progressively lower latitudes (e.g., mid-March to May or early June in Mississippi and Alabama) (Kramer and Smith 1960a; Allan and Romero 1975; Becker 1983; Miller and Storck 1984; Isely *et al.* 1987; Goodgame and Miranda 1993; Annett *et al.* 1996; Post *et al.* 1998; Sammons *et al.* 1999; Greene and Maceina 2000; Cooke *et al.* 2006). Large adult male and female largemouth bass spawn before smaller adults. The earlier hatched young of large bass often gain and maintain a distinct size advantage over the later hatched young of smaller bass, a size advantage that may increase probability of survival to age 1+ (Miller and Storck 1984; Miranda and Muncy 1987; Goodgame and Miranda 1993; Phillips *et al.* 1995; Ludsin and DeVries 1997; Sammons *et al.* 1999; Pine *et al.* 2000). Males use caudal sweeping to excavate circular, depressional nests (0.6–1.0 m diameter) 1 to 2 days before spawning (Kramer and Smith 1962; Cooke *et al.* 2001b). Males can successfully sweep out nests over a variety of substrates (e.g., silt to boulders, stump tops, logs, clay slabs), but coarse gravel and sand and the roots and stems of aquatic vegetation are substrates most often used (Reighard 1906; Miller and Kramer 1971; Allan and Romero 1975; Annett *et al.*

1996; Hunt *et al.* 2002). Most males select nest sites near simple cover (e.g., horizontal log, tree trunk) where they suffer less nest intrusion by brood predators and expend less effort in aggressive actions than males selecting sites near complex cover (e.g., brush piles, patches of aquatic macrophytes) (Annett *et al.* 1996; Hunt *et al.* 2002). Although a few nests have been reported from >6 m depth, most nests are placed in water <4 m deep with average or median depths ranging from 0.40 to 2.1 m (Kramer and Smith 1962; Miller and Kramer 1971; Allan and Romero 1975; Heidinger 1975; Vogele and Rainwater 1975; Hunt *et al.* 2002). Largemouth bass males are solitary nesters. Average internest spacing ranged from 6.2 to 9.4 m in an Arkansas reservoir or about 15 nests/100 m transect (Hunt and Annett 2002), but other studies reported much lower densities of <1 to 3.0 nests/100 m of shoreline (Vogele and Rainwater 1975). Courting males may leave the nest for extended periods and approach a nearby female, using gentle nudges to her opercular area to direct her toward the nest (Cooke *et al.* 2001b). Males may also seem to lose buoyancy, float upward, and turn on their side to flash their lighter ventral side toward nearby females, which also appears to attract the female to the nest (Allan and Romero 1975). While courting the female or guarding embryos or fry in the nest, parental males engage in a number of vigilant and aggressive behaviors (e.g., hovering, pivoting, nest circling, opercle flaring, chasing, biting, parallel swims) (Allan and Romero 1975; Hunt 1995). Once the female is led to the nest, the male uses nips and nudges near her vent and opercle to encourage egg deposition (Cooke *et al.* 2001b). The pair ultimately assumes the head-to-head, broadside orientation of most centrarchids for spawning (Reighard 1906; Allan and Romero 1975). Spawning activity can be intense, involving up to 123 shudders per hour, and a complete spawning sequence with a single female including pauses between spawning bouts can last for over 3.5 hours (Cooke *et al.* 2001b). After the female departs the nest, the male immediately begins vigilance behaviors (e.g., pivoting) and gentle fanning of the eggs. Although males may occasionally mate with more than one female (Reighard 1906), most mating is monogamous. In a North Carolina population subjected to genetic parentage analysis, eggs in 23 of 26 nests were exclusively or almost exclusively composed of full-sib progeny, the products of one male and one female; the other three nests were indicative of serial monogamy (one male with two or three females; DeWoody *et al.* 2000b). In tagged individuals in experimental ponds, six of seven male largemouth bass spawned with one female and only one male spawned with two females (Cooke *et al.* 2001b). Ovaries begin development for the next spawning season in the fall and continue developing over winter (Olmsted 1974; Brown and Murphy 2004, Florida bass × largemouth bass hybrids). Mature ovarian eggs are 0.75 to 1.56 mm diameter, and the yellow to orange, fertilized, water-hardened eggs average 1.60 to 2.09 mm diameter, increasing in diameter with female size (Kelley 1962; Meyer 1970; Merriner 1971a; Cooke *et al.* 2006). Fecundity increases with female size, and ovaries apparently contain one distinct mode of mature ova, suggesting that females release a single batch of eggs (Kelley 1962; Olmsted 1974). The relationship between potential batch fecundity (Y) and total length (X) is described by the power function, $Y = 0.00003X^{3.4067}$ (n = 36, $R^2 = 0.70$, data from Kelley 1962 and Olmsted 1974). At 388 mm TL, a female can potentially produce 19,792 mature eggs in a single batch (range: 4550 eggs at 252 mm TL to 54,732 eggs at 523 TL). The adhesive, fertilized eggs hatch in about 3 to 4 days at 18 to 21°C (Kramer and Smith 1960a; Laurence 1969; Allan and Romero 1975). Newly hatched larvae are 3.6 to 4.1 mm TL (Cooke *et al.* 2006) and at 19°C average 6.2 mm TL (range, 5.9–6.3 mm TL) at the swim-up stage 6.75 days after hatching (Kramer and Smith 1960a; Meyer 1970; Goodgame and Miranda 1993). Male largemouth bass invest 20 to 39 days in parental care from spawning to fry dispersal (Kramer and Smith 1962; Cooke *et al.* 2006). Male defensive behaviors and hence activity and energy expenditures increase through the embryo to swim-up stages (Hunt 1995; Cooke *et al.* 2006). Largemouth bass fry begin leaving the nest about 8 to 11 days after spawning by forming initially tight schools or fry balls that begin to forage away from the nest area. The male bass guards the fry balls by constantly patrolling the areas around the moving fry ball. With growth of the fry, the brood association becomes looser and two or more broods may join, further increasing the peripheral area the male must patrol. The fry remain in swarms until they reach about 28 to 33 mm TL (Kramer and Smith 1962; Allan and Romero 1975; Elliott 1976; Colgan and Brown 1988; Annett *et al.* 1996). Relative to similar-age rock bass fry, largemouth bass fry display reduced predator avoidance responses during their first 3 weeks of free swimming, responses related directly to the extended period of protection provided to the fry by male largemouth bass. About 45 to 50 days after swim-up and after the guarding male parent has left, largemouth bass fry develop agonistic behaviors toward conspecifics, coincidental with the breakup of the large swarms of fry into solitary individuals or pairs (Brown 1984). Juvenile largemouth bass show evidence of natal fidelity. Tagged age-0 largemouth bass in a reservoir remained within a 250-m home range during their first year of life, and 79 to 90% of recaptures were within 58 m of release sites. Of a small number of recaptured yearlings (second summer of life), 56% were still within 58 m of the release site of the previous year (Copeland and Noble 1994; Jackson *et al.* 2002).

Biparental care is documented in a largemouth bass population in a North Carolina stream. Most of 26 nests examined were attended by a female and a guardian male (DeWoody *et al*. 2000b). The attendant female generally faced the nest from 1 to 2 m distance with the attendant male over the nest, but these positions were occasionally reversed. The guardian male showed no aggression toward the female, and the attendant female actively chased away conspecific nest intruders and predators. Nests with attendant females occurred across several stages of brood development, indicating that female nest guarding extended well past spawning and incubation of eggs to the free-swimming fry stage of the brood. A few nests that lacked parental males were guarded solely by females. Biparental care in largemouth bass (or other *Micropterus*) populations is not a general occurrence across populations (Cooke *et al*. 2006), but observation of two individual Florida bass guarding a single nest for 3 days (Carr 1942) and other anecdotal accounts (Miller 1975) suggest that some as yet undocumented degree of biparental care may exist in other populations of largemouth bass or other species of *Micropterus*. The existence of biparental care in the largemouth bass is consistent with several reproductive life history traits (i.e. large body size, large eggs, sexual monomorphism, monogamy, extended parental care; DeWoody *et al*. 2000b).

Nest associates: Golden shiner, *N. crysoleucas* (Kramer and Smith 1960b).

Freshwater mussel host: Confirmed host to *A. ligamentina, A. neislerii, A. plicata, A. suborbiculata, A. ferussacianus, E. complanata, E. fisheriana, L. altilis, L. cardium, L. higginsii, Lampsilis ornata, L. perovalis, L. rafinesqueana, L. siliquoidea, L. subangulata, L. complanata, L. recta, L. subrostrata, M. nervosa, P. grandis, S. undulatus, S. subvexus, V. iris* (reported as *V. nebulosa*), *V. nebulosa*, and *V. vibex* (Lefevre and Curtis 1910, 1912; Young 1911; Howard 1914, 1922; Reuling 1919; Coker *et al*. 1921; Howard and Anson 1922; Arey 1923, 1932; Penn 1939; Neves *et al*. 1985; Waller *et al*. 1985; Waller and Holland-Bartels 1988; Barnhart and Roberts 1997; Haag and Warren 1997; Hove *et al*. 1997; Haag *et al*. 1999; O'Brien and Brim Box 1999; Watters and O'Dee 1999; Khym and Layzer 2000; O'Dee and Watters 2000; O'Brien and Williams 2002; Van Snik Gray *et al*. 2002; Haag and Warren 2003). Putative host to *L. abrupta* (unpublished sources in OSUDM 2006).

Conservation status: Although secure within most of its native range and widely established outside its native range, the largemouth bass is not without major conservation concerns. The genetic integrity of the species in the southern United States is threatened by the widespread and decades-long practice of stocking nonnative Florida bass (or Florida-largemouth hybrids) on top of existing native largemouth bass populations (Philipp *et al*. 2002). Where introduced, Florida bass often rapidly and substantially introgress with native largemouth bass populations, eventually producing hybrid populations with high potential for loss in reproductive fitness and loss in adaptation to local conditions (Philipp *et al*. 1985a, 2002; Fields *et al*. 1987; Cooke *et al*. 2001a; Kassler *et al*. 2002; see account on *Micropterus floridanus*). Even largemouth bass populations in relatively close geographic proximity can differ significantly with respect to growth, survival, reproductive fitness, or physiological responses to the environment, reflecting the adaptation of the stock to the region in which it evolved (Philipp and Claussen 1995; Cooke *et al*. 2001a; Cooke and Philipp 2005, 2006). At least some native populations of largemouth bass in Mexico and perhaps southwest Texas likely represent distinct taxa that could be threatened by further introductions of nonnative largemouth bass or congeners (Edwards 1980; Miller 2005; Lutz-Carillo *et al*. 2006). Two tasks appear primary to the conservation of the genetic integrity of native largemouth bass (Philipp *et al*. 2002): identification of the number and geographic distribution of genetic stocks across the native range of the species and the reconstruction of native stocks now lost or contaminated by past (and present) stocking of nonnative Florida bass, intergrades, or even nonlocal stocks of largemouth bass.

Similar species: All other species of *Micropterus*, except the Florida bass, have more confluent dorsal fins, upper jaws that reach to or barely past the eye, and unbranched pyloric caeca (Page and Burr 1991; see account on Florida bass).

Systematic notes: *Micropterus salmoides* forms a sister pair with *M. floridanus* (Near *et al*. 2004, 2005; see account on *M. floridanus*). At least some native populations of *Micropterus*, currently under the name *M. salmoides*, in the Rio Grande system, appear to represent distinct, but formally unrecognized taxa (Bailey and Hubbs 1949; Edwards 1980; Miller 2005).

Importance to humans: The largemouth bass is the most popular and economically significant freshwater sport fish in North America, perhaps rivaled only by the rainbow trout in its local, regional, and ultimately national economic and social impact. Over its broad native and introduced range in North America, the largemouth bass was the primary impetus over the last 30 years for the founding of hundreds of bass-focused fishing clubs and national angler associations and federations, all of which effectively lobby local, state, and federal agencies and governments and influence fisheries management and conservation (Dean 1996; Shupp 2002; Chen *et al*. 2003; Schramm and Hunt 2007). Broad ecological and habitat tolerances, explosive and aggressive attacks on just about any moving natural or artificial bait, a relatively large size, and excellent table qualities combine as winning characteristics among anglers. Anglers successfully take largemouth bass day or night, across seasons, and in almost every conceivable type of water condition (e.g., Heidinger 1975; Becker 1983; Etnier and Starnes 1993). Largemouth bass anglers range from subsistence fishers in rural areas to a growing cadre of amateur and professional anglers following regional and national largemouth bass tournament trails to compete for hundreds to hundreds of thousands of dollars in cash and prizes (Ross 2001; Shupp 2002; Leonard 2005; Schramm and Hunt 2007). Bass tournaments are often sponsored by large media and corporate interests and broadcast nationally as sporting events. Tournament sponsors manufacture and distribute highly specialized bass fishing equipment (e.g., bass powerboats), bass fishing television shows, "how-to" bass fishing videos, and print media, all of which renders largemouth bass fishing both a spectator and a participatory sport (Ridgway and Philipp 2002). For decades, the largemouth bass in combination with the bluegill has formed the core predator–prey combination used in management of warmwater ponds and small public and private warmwater impoundments (Bennett 1948; Swingle 1949). Historically, the species supported commercial fisheries in the Great Lakes, Ohio, and Illinois (Mills *et al*. 1966; Trautman 1981; Scott and Crossman 1973). For example, before 1900, thousands of barrels of largemouth bass were taken commercially from impoundments in Ohio, and in 1897, an estimated 13,000 pounds of largemouth bass were taken commercially from lakes along the Illinois River.

13.9.8 *Micropterus treculi (Vaillant and Bocourt)*

13.9.8.1 Guadalupe bass

Characteristics: See generic account for general characteristics. Elongate, slightly compressed body depth 0.20 to 0.25 of TL. Mouth large, terminal, lower jaw slightly projecting, upper jaw extends to rear half of eye (in adults). Outline of spinous dorsal fin curved. Juncture of soft and spiny dorsal fins slightly emarginate, broadly connected. Shortest dorsal spine at emargination of fin, 0.5 to 0.6 times length of longest spine. Dorsal soft rays, usually 12, 11 to 13; anal soft rays, usually 10, 9 to 11. Gill rakers, 8. Lateral scales, (55)61 to 69; rows above lateral line (7)8 to 9(10); rows below lateral line, (14)15 to 18(20); cheek scale rows, (10)12 to 14(18); caudal peduncle scale rows, (23)26 to 27(29); pectoral rays, (14)15 to 16. Small scales on interradial membranes at anal and second dorsal fin bases (>60 mm SL). Pyloric caeca, single, usually 10 to 11, (8–13). Tooth patch present on glossohyal (tongue) bone (Hubbs 1927; Hubbs and Bailey 1942; Edwards 1980; Kassler *et al*. 2002).

Size and age: Age 0+ fish average from 82 to 103 mm TL at age 1 (Edwards 1980). Large individuals weigh 500 to 1000 g and attain 250 to 330 mm TL; few live beyond age 3+ (maximum about 400 mm TL, age 6+) (Boyer *et al*. 1977; Edwards 1980; Page and Burr 1991; Koppelman and Garrett 2002). World angling record, 1.67 kg, Texas (IGFA 2006). The oldest individuals in a population are generally females (Edwards 1980).

Coloration: Similar to spotted bass but has 10 to 12 dark vertical blotches along side (diamond shaped posteriorly and darkest in young), usually 16 pectoral rays, and 26 to 27 caudal peduncle scale rows (Edwards 1980; Page and Burr 1991).

Native range: The Guadalupe bass is native to the Edwards Plateau in the Brazos, Colorado, Guadalupe, and San Antonio river drainages, Texas (MacCrimmon and Robbins 1975; Page and Burr 1991; Koppelman and Garrett 2002). Established populations in the Nueces River, Texas, were introduced deliberately in 1973 (Koppelman and Garrett 2002).

Habitat: The Guadalupe bass inhabits gravel riffles, runs, and flowing pools of clear creeks and small to medium rivers (Edwards 1980; Page and Burr 1991). The species is most common in flowing waters of streams (6–22 m wide) in association with large rocks, cypress roots, stumps, or other cover. Individuals overwinter in deep pools with currents, move in spring to shallow, but flowing, backwaters to spawn, and then to deep runs and flowing pools. The species avoids the constant thermal environments of headsprings, extremely silted streams, and the smallest headwater streams. Survival is poor in hypolimnetic-release tailwaters and most reservoirs, except in variable-level reservoirs that provide flowing conditions for at least part of the year (Edwards 1980).

Food: The Guadalupe bass is an opportunistic top carnivore (Edwards 1980). The adult (>90 mm SL) diet is dominated by small fishes, mostly minnows (e.g., *Notropis, Cyprinella, Campostoma*) and other centrarchids, but also includes large numbers of mayfly, dragonfly, dipteran, hemipteran, and megalopteran larvae, a few bees and wasps, and an occasional amphibian. Large adults (>150 mm SL) consume relatively large volumes of crayfish. Fish prey associated with flowing water (e.g., blacktail shiner, darters, channel catfish) are taken most often, an indication of the primary foraging habitat of Guadalupe bass. By volume, the diet of young bass (15–30 mm SL) is dominated by mayfly, odonate, and hemipteran larvae. In bass between 30 and 90 mm SL, increasing volumes of fish are consumed, but invertebrates remain important components of the diet of bass <135 mm SL (Edwards 1980). Dietary comparisons between sympatric populations of Guadalupe bass and largemouth bass indicated decreasing similarity with growth in the numbers and volumes of diet items shared. Where spotted and largemouth basses occurred in sympatry with Guadalupe bass, Guadalupe bass diets were most similar among seasons to those of the spotted bass (Edwards 1980).

Reproduction: Maturity is reached minimally in males at 97 mm TL and age 1+ and in females at 128 mm SL and age 2+ (Hurst *et al.* 1975; Edwards 1980); reported maturation of a female at 70 mm SL (Hurst *et al.* 1975) is perhaps feasible but needs further confirmation (Edwards 1980). With the possible exception of the redeye bass, Guadalupe bass apparently mature at smaller sizes than any other *Micropterus*. Spawning initiation and duration are not well documented, but various observations suggest a mid-March to June spawning period. Male and female gonadosomatic ratios peak in spring, but some individuals taken in summer continue to have elevated ratios. In mid-March, a male was observed guarding a nest and eggs (water temperature 14–17°C), and many large males and females emit freely flowing sex products at that time. Young <30 mm SL are taken from May through August, and recently spent females are observed as late as July (*et al.* Hurst *et al.* 1975; Boyer *et al.* 1977; Edwards 1980). Nesting areas are apart from, but always near, a source of slow to moderately flowing water (i.e. backwaters with water inflow) (Edwards 1980). A single observed depressional nest was oval shaped (41 × 50 cm, 10 cm in depth), placed 1 m from shore on a sloping bank at a water depth of 69 cm and current speed of about 0.3 m/s. The nest was swept into the hard black soil of the creek bank and lined with 5 cm diameter limestone rubble that was covered partially by sticks and leaves. The nest was guarded by a relatively large (280 mm TL) male, and a second individual, suspected to be a female, was also observed near the nest. The nest contained 1406 adhesive eggs, most of which were adhered to the sticks and leaves (Boyer *et al.* 1977). Apparently, nothing else is published on nest building, courtship, spawning, or parental care behaviors. Mature ovarian eggs average from 1.50 to 2.25 mm in diameter, and fertilized water-hardened eggs average 2.1 mm in diameter (Boyer *et al.* 1977; Edwards 1980). Fecundity increases with female size. The relationship between potential batch fecundity (Y) and standard length (X) is described by the linear function, $Y = 29.98X - 3072.20$ (Guadalupe River; $Y = 34.28X - 4144.08$, Llano River; $Y = 57.85X - 5920.62$, LBJ reservoir, equations from Edwards 1980). At 203 mm SL, a female can potentially produce 3013 mature eggs in a single batch (range: 765 eggs at 128 mm SL to 5262 eggs at 278 mm SL, respectively). With growth, young Guadalupe bass occupy increasingly faster and deeper water during their first summer, shifting to deeper-flowing pools to overwinter (Edwards 1980).

Nest associates: None known.

Freshwater mussel host: None known.

Conservation status: The Guadalupe bass is vulnerable throughout its native range (Warren *et al.* 2000; NatureServe 2006). The species has declined dramatically in recent history because of decreased stream flow, reservoir construction, habitat degradation, and extensive, introgressive hybridization with nonnative smallmouth bass (Edwards 1980; Whitmore and Butler 1982; Whitmore 1983; Morizot *et al.* 1991; Koppelman and Garrett 2002). Genetic contamination of the Guadalupe bass from hybridization with nonnative smallmouth bass is pervasive throughout its range, and only five natural populations remain free from introgressive hybridization (Koppelman and Garrett 2002). Genetically uncontaminated Guadalupe bass are being stocked in an attempt to numerically and reproductively overwhelm the hybrid swarms (Koppelman and Garrett 2002).

Similar species: See account on spotted bass and the section on coloration.

Systematic notes: *Micropterus treculi* is a member of a "Gulf of Mexico" clade of *Micropterus*, including all other *Micropterus* except *M. dolomieu* and *M. punctulatus* (Near *et al.* 2003, 2004). Although relationships within the clade are not well resolved, phylogenetic analyses usually recover *M. treculi* as sister to *M. salmoides+M. floridanus* (Kassler *et al.* 2002; Near *et al.* 2003, 2004, 2005). On the basis of morphology, taxonomists usually related *M. treculi* to *M. punctulatus* (e.g., Hubbs and Bailey 1942; Huhbs 1954; Ramsey 1975).

Importance to humans: The Guadalupe bass is designated the State Fish of Texas in recognition of the unique character of both the species and its habitat. Although small relative to congeners, the species is the focus of a popular sport fishery on the Edwards Plateau. The species provides good sport using ultralight gear with spinners and other small bass lures that are fished in riffle areas, flowing pools, or deep eddies below riffles (Boyer *et al.* 1977). The fishery provides the angler with an agile fast water fish occurring in attractive, natural stream settings (Koppelman and Garrett 2002).

13.10 *Pomoxis* Rafinesque

The genus *Pomoxis*, consisting of the sister pair *Pomoxis annularis* and *Pomoxis nigromaculatus*, is sister to a clade inclusive of the genera *Archoplites* and *Ambloplites* (Near *et al.* 2004, 2005). The natural range of the genus, collectively called the crappies, encompasses North America east of the Rocky Mountains from southern Canada to the Gulf of Mexico, excluding the Atlantic Slope from southern Virginia northward (Page and Burr 1991). A fossil species, *Pomoxis †lanei* Hibbard, is known from Miocene deposits in Kansas and Nebraska with the oldest formations being the Rhino Hill Quarry and is dated at 6.6 mya (million years ago) (Uyeno and Miller 1963; Schultz *et al.* 1982; Cross *et al.* 1986). Another undescribed fossil species presumably representing *Pomoxis* was reported from material collected at the Wakeeney local fauna (Ogallala Formation) in Kansas dating to about 12 mya (Wilson 1968; Tedford *et al.* 1987).

The white crappie and black crappie show wide overlap in distribution across their large ranges and frequently co-occur in the same water body. Nuclear-encoded allozyme data indicate that some sympatric populations of white crappies and black crappies in reservoirs introgress through hybridization, although other sympatric populations do not (Maceina and Greenbaum 1988; Hooe and Buck 1991; Dunham *et al.* 1994; Epifanio and Philipp 1994; Smith *et al.* 1994, 1995; Travnichek *et al.* 1996). Estimates of the degree of hybridization among reservoirs is variable (e.g., none to >40% of individuals,), but second-generation (or higher) hybrids are usually less common than first-generation hybrids and contribute little to recruitment (Smith *et al.* 1994; Dunham *et al.* 1994; Travnichek *et al.* 1996). Within-reservoir differences in species abundances and habitats or among-reservoir differences in physicochemical characteristics are not related in any obvious way to the degree of hybridization. Some speculate that hybridization may be related to contact between the species in artificial environments where habitats or physical conditions limit species recognition or species segregation during spawning, particularly in geographical areas at the historical border of the range of the white crappie (Travnichek *et al.* 1996, 1997; Epifanio *et al.* 1999).

A hallmark of the genus *Pomoxis* is the capacity of both species to maintain high recruitment and rapid growth to harvestable sizes under high mortality or fishery exploitation rates. Sustainable sport fishery exploitation rates of crappies as high as 40 to 60% per year are observed in many impoundments (Colvin 1991; Larson *et al.* 1991), but because of their capability to proliferate, crappies are prone to overpopulation and stunting, especially in small or resource-limited reservoirs (Hooe and Buck 1991; Hooe *et al.* 1994). Crappies were exploited commercially in natural lakes from Florida to Canada well into the twentieth century (e.g., Schoffman 1940, 1960, 1965; Huish 1954; Scott and Crossman 1973; Trautman 1981; Schramm *et al.* 1985). From 1938 to 1955, crappies were liberally harvested in a commercial fishery in Reelfoot Lake, Tennessee, and supported a thriving sport fishery. Soon after cessation of commercial fishing the population was reportedly overrun by smaller crappies (Schoffman 1960, 1965). As recently as 1976 to 1981, the black crappie was commercially fished in Lake Okeechobee, Florida. Commercial fishers and anglers removed about 3.8 million kg of the species (about 833,000 kg/yr; 65% of annual average standing crop) from the lake until the fishery collapsed in 1981 because of highly variable recruitment (Schramm *et al.* 1985; Miller *et al.* 1990).

From a management perspective, and in spite of the ability to proliferate, a perplexing characteristic of the genus is the near unpredictability of survival of fishes beyond their first year of life. Annual recruitment of both crappie species is notoriously erratic, often quasi-cyclical, and highly variable from year to year within a given population. Variability in postspawning larval abundance and subsequent recruitment of both crappie species can often be related to complex interactions among population dynamics and lake conditions or reservoir operations. These often involve combinations of factors such as larval densities, hatch times, harvest rates, water body productivity, prespawning water temperatures, water retention time, water elevation, or dam discharge rates that may predict crappie recruitment in some, but not other waters (e.g., Beam 1983; McDonough and Buchanan 1991; Mitzner 1991; Allen and Miranda 1998, 2001; Maceina and Stimpert 1998; Sammons and Bettoli 1998; Miranda and Allen 2000; Pine and Allen 2001; Sammons *et al.* 2001, 2002; Dubuc and DeVries 2002; Maceina 2003; St. John and Black 2004; Dockendorf and Allen 2005; Bunnell *et al.* 2006).

The black crappie and white crappie support a popular sport fishery and on a kilogram per hectare basis are the most harvested fish in reservoirs of the United States (Miranda 1999). Of all freshwater anglers (exclusive of the Great Lakes) in the United States, an estimated 24% (6.7 million) of anglers spent 21% (95 million days) of fishing days seeking crappies (USFWS 2002). These percentages compare favorably with popularity of sport fisheries for catfish, panfish, and trout. On some southern US reservoirs much if not most (>30%) of the angling effort is directed at crappies (e.g., Larson *et al.* 1991; Reed and Davies 1991; St. John and Black 2004). A growing contingency of crappie anglers are considered "specialists," similar to many black bass anglers, because they fish year round for crappies to the near exclusion of other species. The relatively recent advent of crappie clubs and fishing tournaments, dubbed crappiethons, are further evidence of the continued and growing popularity of sport fishing for these centrarchids (Larson *et al.* 1991; Allen and Miranda 1996).

Generic characteristics: Deep, extremely compressed body, depth about 0.33 to 0.48 of SL. Long to very long predorsal region with sharp dip over eye in dorsal profile. Dorsal fin base equal to or shorter than distance from center of eye to dorsal fin origin. Head small. Eye large, diameter equal to or slightly greater than snout length. No black teardrop; no black spot in soft dorsal fin. Dorsoposterior margin of opercle shallowly emarginate. Preopercle posterior margin serrate. Long dorsal fin, 6 to 8 spines, 13 to 18 rays, 20 to 24 total; and long anal fin, 5 to 8 spines, 14 to 18 rays, 23 to 24 total. Spiny and soft dorsal and anal fins continuous, smoothly rounded, similar in length, and nearly symmetrical. Emarginate to shallowly forked caudal fin. Rounded pectoral fin. Long, slender gill rakers, 25 to 32. Ctenoid scales. Lateral line complete. Lateral line scales, 34 to 50; cheek scale rows, 5 to 6; branchiostegal rays, 7. Teeth on entopterygoid and glossohyal (tongue, two patches) bones (Bailey 1938; Keast 1968a; Trautman 1981; Becker 1983; Smith 1985; Page and Burr 1991; Etnier and Starnes 1993; Mabee 1993; Jenkins and Burkhead 1994; Smith *et al.* 1995).

Similar species: See account on flier.

13.10.1 Pomoxis annularis *Rafinesque*

13.10.1.1 White crappie

Characteristics: See generic account for general characteristics. Deep, extremely compressed body, depth usually 0.33 to 0.48 of SL. Very long predorsal region with sharp dip over eye in dorsal profile. Dorsal fin base shorter than distance from center of eye to dorsal fin origin. Large, supraterminal, oblique mouth, lower jaw projecting, supramaxilla moderate ($\leq$2 times length of maxilla), upper jaw reaching to or slightly beyond middle of eye. Opercular spot black. Long dorsal fin, (4)5 to 6(8) spines, (12)14 to 15(16) rays; and long anal fin, 6 to 7(8) spines, 16 to 19 rays. Pectoral rays, (14)15(16); vertebrae, 30 to 32(14+18) (Bailey 1938; Trautman 1981; Becker 1983; Page and Burr 1991; Etnier and Starnes 1993; Mabee 1993; Jenkins and Burkhead 1994; Smith *et al.* 1995).

Size and age: Typically reach 131 to 173 mm TL at age 1, but first-year growth is highly variable across latitudes and among habitats (range, 58–310 mm TL, Siefert 1969a; Carlander 1977). Large individuals measure 350 to 400 mm TL, weigh 500 to 800 g, and reach age 6+ to 8+ (maximum 530 mm TL, age 9+) (Carlander 1977; Page and Burr 1991; Etnier and Starnes 1993). World angling record, 2.35 kg, Mississippi (IGFA 2006).

Coloration: Gray-green above with silvery blue sides and upper back vaguely barred with about 6 to 10 chainlike double vertical bands (widest at top) as well as dark blotches and green flecks. Chainlike bars and mottling often faint in individuals from turbid water. Whitish to silvery below. Dorsal, anal, and caudal fins with many wavy dark bands and spots. Males become darker during the breeding season (Page and Burr 1991; Etnier and Starnes 1993).

Native range: The white crappie is native to the Great Lakes, Hudson Bay (Red River), and Mississippi River basins from New York and southern Ontario west to Minnesota and South Dakota and south to the Gulf of Mexico and in Gulf drainages from Mobile Bay, Georgia and Alabama, west to the Nueces River, Texas (Page and Burr 1991). The species has been introduced and is established over most of the coterminous United States (Fuller *et al.* 1999).

Habitat: The white crappie inhabits sand- and mud-bottomed pools and backwaters of creeks and small to large rivers, lakes, ponds, and reservoirs (Page and Burr 1991). The greater adaptability of the white crappie to turbid waters than the black crappie is often noted. Higher relative abundance or success in turbid habitats suggests that the white crappie is more adapted to turbid conditions than the black crappie (e.g., Carlander 1977; Trautman 1981; Ellison 1984; Etnier and Starnes 1993; Miranda and Lucas 2004). Even though the difference in turbidity tolerance is frequently noted, both crappie species occur in turbid and clear water habitats, and an obvious mechanism or adaptation explaining the apparent difference in tolerance is lacking (e.g., Barefield and Ziebell 1986). Some indirect evidence (e.g., growth, survival) suggests that white crappies can feed more efficiently in turbid waters than black crappies or that white crappies compete poorly in clear waters with other centrarchids (e.g., Carlander 1977; Ellison 1984; Pope 1996). White crappies move extensively, often show distinct diel activity patterns, and can show persistent occupation of home activity areas in the summer. In rivers in Missouri, tagged individuals covered 34 to 42 km in 21 to 91 days (Funk 1957) and others have noted movements up to 30 km (review in Hansen 1951; Siefert 1969a). Increased movement in spring and early summer is attributed to aggregation in spawning areas and postspawning foraging (Guy *et al.* 1994). Adult white crappies show high levels of nocturnal activity (see section on food), but overall patterns of movement and activity vary seasonally and daily among seasons (e.g., Hansen 1951; Morgan 1954; Greene and Murphy 1974; Markham *et al.* 1991; Guy *et al.* 1994). In an Ohio reservoir, diel movement of large white crappie (271–352 mm TL) in summer rapidly increased at dusk when light intensity was zero, peaked at night (average 47 m/h), and declined at dawn. Movement was low throughout the day (average 17 m/h). During the day, the species was associated with steeply sloped bottoms and the presence of structure (e.g., tree stumps, logs, rocks). Individuals tended to occupy deeper water during the day than at night (e.g., 5.4 vs 4.3 m, respectively), generally staying within 0.5 m of the bottom. Median summer home activity areas were 0.49 to 0.63 ha during the day and 1.25 ha at night (Markham *et al.* 1991). In a shallow, homogeneous glacial lake in South Dakota, movement patterns of large radio-tagged white crappie tracked from April to September were more extensive and less patterned. Over the tracking period, median movement was 73.2 m/h (range: 0–1,523 m/h) and was highest in May (102.1 m/h) and July (82.4 m/h). Diel movement patterns were indistinct or variable, but tended to peak at dawn and dusk. Median home activity area was large relative to the reservoir study (15.8 ha) and varied considerably (range: 0.1–85.0 ha) (Guy *et al.* 1994). The larger home range, relative to the other study, was attributed to greater foraging demands or the lack of cover and bottom structure in the homogeneous habitat of the lake. Cover or structure tends to hold individuals within a limited area for prolonged periods (Markham *et al.* 1991; Guy *et al.* 1994).

Food: The white crappie is primarily a midwater, particulate-feeding zooplanktivore and invertivore that shifts to piscivory at a relatively large size (~ 160 mm TL) compared to other piscivorous centrarchids (O'Brien *et al.* 1984). Numerous, long gill rakers likely play an important functional role in the extended period of zooplanktivory (Wright *et al.* 1983). Food of large individuals (>160 mm TL) consists primarily of small fishes (e.g., clupeids, other white crappies and sunfishes, minnows, silversides), zooplankton, immature aquatic insects (e.g., chironomid larvae and pupae, burrowing mayflies), and amphipods (e.g., Hansen 1951; Morgan 1954; Hoopes 1960; Whiteside 1964; Siefert 1969a; Mathur 1972; Greene and Murphy 1974; Ellison 1984; Muoneke *et al.* 1992). Large white crappies are among the best documented of any centrarchid for their nocturnal feeding and high levels of nocturnal activity (see section on habitat). Large individuals feed at dusk, sporadically throughout the night, and intensively at dawn, feeding very little or not at all during the day (Childers and Shoemaker 1953; Greene and Murphy 1974). In lentic waters, intermediate-size fish (80–150 mm TL) are pelagic zooplanktivores that begin feeding at or near dawn and continue feeding throughout the day (O'Brien *et al.* 1984; Wright and O'Brien 1984). These pelagic-dwelling individuals can make diel vertical migrations to exploit vertically migrating zooplankton and dipteran larvae and pupae and to respond to changing levels of temperature, light, and DO (O'Brien *et al.* 1984). Empirical associations of white crappie abundance and abundance of other fishes in wild populations and mesocosm experiments indicate that 130 to 199 mm TL white crappie are highly effective predators that rapidly find and eat larval fishes (e.g., bluegills, walleye). Predation by white crappies is so effective it could drastically limit recruitment of the prey fish species (Kim and DeVries 2001; Quist *et al.* 2003). Young-of-the-year white crappies feed most heavily during daylight hours on crustacean zooplankton (e.g., copepods and cladocerans) and small dipteran larvae and pupae, but some feeding occurs continuously over a 24-hour period (Siefert 1968, 1969a; Mathur and Robbins 1971; Overmann *et al.* 1980; DeVries *et al.* 1998). Individuals can actively search for, pursue, and capture zooplankton prey down to water temperatures of at least 7°C (O'Brien *et al.* 1986).

The white crappie is adapted behaviorally and visually for detecting zooplankton prey, but foraging success is affected by prey size, prey movement, light intensity, and turbidity. White crappies use a stereotyped saltatory (pause-travel) search strategy in which they visually locate and attack individual prey. In this strategy, they search briefly for a prey item while stationary and, if they do not locate prey, swim a short distance before stopping to scan again (O'Brien 1979; O'Brien *et al.* 1986, 1989; Browman and O'Brien 1992). The white crappie retina has a high density of cones in the far temporal region along the eye's horizontal meridian, an apparent adaptation for detecting open-water zooplankton. Highest probabilities and maximum distances that white crappie will pursue small zooplankters (1–2 mm) are concentrated in a 60-degree forward-directed pie-shaped wedge of limited height (Browman *et al.* 1990) in which the species is better able to discriminate the absolute size of prey (O'Brien *et al.* 1985). The wedge-shaped field of maximum foraging corresponds well with the position of the high-density photoreceptor region on the retina (Browman *et al.* 1990). Under well-lit, low-turbidity conditions (80 lux, 1 NTU), the distance at which individuals (~ 160 mm TL) can detect prey (reactive distance) increases from about 4 to 30 cm as prey size increases from 1 to 3 mm, and reactive distance for moving prey increases about threefold. For 3-mm prey, white crappie reactive distance is little affected by decreases in illumination from 106 to 10 lux, but from 10 lux to 0.97 lux, reactive distance decreases from about 25 to 6 cm. Differences in reactive distance across prey sizes (1–3 mm) at the lowest light intensities are minimal. Reactive distance to a 2.4-mm prey at 80 lux decreases as an approximate log function of turbidity from about 20 cm at 1 NTU to 5 cm at 33 NTU (Wright and O'Brien 1984).

Reproduction: Maturity is usually reached at age 2+ to age 3+ and a minimum size of about 140–180 mm TL, although stunted individuals in dense populations reportedly spawn at 110 mm TL (Morgan 1951a, 1954; Whiteside 1964; Hansen 1951; Siefert 1969a; Trautman 1981). The white crappie is among the earliest, lowest-temperature spawners in the family. The testes and ovaries enlarge and continue developing in the fall and over winter (Morgan 1951b; Whiteside 1964), which is likely an adaptation for early spawning. Spawning occurs at water temperatures of 11 to 27°C with most spawning taking place at 16 to 20°C. The duration of the spawning period is variable, lasting from 17 to 53 days, and depending on latitude, spawning activity occurs from late March to June or mid-July (Hansen 1951; Morgan 1954; Whiteside 1964; Siefert 1969a; Carlander 1977; McDonough and Buchanan 1991; Pope and DeVries 1994; Travnichek *et al.* 1996; Sammons *et al.* 2001). Year-to-year fidelity to nesting areas is not apparent (Hansen 1965). Male white crappies have less fastidious nest-building habits than some centrarchids. Males establish individual territories but apparently do not use caudal sweeping to clear the nesting area. The male remains upright with the abdomen touching or nearly touching the substrate and uses vigorous 3- to 5-second bursts of fin and body movements to sweep out a roughly circular area (about 15–30 cm diameter), actions which remove only the loosest bottom material. Nest-clearing stops before the well-defined depression typical of most centrarchids is created (Hansen 1965; Siefert 1968). Interestingly and atypical among centrarchids, the female often engages in similar nest cleaning behaviors just before spawning and after egg deposition. Substrate at the nest site appears less important to the male than being near some protective cover or bottom vegetation (Siefert 1968). Nests are located on sod clumps, clay, gravel, rock piles, hollows made among aquatic plants, filamentous algae, or roots as well as the surfaces of boulders, rootwads, and submerged brush or trees (Hansen 1943, 1951, 1965; Breder and Rosen 1966). Nests are placed at water depths of 0.1 to 1.5 m (anecdotally up to 6 m, Hansen 1965). Nest spacings suggest colonies (35–50 nests/colony, 46–76 cm apart), and solitary nests are rare (3 of 150), but nests along shorelines (3–15 nests) are in linear arrangements up to 1.2 m apart (Hansen 1965). Nest-guarding males repeatedly repulse approaching females until the female finally stops retreating from the male's territory when chased, and the male accepts the female (Siefert 1968). The female circles the nest alone but ultimately moves over the bottom of the nest in a head-to-head, broadside position with the male. As both quiver and move forward with vents touching, she slides under the male, causing the pair to move in a curve as gametes are released. Each quivering act lasts about 4 seconds with intervals of 30 seconds to 20 minutes, at which time females often leave the nest. Spawning with a single female can continue from 45 minutes to 2.5 hours (Siefert 1968). In spawning pens, one female spawned in the nest of two different males, and on two occasions an intruding male joined a spawning female and guardian male to steal fertilizations (Siefert 1968). Eggs in two distinct stages of development in two nests suggested that multiple spawnings occurred over a 2-day period (Siefert 1968). Male white crappie remain relatively motionless over the nest and apparently do not engage in rim circling, but do display (opercle flare) to neighboring males or rush and attack (butt, snap, bite) territorially intruding males and females (Hansen 1965; Siefert 1968). During incubation, the male fans the eggs with constant motion of the pectoral fins (Hansen 1943; Breder and Rosen 1966). Fertilized eggs, which are almost completely covered with minute debris, often occur in clumps of three or more and are attached to gravel, leaves, twigs, grass, algae, or plants in and well outside the periphery of and even above the nest (Hansen 1943, 1965; Siefert 1968). Mature ovarian eggs are small, ranging from 0.82 to 0.92 mm in diameter, and fertilized water-hardened eggs average 0.89 mm diameter (Hansen 1943; Morgan 1954; Whiteside 1964). Size-adjusted batch fecundities are higher than any other centrarchid except the black crappie (see accounts on *Archoplites* and *Centrarchus*), but female fecundity shows high interannual variation within populations and high variation among populations (Mathur *et al.* 1979; Dubuc and DeVries 2002; Bunnell *et al.* 2005). Some females retain ripe eggs throughout the spawning period (Morgan 1954; Whiteside 1964), and gonadosomatic values and larval densities may each show two or more temporally separate peaks (Dubuc and DeVries 2002), patterns which are suggestive of partial release of a single batch over a protracted period, production of two or more batches by a female, or asynchrony in maturation of females. Fecundity increases with female size. The relationship between number of mature eggs (Y) and TL (X) is described by the function $\log Y = -5.301 + 4.24 \log X$ (formula from data in Morgan 1954, average of 20 length classes, 159–330 mm TL, for 50 females, $R^2 = 0.87$, see also Mathur *et al.* 1979). At a mean size of 230 cm TL, a female potentially can produce 51,609 mature eggs in a single batch (range: 10,787 eggs at 159 cm TL to 238,506 eggs at 330 cm TL). Hatching occurs in 1.8 to 2.1 days at 18.3 to 19.4°C (3.9 days at 14.4°C, about 1 day at 22.8°C) (Morgan 1954; Siefert 1968). Hatchlings are of 1.22 to 2.74 mm TL, and swim-up larvae disperse on average at 4 days post hatch (range: 2.1 to 6.8 days) at a size of 4.1 to 4.6 mm TL (Morgan 1954; Siefert 1968, 1969b; Sweatman and Kohler 1991; Browman and O'Brien 1992). Male parental care from egg deposition to dispersal typically lasts for 6 days, but, on the basis of developmental information, could range from 4 days at 22 to 23°C to 11 days at 14 to 15°C (Siefert 1968). Larvae disperse from nesting areas to forage in open water (Siefert 1969a; Overmann *et al.* 1980).

Nest associates: None known.

Freshwater mussel host: Confirmed host to *A. ligamentina, A. plicata, A. suborbiculata, E. complanata, L. cardium, L. siliquoidea, L. complanata*, and *L. recta* (Young 1911; Lefevre and Curtis 1912; Howard 1914; Coker *et al.* 1921; Barnhart and Roberts 1997). Putative host to *L. reeveiana* (unpublished sources in OSUDM 2006).

Conservation status: The white crappie is secure throughout its native range (Warren *et al.* 2000; NatureServe 2006).

Similar species: The black crappie has a shorter predorsal region, usually 7 to 8 dorsal spines, and no dark bars on sides. These phenotypic characters are not entirely reliable in separating the two crappie species where both species and their hybrids co-occur (Dunham *et al.* 1994; Smith *et al.* 1995).

Systematic notes: *Pomoxis annularis* forms a sister pair with *P. nigromaculatus*. The pair is basal to a clade comprised of the genera *Archoplites* and *Ambloplites* (Roe *et al.* 2002; Near *et al.* 2004, 2005). Comparative studies of variation across the range of *P. annularis* are lacking.

Importance to humans: White crappies are a popular sport fish and like black crappies can maintain recruitment and growth that can sustain extremely high levels of exploitation as sport fisheries (e.g., 60% for age 3 and older fish, Colvin 1991). In southern reservoirs, many thousands of crappies are harvested by anglers in the weeks before spawning when fishes, loosely aggregated near cover, go on a feeding spree, perhaps in response to rising water temperatures or preparatory to spawning (Etnier and Starnes 1993; Allen and Miranda 1996; Miranda and Dorr 2000; Dorr *et al.* 2002). During this time, white crappies are taken easily by anglers using small jigs, streamers, or minnows fished near underwater structure, where fishes are often caught one after the other. Later in spring, white crappies appear most vulnerable to night fishing with minnows below lanterns (Etnier and Starnes 1993).

13.10.2 Pomoxis nigromaculatus *(Lesueur)*

13.10.2.1 Black crappie

Characteristics: See generic account for general characteristics. Deep, extremely compressed body, depth usually 0.37 to 0.45 of SL. Long predorsal region with sharp dip over eye in dorsal profile. Dorsal fin base about equal to or greater than distance from posterior rim of eye to dorsal fin origin. Large, supraterminal, strongly oblique mouth, lower jaw projecting, supramaxilla moderate (≤ 2 times length of maxilla), upper jaw reaching to or slightly beyond middle of eye. Opercular spot black. Silvery sides profusely speckled and mottled. Long dorsal fin, usually (6)7 to 8(10) spines, 14 to 16 rays; and long anal fin, 6 to 7(8) spines, 16 to 19 rays. Pectoral rays, (13)14(15); vertebrae, 31 to 33(14 + 18 or 19) (Bailey 1938; Keast and Webb 1966; Trautman 1981; Becker 1983; Page and Burr 1991; Etnier and Starnes 1993; Mahee 1993; Jenkins and Burkhead 1994; Smith *et al.* 1995).

Size and age: Typically reach 122 to 160 mm TL at age 1 but first-year growth is highly variable among habitats and apparently less so among latitudes (range, 48–301 mm TL, Carlander 1977). Large individuals measure 300 to 400 mm TL, weigh 400 to 500 g, and reach age 6+ to 8+ (maximum 560 mm TL, 2.72 kg, age 13+) (Carlander 1977; Page and Burr 1991; Etnier and Starnes 1993). World angling record, 2.05 kg, Nebraska and Virginia (IGFA 2006).

Coloration: Gray-green above with upper back and silvery blue sides marked with wavy black lines, dark blotches, and green flecks. Silvery below. Dorsal, anal, and caudal fins with many wavy black bands and pale spots. Males become darker during the breeding season (Page and Burr 1991; Etnier and Starnes 1993; Jenkins and Burkhead 1994). The presence of a black predorsal stripe (colloquially known as the black-nose or black-stripe crappie) in some individuals is the expression of a dominant trait controlled by a single gene (Gomelsky *et al.* 2005).

Native range: The native range presumably includes Atlantic Slope drainages from Virginia to Florida, Gulf Slope drainages west to Texas, and the St. Lawrence River-Great Lakes and Mississippi basins from Quebec to Manitoba and south to the Gulf of Mexico (Page and Burr 1991). The wide introduction and establishment of the black crappie renders accurate determination of the native range difficult (Page and Burr 1991; Fuller *et al.* 1999). As the introduced black crappie became abundant in some California waters, the only native centrarchid, the Sacramento perch, declined or disappeared (Moyle 2002). Historical shifts in distribution and relative abundance suggest that the black crappie has declined or has been replaced by the white crappie because of increased turbidity of waters (e.g., South Dakota, Carlander 1977; Illinois, Smith 1979; Ohio, Trautman 1981; Wisconsin, Becker 1983). In some reservoirs, the black crappie hybridizes extensively with the white crappie (see account on *P. annularis*).

Habitat: The black crappie inhabits lakes, ponds, sloughs, and backwaters and pools of streams and rivers. The species is most common in lowland habitats, large reservoirs, and navigation pools of large rivers but is rare in upland rivers and streams. The black crappie is usually associated with clear waters, absence of noticeable current, and abundant cover (e.g., aquatic vegetation, submerged timber) (Carlander 1977; Werner *et al.* 1977; Conrow *et al.* 1990; Page and Burr 1991; McDonough and Buchanan 1991; Keast and Fox 1992; Etnier and Starnes 1993; Pflieger 1997). The species is apparently moderately tolerant of oligohaline conditions, occasionally entering tidal waters (usually <5.0-ppt salinity) to feed on small fish and shrimp (Rozas and Hackney 1984; Moyle 2002). In a whole-lake acidification experiment, black crappies nested from pH 5.6 to 4.7, but no larvae or post larvae were observed at pH 4.7 (Eaton *et al.* 1992; see also McCormick *et al.* 1989). Along a bog lake successional gradient in Wisconsin, the species was rare or absent in lakes with pH <6.0 (Rahel 1984). Field and laboratory observations indicate that the black crappie is tolerant of long exposures to extremely low temperatures (<1°C) and DO (ca. 1 ppm), particularly in winter (e.g., Cooper and Washburn 1946; Moyle and Clothier 1959; Siefert and Herman 1977; Carlson and Herman 1978; Knights *et al.* 1995).

Black crappies move to shift seasonal habitats or track resources, to avoid extreme physical conditions, and in response to environmental changes. In the St. Johns River, Florida, 38% of recaptured individuals emigrated at least 5 km from the point of capture, and three fish traveled over 99 km (Snyder and Haynes 1987 in Parsons and Reed 2005). In a series of small, interconnected glacial lakes, up to 92% of recaptured black crappies had emigrated from the lake of origin to another lake (Parsons and Reed 2005). In Wisconsin, radio-tagged black crappies moved among a series of small, shallow finger lakes to overwinter in oxygenated refuges that were distinct from summer and fall activity areas. Individuals avoided areas with DO concentrations <2 mg/l despite physiological advantages of warmer water temperatures (>1°C) and lower currents in those areas (Knights *et al.* 1995). In a South Dakota lake, mean movement in spring and summer was highest in April and July (about 130 m/h), and highest diel movement was at night and early morning. Increased movement also was correlated highly with increased barometric pressure (Guy *et al.* 1992).

Food: The black crappie is primarily a midwater invertivore, usually shifting to piscivory at a relatively late age and large size compared to other piscivorous centrarchids (up to age 3+ in northern populations) (Seaburg and Moyle 1964; Keast and Webb 1966; Keast 1985c). A variety of fishes (e.g., centrarchids, minnows, yellow perch, clupeids), aquatic insects (e.g., chironomid, mayfly, and odonate larvae), and crustaceans (e.g., amphipods, freshwater shrimp) usually dominate diets of the largest individuals (>160 mm TL). Winged insects are occasionally taken in the summer months (McCormick

1940; Reid 1950b; Seaburg and Moyle 1964; Keast and Webb 1966; Keast 1968a, 1985c; Ball and Kilambi 1972; Becker 1983; Ellison 1984; Keast and Fox 1992; Liao *et al.* 2002). The zooplankton-dominated diet of young black crappie can be continued until individuals reach a relatively large size (160–200 mm TL), a feeding strategy likely associated with the possession of numerous, long gill rakers (Keast and Webb 1966; *et al.*Keast 1968a, 1980, 1985c; Bulkley *et al.* 1976; Overmann *et al.* 1980; Ellison 1984; Hanson and Qadri 1984; Schael *et al.* 1991; Pope and Willis 1998; Pine and Allen 2001; Dubuc and DeVries 2002; see account on *P. annularis*). Young-of-the-year tend toward diurnal or crepuscular feeding, but both adults and young may feed at virtually any hour of the day or night. Large black crappies are one of the most active nocturnal feeders among centrarchids; during the day, individuals may remain in the same location for several hours or all day. Peak movement and feeding occur at dawn or dusk, but movement and feeding also peak at night (Childers and Shoemaker 1953; Keast 1968a; Helfman 1981; Ellison 1984; Guy *et al.* 1992; Keast and Fox 1992; Shoup *et al.* 2004). Black crappies often exploit small dipteran larvae (*Chaoborus*) and pupae (*Chironomus*) as these insects rise in the water column at dusk and night (Keast 1968a; Keast and Fox 1992). Individuals tend to move to deeper offshore waters during the day and shallower depths or inshore waters at night, presumably to feed, but the extent of these movements and movement patterns varies seasonally (Helfman 1981; Guy *et al.* 1992; Keast and Fox 1992). The black crappie can feed actively at water temperatures as low as 6.5°C (Keast 1968b).

Reproduction: Maturity is reached at age 2+ to 4+ and a minimum size of about 178 mm TL (Huish 1954; Cooke *et al.* 2006). Most nesting and spawning occur at water temperatures of 14 to 22°C (to 26°C) with peak activity (most active nests) at about 18°C (Carlson and Herman 1978; Becker 1983; Colgan and Brown 1988; Pine and Allen 2001; Cooke *et al.* 2006). Spawning is most protracted in Florida, occurring over a 12-week period from late January to May with peaks in March and April. The spawning season is later (April to June or even July in northern lakes) and shorter (21 to 37 days) at more northerly latitudes (Reid 1950b; Huish 1954; Becker 1983; Keast 1985c; Pope *et al.* 1996; Travnichek *et al.* 1996; Pope and Willis 1998; Pine and Allen 2001; Cooke *et al.* 2006). The ovaries enlarge and continue developing in the fall and over winter (Schloemer 1947; Morgan 1951a), which is likely an adaptation for early spring spawning. In South Dakota waters, male black crappies move 0.4 to 6.0 km to establish spawning sites (Pope and Willis 1997). In the spawning area, the male establishes a territory and prepares a saucer-shaped depressional nest (20 to 23 cm diameter) in variable substrates (gravel, sand, clay, or even softer) and water depths (0.25 to 6.1 m). Nests are placed in areas protected from wind and waves, usually at the base of vegetation (e.g., cattails), near the edge of floating or emergent plant beds, or near other simple cover (e.g., logs) (Reid 1950b; Carlander 1977; Siefert and Herman 1977; Pope and Willis 1997). Nests may be closely spaced (3.3 nests/m^2) or more loosely aggregated (1.8 m apart) (Breder and Rosen 1966; Carlander 1977; Becker 1983). Reproductive behaviors are presumably similar to those of the white crappie, but little detail is available for comparison. In experimental tanks with two nesting males, females on occasion spawned with both males and in one instance, a male spawned with two females (Siefert and Herman 1977). Eggs are demersal, adhesive, and whitish to yellowish in color (Scott and Crossman 1973; Barwick 1981). Mature ovarian eggs range from 0.68 to 1.05 mm diameter, water-hardened eggs average 0.93 mm diameter (range: 0.7591–1.03 mm), and water-hardened, fertilized eggs average 1.27 mm diameter (Merriner 1971a; Barwick 1981; Cooke *et al.* 2006). Size-adjusted batch fecundities are higher than any other centrarchid except the white crappie (see accounts on *Archoplites* and *Centrarchus*), but female fecundity can be highly variable between years or among populations (Dubuc and DeVries 2002). One to three distinct size classes of maturing ova are reported in ovaries of mature females, suggesting that some females may produce multiple batches of eggs (Barwick 1981; Pope *et al.* 1996). In controlled settings, the number of eggs released per spawn (average 66,130/243 mm TL female; Siefert and Herman 1977) falls within the range estimated for a 246 mm TL female (see subsequent), suggesting single-batch production. Fecundity increases with female size. The relationship between number of mature eggs (Y) and TL (X) is described by the power functions $\log Y = -3.0196 + 3.243 \log X$ and $\log Y = -6.2192 + 4.6580 \log TL$ (formulas from Barwick 1981, $n = 59$, $R^2 = 0.57$, and Baker and Heidinger 1994, $n = 11$, $R^2 = 0.74$, respectively). At a mean size of 246 mm TL, a female potentially can produce 54,225 to 82,751 mature eggs in a single batch (range: 10,836–13,168 eggs at 159 mm TL to 143,368–334,396 eggs at 332 mm TL). Hatching occurs in 2.4 days at 18.3°C, newly hatched larvae are 2.3 mm TL, and swim-up larvae are about 4 to 5 mm TL (Merriner 1971b; Siefert 1969b; Bulkley *et al.* 1976; Chatry and Conner 1980; Brown and Colgan 1985b). Black crappie maintained overwinter at DO concentrations as low as 2.6 mg/l successfully spawned (larvae survived to swim-up) during a simulated spring-to-summer rise in temperature (Carlson and Herman 1978). Spawning did not occur in trials with constant DO of 1.8 mg/l or diurnally fluctuating levels of 1.8 to 4.1 mg/l. No differences in number of embryos, hatching success, or survival through swim-up were detected at DO levels as low as 2.5 mg/l, but at that level individuals started and finished spawning earlier (i.e. at lower temperatures) than those exposed to higher DO concentrations (Siefert and Herman 1977). The male vigorously guards the nest, eggs, and larvae from predation by frequent nest predators, especially *Lepomis* spp. At the northern edge of the range, the entire cycle of male parental care lasts for about 7 to 11 days from egg deposition until swim-up larvae disperse (Colgan and Brown 1988; Cooke *et al.* 2006). The male feeds opportunistically during this period on invertebrates occurring on vegetation near the nest (e.g., amphipods) (Reid 1950b; Colgan and Brown 1988; Breder and Rosen 1966).

Nest associates: None known.

Freshwater mussel host: Confirmed host to *A. ligamentina, A. plicata, A. ferussacianus*, and *L. siliquoidea* (Howard 1914, 1922; Coker *et al.* 1921; Hove *et al.* 1997). Putative host to *L. compressa* (unpublished sources in OSUDM 2006).

Conservation status: The black crappie is secure throughout its native range (Warren *et al.* 2000; NatureServe 2006).

Similar species: The white crappie has a longer predorsal region, usually six dorsal spines, and vague but usually discernible dark bars on sides (see account on white crappie).

Systematic notes: *Pomoxis nigromaculatus* forms a sister pair with *P. annularis* (see account on *P. annularis*). Comparative analyses across the range of the species are lacking.

Importance to humans: Catchability, edibility, and liberal catch limits in most waters make the black crappie a highly sought and important sport fish throughout its rather large range. The species is easily caught on minnows, worms, and a variety of artificial lures; dry flies are taken occasionally. Black crappies tend to aggregate and at dusk are often caught one after the other as quickly as the hook can be rebaited. Because it remains active in cold waters, the species is also a popular target for ice fishing enthusiasts (Scott and Crossman 1973; Becker 1983). The flesh is white, flaky, and tasty, comparing favorably as table fare with the highly acclaimed walleye (*Sander vitreum*) (Scott and Crossman 1973; Becker 1983).

13.11 Identification keys to genera and species

Dichotomous keys are presented for identification of genera within the family and species within each genus. The characters used primarily follow and are illustrated in Becker (1983), Page and Burr (1991), Etnier and Starnes (1993), Jenkins and Burkhead (1994), Pflieger (1997), Ross (2001), Boschung and Mayden (2004), Marcy *et al.* (2005), and other taxa-specific sources given in the generic and species accounts. The species keys here are aimed primarily at identifying adults. Young individuals of many centrarchids can be a challenge to correctly identify to species, but illustrations and characters useful in differentiating juveniles are available in Ramsey and Smitherman (1972), Etnier and Starnes (1993), and Jenkins and Burkhead (1994).

13.11.1 Key to genera of Centrarchidae

1a. Anal fin with 4 to 5 or more spines.

Go to 2

1b. Anal fin with 3 spines.

Go to 6

2a. Anal fin base shorter than dorsal fin base; anal fin with 12 or fewer soft rays; moderately laterally compressed to elongate body.

Go to 3

2b. Anal fin base about equal to dorsal fin base; anal fin with 13 or more soft rays; deep, laterally compressed body.

Go to 5

3a. Caudal fin bilobed or concave; scales ctenoid; gill rakers long or moderately long, 7 or more on first arch.

Go to 4

3b. Caudal fin rounded; scales cycloid (scale shape percoid-like with anterior margin truncate and scalloped but ctenii are lacking); gill rakers moderately long, stout, 5 to 7 on first arch.

Acantharchus pomotis, mud sunfish

4a. Red eye in life. Gill rakers moderately long, 7 to 16 on first arch; branchiostegal rays usually 6. Dorsal fin with 10 to 12 spines, 11 to 12 rays; anal fin with 5 to 7 spines, 10 to 11 rays.

Ambloplites

4b. Eye not red in life. Gill rakers long, slender, 25 to 29 on first arch; branchiostegal rays usually 7. Dorsal fin with 12 to 14, usually 13 spines, 10 to 12 rays; anal fin with 6 to 8, usually 7 spines, 10 to 12 rays.

Archoplites interruptus, Sacramento perch

5a. Dorsal fin with 5 to 8 spines, 14 to 16 rays; anal fin with 6 spines, 17 to 19 rays; no teardrop; laterally compressed oblong body; rounded pectoral fin.

Pomoxis

5b. Dorsal fin with 11 to 13 spines, 12 to 15 rays; anal fin with 7 to 8 spines, 13 to 17 rays; large black teardrop; short, deep extremely laterally compressed body; long, pointed pectoral fin.

Centrarchus macropterus, flier

6a. Body elongate, depth goes into SL three or more times; lateral scale rows 55 or more; dorsal fins nearly separate, deeply notched.

Micropterus

6b. Body deeper, laterally compressed, depth goes into SL less than three times; lateral scale rows less than 55; dorsal fins continuous.

Go to 7

7a. Caudal fin truncate or rounded, not concave or bilobed; black teardrop.

Enneacanthus

7b. Caudal fin concave or bilobed; no black teardrop.

Lepomis

13.11.2 Key to species of Ambloplites

1a. Cheek naked or partly scaled, if present cheek scales are tiny or small and deeply embedded; body often with distinct round pale spots (iridescent gold to white in life) on upper side and head (found only in the Roanoke, Tar, and Neuse river drainages of Virginia and North Carolina).

Ambloplites cavifrons, Roanoke bass

1b. Cheek fully scaled, the scales moderate to large size and only slightly to moderately embedded; body lacking distinct pale spots.

Go to 2

2a. Color pattern of sides of body dominated by freckled pattern (scattered dark brown spots); no black edge on anal fin of large male (found only in the White River basin, Arkansas and Missouri, and Sac and Pomme de Terre drainages of the Osage River basin).

Ambloplites constellatus, Ozark bass

2b. Sides lack freckled pattern but are dominated by regularly arranged horizontal rows of brown-black spots or broad irregular vertical dark blotches; distinctive black edge on anal fin of large male, present or absent.

Go to 3

3a. Color pattern of sides of juveniles and adults dominated by broad irregular vertical brownish or grayish blotches; large male lacks black edged anal fin; breast scale rows (between bases of pectoral fins) usually ≤20.

Ambloplites ariommus, shadow bass

3b. Color pattern of sides of adults dominated by regularly arranged horizontal rows of brown-black spots (young patterned similar to *A. ariommus*); large male with distinctive black edge on anal fin; breast scale rows (between bases of pectoral fins) usually 21 to 25.

Ambloplites rupestris, rock bass

13.11.3 Key to species of Enneacanthus

1a. Six distinct bold black bars on sides contrast with pale to opalescent ground color, often with rose or pink blush; first bar on head passes through eye, forming a distinct black teardrop; the third black bar, extending from the anterior dorsal fin to the pelvic fin forms a distinct black blotch on the first 2 to 3 anterior membranes of the spiny dorsal fin; sixth bar on caudal peduncle is often faint; 3 to 4 incomplete bars often occur between complete bars; juncture of spiny and soft dorsal fin noticeably notched; second dorsal and anal fin not enlarged in breeding male.

Enneacanthus chaetodon, blackbanded sunfish

1b. Sides of body lack distinct bold black vertical bars on light background (may have dark to faint bars on dusky background); anterior dorsal fin membranes lack distinct black blotch, fin membranes mostly with uniformly dusky or dark pigmentation with rows of pale spots in soft-rayed portion; dorsal fin smooth in profile, not deeply notched; second dorsal and anal fins enlarged in breeding male.

Go to 2

2a. Body side pattern of males dominated by 5 to 8 dark to faint vertical bars (darkest on large individuals); rows of greenish-copperish to purple-gold crescent-shaped spots along side; black spot on ear tab larger than eye pupil; usually 19 to 22 scales around caudal peduncle

Enneacanthus obesus, banded sunfish

2b. Body side pattern of large young and adults dominated by rows of iridescent blue, silver, or pale round spots; bars on sides indistinct in adults; black spot on ear tab two-thirds the size of eye pupil; usually 16 to 18 scales around caudal peduncle.

Enneacanthus gloriosus, bluespotted sunfish

13.11.4 *Key to species of* Pomoxis

1a. Dorsal fin base shorter than distance from eye to dorsal fin origin; dorsal spines, usually 5 to 6; cheek scale rows, usually 4 to 5; mottling on sides forming 8 to 10 dark, irregular, but discernible, vertical bars.

Pomoxis annularis, white crappie

1b. Dorsal fin base about as long as distance from eye to dorsal fin origin; dorsal spines, usually 7 to 8; cheek scale rows, usually 6; sides randomly mottled with dark pigment (may be vertically barred in young).

Pomoxis nigromaculatus, black crappie

13.11.5 *Key to species of* Lepomis

1a. Sensory pits on top of head between eyes greatly enlarged, their width about equal to distance between them; sensory pores on edge of opercle greatly elongated, slit-like; ear flap, elongate, flexible, angled upward, black with wide white edge; gill rakers, long, slender, length of longest about 4 to 5 times their basal width.

Lepomis humilis, orangespotted sunfish

1b. Sensory pits between eyes not greatly enlarged, their width much less than the distance between them; sensory pores on edge of preopercle, not slit-like; ear flap size, orientation, and pigmentation variable; gill rakers variable.

Go to **2**

2a. Pectoral fins long and moderately sharply pointed, extending to or beyond anterior rim of eye when bent forward.

Go to **3**

2b. Pectoral fins shorter with tips rounded, not extending to anterior rim of eye when bent forward.

Go to **5**

3a. Large dark spot at rear of dorsal fin (faint in young); ear flap black to margin; gill rakers long, slender, length of longest four or more times their basal width; dark bars on sides (absent in turbid water; thin and chainlike in young).

Lepomis macrochirus, bluegill

3b. No dark spot at rear of dorsal fin; sides usually with scattered dark spots (may form single vertical bars in young); ear flap with pale margin or spot at tip; gill rakers short, longest about two times longer than basal width.

Go to **4**

4a. Pectoral fins long, extending to about 3 to 5 scale rows below dorsal fin base when angled upward; second dorsal fin with many bold dark brown wavy lines and spots; wavy blue lines on cheek and opercle of adult; sides below lateral line marked with dusky spots (orange in life); body of adults deep, depth about 0.5 of SL; profile of head in adults rounded.

Lepomis gibbosus, pumpkinseed

4b. Pectoral fins very long, extending to or beyond dorsal fin base when angled upward; second dorsal fin uniform or with vague dark mottling but lacks bold wavy lines or spots; no blue lines on cheek and opercle; sides below lateral line uniformly pigmented, not marked with dusky spots; body of adults somewhat elongate, depth about 0.4 of SL in adults; profile of head more or less pointed.

Lepomis microlophus, redear sunfish

5a. Tooth patch on tongue; 3 to 4 dark bars (red-brown in life) radiating backward from eye across cheeks and opercles.

Lepomis gulosus, warmouth

5b. No tooth patch on tongue; no dark bars radiating backward from eye.

Go to 6

6a. Lateral line incomplete or interrupted; gill rakers long, slender, longest 6 to 8 times longer than their basal width; dark spot usually at rear of soft dorsal fin (indistinct in large specimens); coloration relatively subdued, dusky, no bright blue, red, orange, or yellow colors on head or body; small, adults usually <75 mm SL.

Lepomis symmetricus, bantam sunfish

6b. Lateral line complete, not interrupted (occasionally interrupted in *Lepomis peltastes*, which has short, stubby gill rakers and wavy blue lines on cheek and opercle); dorsal spot variable; coloration variable.

Go to 7

7a. Mouth relatively large and moderately oblique, the upper jaw extending well past anterior rim of eye in large specimens.

Go to 8

7b. Mouth relatively small and moderately to very oblique, the upper jaw seldom extending past anterior rim of eye.

Go to 9

8a. Ear flap short, the black portion inflexible and appearing as a round spot, posterior edges pale; large dark spot usually evident at rear of dorsal and anal fins; gill rakers long and slender, length of longest 4 to 6 times their basal width; lateral scales, usually 45 to 50; scales below lateral line, usually 16 to 19; body relatively elongate, robust, and basslike.

Lepomis cyanellus, green sunfish

8b. Ear flap long, narrow, and flexible in adults, black to posterior margin, outlined above and below by pale or blue lines; no large dark spot at rear of dorsal or anal fin; gill rakers moderate, length of longest two times basal width in adults; lateral scales, usually 41 to 50; scales below lateral line, usually 14 to 16; body deep, not basslike.

Lepomis auritus, redbreast sunfish

9a. Ear flap, elongate, thin, and flexible; wavy blue to blue-green lines on cheek and opercle in life; gill rakers, short, stubby, knoblike, length of longest about equal to their basal width in adults.

Go to 10

9b. Ear flap short, stiff; no wavy blue lines on cheek and opercle; gill rakers not stubby or knoblike, moderate to long, length of longest about two to six times their basal width.

Go to 12

10a. Ear flap with black center, bordered in pale to white, angled upward at about 45 degrees and in adult males posterior edge marked with red spot; lateral scales, usually 35 to 37; pectoral rays, usually 12 to 13 (found only in Great Lakes basin and a few scattered localities in the upper Mississippi basin).

Lepomis peltastes, northern longear sunfish

10b. Ear flap, variously oriented, with black center and pale to white borders, but lacks distinct posterior red spot (not found in Great Lakes basin).

Go to 11

11a. Cheek scales, usually 3 to 4; pectoral rays, usually 12 to 13; ear flap often angled noticeably upward, center black and often flecked with silver or greenish streaks, margin pale white to greenish; lateral line brick red in life; blue-green marks (brown in preserved fish) on lower side of head tend to be broken, appearing as freckles or short streaks; body profile somewhat rounded, greatest depth usually beneath or behind the dorsal fin origin.

Lepomis marginatus, dollar sunfish

11b. Cheek scales, usually 5 to 6; pectoral rays, usually 13 to 14; ear flap orientation variable, usually horizontal or angled slightly upward, center black, entire margin whitish, flushed with orange-red, or with 2 to 9 red spots scattered along the margin (some populations lack pale margins); lateral line not red in life; blue-green marks (brown in preserved fish) on lower side of head tend to form long continuous streaks; body profile more elongate, the greatest depth usually before the dorsal fin origin in specimens <150 mm SL.

Lepomis megalotis, longear sunfish

12a. Discrete black spots on scales form irregular horizontal rows of spots on sides and dorsum, especially prevalent on lower sides; cheek and opercle often speckled with small discrete dark spots; breeding males lack red-orange on breast, belly, and on sides (these may be yellowish to pinkish); breast scale rows, usually 15 to 18; cheek scales, usually 5 to 7; scales above lateral line, usually, 7 to 8; scales below lateral line, 13 to 15; caudal peduncle scales, usually 8 to 10.

Lepomis punctatus, spotted sunfish

12b. Pale areas (red-orange in breeding males) at anterior scale bases form horizontal rows of triangular-shaped spots along sides; discrete black spots lacking at scale bases; cheek and opercle lack speckling of small discrete dark spots (often with a few dusky to dark streaks); breeding males with red-orange color on sides, breast, belly, dorsal margin of ear tab, and quadrate patch on side above ear tab; breast scales, usually 12 to 15; cheek scales, usually 4 to 6; scales above lateral line, usually, 6 to 7; scales below lateral line, 12 to 14; caudal peduncle scales, usually 7 to 9.

Lepomis miniatus, redspotted sunfish

13.11.6 Key to species of Micropterus

1a. Spinous and soft dorsal fins separated by deep notch, if connected, only by a small membrane; length of last dorsal spine less than half the length of longest dorsal spine; upper jaw extends beyond posterior rim of eye in adults; dark lateral band present; caudal fin of juveniles bicolored, the base lighter than posterior portion; pyloric caeca branched at base.

Go to **2**

1b. Dark lateral band present or absent, sides often marked by conjoined blotches or vertically elongate bars; spinous and soft dorsal fins well connected, the notch between the fins shallow; length of last spine more than half the length of longest spine; upper jaw usually not extending beyond posterior rim of eye; caudal fin of juveniles tricolored, often sharply contrasted dark middle region separating orange or yellow base from white (or clear) posterior (faint to lacking in *M. coosae*), with or without prominent tail spot; pyloric caeca unbranched.

Go to **3**

2a. Lateral scales, usually 69 to 73; caudal peduncle scales, usually 28 to 31 scales (occurs as a native only in peninsular Florida, but widely introduced in the southern United States)

Micropterus floridanus, Florida bass

2b. Lateral scales, usually 58 to 67; caudal peduncle scales, usually 26 to 28.

Micropterus salmoides, largemouth bass

3a. Side uniformly pigmented or with series of broad, indistinct vertical bars, lower sides without distinct rows of horizontal spots, juveniles lack a distinct black caudal spot; scales above lateral line, usually 12 to 13; scales below the lateral line, usually 19 to 23.

Micropterus dolomieu, smallmouth bass

3b.. Side with a distinct narrow midlateral horizontal band (or series of partly joined quadrate blotches) or a midlateral band consisting of a series of vertically elongate blotches (may be indistinct); juveniles may or may not have a distinct caudal spot; scales above lateral line, usually 6 to 9; scales below lateral line, usually <20.

Go to 4

4a. Side with a dark, usually distinct and narrow, midlateral horizontal stripe (or series of partly joined blotches, not elongated vertically) and lower sides with rows of small black spots; middle band on caudal fin and black caudal spot of juveniles distinct; tooth patch on tongue.

Micropterus punctulatus, spotted bass

4b. Side with a series of vertically elongate to quadrate blotches (often indistinct or faint in adults).

Go to 5

5a. Caudal fin orange with white (or clear) upper and lower outer edges; tail spot prominent in juveniles; tooth patch on tongue; sides marked with dark confluent irregular blotches or stripe; tinges of red or orange on fins; young lacking sharply contrasting caudal fin pigmentation; 5 to 8 well-developed rows of dark spots on ventrolateral scales.

Micropterus coosae, redeye bass

5b. Caudal fin without white (or clear) upper and lower outer lobes; tooth patch on tongue present or absent.

Go to 6

6a. No tooth patch on tongue; sides marked with 10 to 15 dark vertically elongate midlateral bars with 6 to 8 supralateral bars extending into the interspaces of the midlateral bars; 5 to 7 rows of weakly developed spots on ventrolateral scales, frequently forming wavy lines; quadrate to rectangular dark tail spot in adults, lacking or faint in young; caudal peduncle scales, usually 30 to 33; lateral line scales, usually 72 to 77 (found as native only in the Apalachicola River system, Alabama and Georgia).

Micropterus cataractae, shoal bass

6b. Tooth patch on tongue; sides variously marked; caudal peduncle scales, usually <31; lateral line scales, usually <69.

Go to 7

7a. Upper jaw extending to or beyond rear margin of eye in adults; sides marked with a series of about 12 vertically elongate lateral blotches, anteriorly much wider than interspaces, fusing on the caudal peduncle, to form a relatively uniform lateral band; caudal spot prominent in young; caudal peduncle scales, usually 27 to 31; lateral line scales, usually 57 to 65 (found as native only in Suwannee and Ochlockonee river systems, Florida).

Micropterus notius, Suwannee bass

7b. Upper jaw extending to or slightly beyond middle of eye; sides marked with a series of about 13 vertically elongate lateral blotches, being broadly diamond shaped, especially on the caudal peduncle; dark spots on scales form distinct continuous lines on lower sides; caudal spot prominent in young; caudal peduncle scales, usually 26 to 27; lateral line scales, usually 61 to 69 (found only on the Edwards Plateau of Texas in the Brazos, Colorado, Guadalupe, and San Antonio rivers and upper Nueces River, where introduced).

Micropterus treculi, Guadalupe bass

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Centrarchidae Species List with Latin Name and Common Name

Acantharchus pomotis, mud sunfish
Ambloplites ariommus, shadow bass
Ambloplites cavifrons, Roanoke bass
Ambloplites constellatus, Ozark bass
Ambloplites ruprestris, rock bass
Archoplites interruptus, Sacramento perch
Centrarchus macropterus, flier
Enneacanthus chaetodon, blackbanded sunfish
Enneacanthus gloriosus, bluespotted sunfish
Enneacanthus obesus, banded sunfish
Pomoxis annularis, white crappie
Pomoxis nigromaculatus, black crappie
Lepomis auritus, redbreast sunfish
Lepomis cyanellus, green sunfish
Lepomis gibbosus, pumpkinseed
Lepomis gulosus, warmouth
Lepomis humilis, orangespotted sunfish
Lepomis macrochirus, bluegill
Lepomis morginatus, dollar sunfish
Lepomis megalotis, longear sunfish
Lepomis microlophus, redear sunfish
Lepomis miniatus, redspotted sunfish
Lepomis peltastes, northern longear sunfish
Lepomis punctatus, spotted sunfish
Lepomis symmetricus, bantam sunfish
Micropterus henshalli, Alabama bass*
Micropterus cataractae, shoal bass
Micropterus coosae, redeye bass
Micropterus dolomieu, smallmouth bass
Micropterus floridanus, Florida largemouth bass
Micropterus notius, Suwannee bass
Micropterus punctulatus, spotted bass
Micropterus salmoides, largemouth bass
Micropterus treculi, Guadalupe bass

*Note: *M. henshalli* (Alabama bass) was elevated to the species level in 2008 when this book was "in press". Hence, in this book and index it is referred to as a subspecies of *M. punctulatus* (spotted bass).

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Note: Only Latin binomials have been used here. Please consult the previous page for a complete species list with common names cross-referenced with Latin binomials.