Chapter 15   Ictaluridae: North American Catfishes

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The North American Catfishes, family Ictaluridae, comprising 50 species in seven genera, is the largest family of freshwater fishes indigenous to North America. The family name Ictaluridae is from the Greek, *ichthys*, meaning fish, and *ailouros* (Latinized *aelurus*), meaning cat (Boschung & Mayden 2004). The Chiapas Catfish family, Lacantuniidae (Rodiles-Hernández et al. 2010), is presently known only from the Rio Usumacinta basin, Chiapas, Mexico, and is south of the general area covered here.

Ictalurids are recognized easily as Catfishes (Siluriformes) even by small children because of the barbels, or whiskers, similar to cat whiskers, that adorn the face. Technically, they are ostariophysan fishes having a sound-producing and sound-receiving mechanism intimately tied to a bony Weberian apparatus, swim bladder, and gut. Their skin and barbels have cutaneous taste buds and alarm substance cells. These structures play a prominent role in social behavior and are essentially the exclusive means of locating food by a touch-taste sensory system.

Nearly everyone who mishandles a Catfish becomes acutely aware of the sting associated with the spines or the skin around the spines (Fig. 15.1). Not as well known to fishers is the possibility of strong allergic reactions to the sting or the bacterial infections that arise when one does not remove a piece of spine from under the skin. Amputations of digits from severe infection (Baack et al. 1991) and general anaphylactic shock (BMB pers. obs.) occur among people sensitive to venoms.

Excluding the Bowfin (*Amia calva*) and Sunfishes (Centrarchinae), ictalurids exhibit the most extreme examples of parental care among any of the freshwater fishes on the North American continent. With one or two exceptions, all epigean species are cavity nesters, depositing eggs pri-

marily during the summer months and then guarding the hatchlings for about two weeks (Table 15.1); parents of the Bullheads (genus *Ameiurus*) often stay with their young for extended periods, and the black-colored young can be seen in clear streams or lakes as a densely packed swarm or ball (Fig. 15.2). Ictalurids are often nocturnal or crepuscular in habits, usually seeking shelter during daylight hours; they occupy a wide range of habitats, including lentic

Figure 15.1. X-ray of an imbedded catfish spine in a hand (second finger from left) (from Blomkalns & Otten 1999; used with permission of The Wilderness Medical Society, Salt Lake City, Utah).

Table 15.1. Life history information for North American Catfishes, Ictaluridae, compiled from numerous sources used in the text (see literature cited). The Blue Catfish, *Ictalurus furcatus*, and Channel Catfish, *I. punctatus*, are exemplars for *Ictalurus*.

	Ameiurus	Ictalurus	Noturus	Pylodictis
Number of extant species	7	10	29	1
Primary or secondary fresh water	Primary fresh water	Primary fresh water	Primary fresh water	Primary fresh water
Maximum size recorded in length and weight	28–62 cm TL (11.0–24.4 inches) 3.5 kg (7.8 pounds), but usually much lighter—a 0.9 kg (2 pound) bullhead is large	Known maximum sizes range from about 100–165 cm TL (39.4–65.0 inches); historically maximum weights from 26.3–142.9 kg (58–315 pounds), most records are now about 59.0–63.5 kg (130–140 pounds) (Blue Catfish)	36–265 mm SL (mean 102 mm) (1.4–10.4 inches, mean 4.0 inches); 2–482 g (.07 ounces to 1 pound 1 ounce)	155 cm TL (5 feet 8 inches); 55.8 kg (123 pounds)
Maximum age	5–8 years; maximum recorded is 11 years	18–27 years (probably much older in both exemplars)	1–9 years	28 years
Age and size at first reproduction	2–4 years; 152–250 mm TL (6.0–9.8 inches)	2–12 years, modally 4–5 years; 170–550 mm TL (6.7–21.7 inches)	1–4 years; 30–87 mm SL (1.2–3.4 inches)	2–5 years; most at 50–75 cm TL (19.7–29.5 inches) and 1.5–4.0 kg (3.3–8.8 pounds)
Iteroparous versus semelparous	Iteroparous	Iteroparous	Iteroparous and semelparous	Iteroparous
Fecundity estimates from ovarian counts	about 2,500–5,000	8,800 eggs/kg for fish 0.45–1.8 kg (4,000 eggs/pound for fish 1–4 pounds); 6,600 eggs/kg for fish >1.8 kg (4,000 eggs/pound for fish >4 pounds)	14–570; mean across all species studied is about 100	4,076–31,579 or in another study 2,391–5,749 eggs/kg (1,087 to 2,613 eggs/pound)
Mature egg diameter	2.00–4.65 mm (0.08–0.18 inches)	3.20–4.25 mm (0.13–0.17 inches)	2.0–3.8 mm (0.08–0.15 inches)	2.56–3.44 mm (0.10–0.14 inches)
Egg deposition sites	Cavity structures, both artificial and natural, or saucer-shaped nests, usually in shaded areas (nest in both lentic and lotic waters)	Very poorly known in wild; few nests described in literature but mostly in cavities, under logs and rocks, in bank holes; spawning substrate clean sand or gravel; use large milk jugs, wooden "nail" kegs, and other structures in culture settings	Cavities beneath stones, logs and boards or in cans, bottles, and bivalve shells	Hollow logs, large artificial nest boxes placed in streams, car bodies, large metal drums, chambers in banks, root masses from downed trees
Clutch size in nest	1,163 ± 95 eggs in a Michigan study	Not known for natural setting; 7,500 to 57,500 in a culture setting in California (estimate based on 17.6 eggs/g, 500 eggs/ounce)	Grand mean is 101; means are from about 17 to 200; embryos are in a single mass attached to each other and not to other surfaces	about 100,000 (based on only 1 individual)
Range of nesting/spawning dates and temperatures	June-July peak (extremes are late May and late August) months; 23–27°C (73.4–80.6°F)	April to June as beginning date (depending on latitude), but genuine nesting peaks in June and July throughout range; 21–29°C (69.8–84.2°F)	May-September; peaks in June-July; 24–30°C (75.2–86.0°F) for 90% of species studied	June-July peak spawning months; 24–28°C (75.2–82.4°F) ideal temperatures

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	Ameiurus	*Ictalurus*	*Noturus*	*Pylodictis*
Habitat of spawning sites; average water depth	Both lentic and lotic habitats (e.g., streams, lakes, ponds); <1 m (39.4 inches); often in shaded areas	Riverine habitats; artificial culture settings are ponds and troughs; <1 m (39.4 inches)	Mostly riverine above and below riffles (also pools); rarely in lakes; <0.5 m (19.7 inches)	Riverine settings; artificial nest boxes set in streams are successful; <2 m (78.7 inches)
Incubation period; larval type at hatching	6–9 days at 21–23°C (73.4°F); mesolarva	6–7 days at 24–26°C (78.8°F); mesolarva	5.8–9.0 days at 24–26°C (75.2–78.8°F); mesolarva	6–7 days at 23.9–27.8°C (82.0°F); probably a mesolarva
Mean size at hatching	9.0–9.8 mm TL (0.35–0.39 inches)	8.5–9.5 mm TL (0.33–0.37 inches)	3.4–10.0 mm TL (0.13–0.39 inches); grand mean is 7.0 mm TL (0.28 inches)	Not accurately known, but one report is 5 mm TL (0.20 inches), the other is 11 mm TL (0.43 inches), likely about 7 mm TL (0.28 inches)
Parental care	Uniparental and biparental care of nest and embryos known (egg-fanning and mouthing); parent(s) stay with young until they are about 25–50 mm TL (1.0–1.97 inches); young form black "ball" and move together guarded by parent(s)	Apparently mostly uniparental care of nest and embryos (egg-fanning and mouthing); parent (usually male) stays with young until they are about 25 mm TL (1.0 inches); young not known to travel together in tight school as in *Ameiurus*	Male parental care seems to dominate, and male does not feed during incubation, fanning, and mouthing of embryos; male stays with young until ≥10 days post-hatching (yolk is absorbed, hatchlings have pigment)	In aquarium, male guarded eggs and stayed with hatchlings; fanning of embryos observed but no egg-mouthing (based on 1 individual)
Major dietary items	Omnivores; adults consume insects, crustaceans, and some fish; crepuscular feeding periodicity known and generally opportunistic in dietary items	Omnivores, but at about 10–15 cm TL (3.9–5.9 inches) switch principally to crustaceans and fishes; spawning usually halts feeding; bivalves and fishes may be major diet item of Blue Catfish	Benthic invertivores with crepuscular feeding periodicity; usually eat insect larvae and small crustaceans; only largest species consume small fishes and crayfish	≤10 cm TL (3.9 inches) insects are frequently eaten, between 10 and 25 cm TL (3.9 and 9.8 inches) individuals become solitary and consume insects, fishes, and crayfishes; a lie-in-wait predator
General year-round habitat	Small to large streams and rivers, reservoirs, and wetlands; sometimes associated with upland reaches (White Catfish), vegetation, or other structure	Medium-sized streams (Channel Catfish) to large rivers and reservoirs; usually associated with structure and banks; may extensively use floodplains during flooding	Headwater streams to large rivers, but most in small-medium streams and rivers; gravel, cobble, and boulder riffles in upland streams; undercut banks, detritus, and woody debris in lowland streams; sometimes found in bivalve shells	Medium-sized to large streams and rivers and reservoirs; associated with woody structure or rocky substrate

(continued)

	Ameiurus	*Ictalurus*	*Noturus*	*Pylodictis*
Migratory or diadromous	≤200 km (124 miles) movement but usually higher site fidelity and <5 km (3.1 miles); more extensive movement during autumn and winter	Significant long-distance movement (≤600 km, 373 miles) associated with spawning and overwintering	Little studied but maximum of 225 m (246 yards) (Neosho Madtom); most studies show restricted movement but with low recapture rates	Significant long-distance movement (>600 km, 373 miles) possible usually in spring, but often establish small home ranges of about 1 km (0.6 miles) and remain nearby
Imperilment status	Currently stable over historic range; some species vulnerable	U.S. species stable and widely stocked; several central American species vulnerable to overexploitation, hybridization, and habitat destruction	Many species imperiled due to habitat destruction or restricted range, but several species widespread and stable	Currently stable over historic range, but populations can be vulnerable to overexploitation

	Prietella	*Satan*	*Trogloglanis*
Number of extant species	2	1	1
Primary or secondary fresh water	Primary fresh water	Primary fresh water	Primary fresh water
Maximum size recorded in length and weight	60 mm SL (2.4 inches), maximum weights not known	117 mm SL (4.6 inches), maximum weights not known	90 mm SL (3.5 inches), maximum weights not known
Maximum age	Not known, but cave organisms are thought to be long-lived (10+ years)	Not known, but cave organisms are thought to be long- lived (10+ years)	Not known, but cave organisms are thought to be long-lived (10+ years)
Age and size at first reproduction	Unknown	Unknown	Unknown
Iteroparous versus semelparous	Unknown	Unknown	Unknown
Fecundity estimates from ovarian counts	Unknown	Unknown	200 at different stages of development
Mature egg diameter	Unknown	Unknown	Unknown, largest egg of largest specimens was 0.5 mm
Egg deposition sites	Unknown	Unknown	Unknown
Clutch size in nest	Unknown, but nest may not be necessary	Unknown, but nest may not be necessary	Unknown, but nest may not be necessary
Range of nesting/spawning dates and temperatures	Unknown	Unknown	Unknown
Habitat of spawning sites; average water depth	Unknown, but in cave or subterranean waters	Unknown, but in artesian wells or subterranean waters	Unknown, but in artesian wells or subterranean waters
Incubation period; larval type at hatching	Unknown	Unknown	Unknown
Mean size at hatching	Unknown	Unknown	Unknown
Parental care	Unknown	Unknown	Unknown
Major dietary items	Unknown	Shrimps, amphipods, isopods, other blindcats	Fungal growths and dead or dying organisms

	Prietella	*Satan*	*Trogloglanis*
General year-round habitat	Dark zone of subsurface karst springs and streams, in still pool over silt and rock substrate or in deeper, high-flow streams	San Antonio Pool of Edwards Aquifer near San Antonio, TX at depths of 300–600 m (984–1,969 feet)	San Antonio Pool of Edwards Aquifer near San Antonio, TX at depths of 300–600 m (984–1,969 feet)
Migratory or diadromous	Unknown, but has been found near pump sites as well as in deep water of caves	Unknown, but does get pumped out at well openings	Unknown, but does get pumped out at well openings
Imperilment status	Federally endangered (both U.S. and Mexican governments)	Not federally protected in United States, but has highest endangerment status by NatureServe	Not federally protected in United States, but has highest endangerment status by NatureServe

Figure 15.2. Male Brown Bullhead, *Ameiurus nebulosus*, guarding young in Otis Reservoir, East Otis, Massachusetts, June 2005 (courtesy of Kristin Coffey).

and lotic systems, pools and riffles of streams, occurring from montane areas to tidal fresh water.

Species of Ictaluridae are among the most economically important fishes in North America. The Channel Catfish (*Ictalurus punctatus*) (Fig. 15.3) is grown in farm or aquaculture ponds in the midwestern and southern United States and in the Central Valley of California (Moyle 2002). In fact, U.S.-grown Catfish served in restaurants of North America are almost certainly of this species. All the large ictalurids are sought by both recreational and commercial fishers. Angling for Catfishes, especially in the Midwest and South, is one of the most familiar pastimes of adults and children. Additionally, a number of fishers participate in a regulated recreational fishery in which large Flathead Catfish (*Pylodictis olivaris*), Blue Catfish (*Ictalurus furcatus*), and Channel Catfish are hand-extracted from their nesting sites, a pastime referred to as hogging, tickling, noodling, grabbing, grabbling, or hand-grappling (Jackson et al. 1997). Madtoms (genus *Noturus*) and other ictalurids are used and sold as bait, and most of the species are kept in home aquaria by fish enthusiasts throughout North America. Some Catfish species are also important as research animals. The Brown Bullhead (*Ameiurus nebulosus*) (Fig. 15.4) is one of the most prominent laboratory experimental fishes in Europe and North America with studies of behavior and the sense organs dating back at least to the early 1900s.

DIVERSITY AND DISTRIBUTION

North American Catfishes, previously known as freshwater Catfishes or bullhead Catfishes, consist of some of our most familiar species, and in contrast, some species rarely

Figure 15.3. (*upper*) The Channel Catfish, *Ictalurus punctatus*, shown here in the Elk River, Grove, Oklahoma, October 2008, is the most widespread (and widely introduced) species in the genus. (*lower*) The Headwater Catfish, *Ictalurus lupus*, is superficially similar to the Channel Catfish, but is restricted to the Rio Grande drainage, Texas, New Mexico, and Mexico; the Nueces River, Texas; and northeastern Gulf tributaries in Mexico. The species formerly occurred in the San Antonio Bay and Colorado River drainages (Bean et al. 2011; Page & Burr 2011). This individual was photographed in October in a large artesian spring, San Solomon Springs, Balmorhea State Park, Pecos River drainage, Texas (courtesy of © Engbretson Underwater Photography, *upper*, and © Jennifer Idol / Engbretson Underwater Photography, *lower*).

Figure 15.4. Brown Bullhead, *Ameiurus nebulosus*, in the Buffalo River, Arkansas, October 2005 (courtesy of © Engbretson Underwater Photography).

are seen by fishers or even ichthyologists. The large fork-tail Catfishes of the genus *Ictalurus* comprise eight species (Table 15.2) at least four of which are familiar and popular sport and food fishes in the United States and Mexico.

Within the genus, at least two species are polytypic (Table 15.2). The genus *Pylodictis* is monotypic containing the prominent sport and food fish, the large Flathead Catfish (Fig. 15.5). The medium-size bullheads (genus *Amei-*
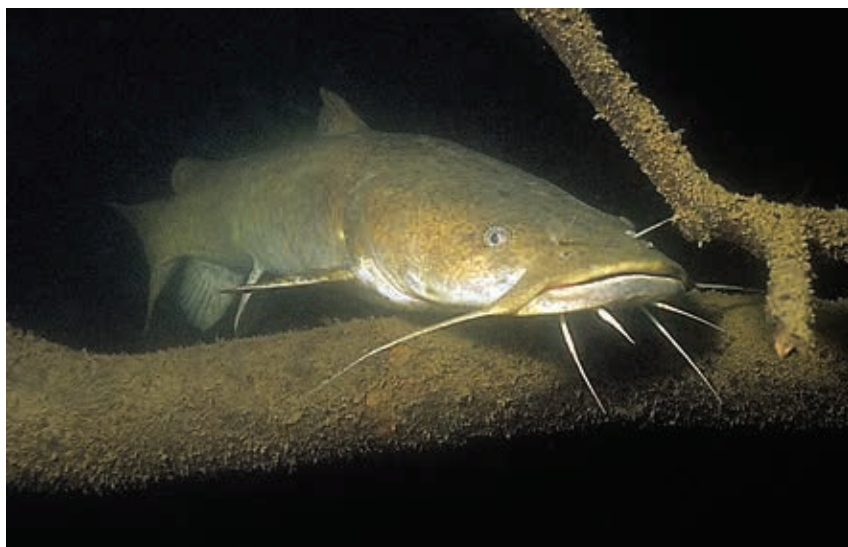
Figure 15.5. Flathead Catfish, *Pylodictis olivaris,* at night in Table Rock Lake, Branson, Missouri, October 2007 (courtesy of © Engbretson Underwater Photography).

Figure 15.6. Close-up of a Stonecat, *Noturus flavus,* illustrating the distinctive nape markings only found on populations in the Tennessee and Cumberland River drainages. Intraspecific morphological and genetic distinctiveness is prevalent among species of North American Catfishes, particularly so in madtoms (genus *Noturus*) (courtesy of MGB at Shoal Creek, Goose Shoals, Lauderdale County, Alabama, January 2011).

urus) are represented by seven species at least six of which show some evidence of polytypy (Table 15.2). The mostly small and cryptic madtoms (genus *Noturus*) currently comprise 29 species, but of these, 15 show evidence of polytypy (Fig. 15.6). Finally, the rare, blind Catfishes include two monotypic genera *Satan* and *Trogloglanis* in Texas and the genus *Prietella* with two species in Mexico, one of which also occurs in southern Texas (Yuhas 2016; Figs. 15.7 and 15.8). A great size range characterizes the family, from the largest Blue Catfish (Fig. 15.9) attaining a

length of at least 1.65 m TL (5.4 feet) and historically >143 kg (315 pounds) to the diminutive Pygmy Madtom (*Noturus stanauli*) at 36 mm SL (1.4 inches) and 2 g (0.07 ounces) (Fig. 15.10).

The Ictaluridae ranges from southern Canada east of the Rocky Mountains south to Belize and Guatemala with most species occurring in the United States and only a few extending into either Canada or Mexico. The taxonomy of *Ictalurus* in Mexico is unclarified, but ≥4 species (one undescribed) inhabit drainages on the Pacific Coast of Mexico and perhaps four occur along the Gulf Slope of Mexico (Miller et al. 2005; Fig. 15.11). Although Lundberg (1970) suggested the Blue Catfish ranged to Central America, later taxonomic work showed that the species south of the Rio Grande drainage on the Gulf Slope is a distinct species, *Ictalurus meridionalis* (Rodiles-Hernandez et al. 2010). The Flathead Catfish occurs natively in the eastern United States, south to Mexico (Fig. 15.12). Bullheads range widely over the eastern United States (Fig. 15.13), and their native range is difficult to determine with accuracy because they have been transplanted frequently for decades. Madtoms (Fig. 15.14) are found primarily in the eastern United States, mostly east of the Great Plains, and barely reach southern Canada and northern Mexico. The blindcats are only in Texas and Mexico (Fig. 15.15) in subterranean habitats.

North American Catfishes as Non-natives

The Channel Catfish, Blue Catfish, Flathead Catfish, and six species of *Ameiurus* have been introduced widely outside their native ranges across the United States and inter-

Figure 15.7. The stygobitic Mexican Blindcat, *Prietella phreatophila*, was thought to occur only in caves south of the Rio Grande drainage in Coahuila, Mexico, but individuals were discovered north of the river in 2016 in a cave near Del Rio, Texas. Adult (*upper*) and juvenile (*middle*) from Catfish Parlor Cave, Val Verde County, Texas, the only known locality for the species in the United States and a pair of individuals (*lower*) from an undisclosed cave in Coahuila, Mexico (*upper* and *middle* courtesy of © Jean Krejca; *lower* photograph © Danté Fenolio 2013; www.anotheca.com; used with permission; image courtesy of Dean Hendrickson, Texas Memorial Museum).

continentally. Other species, even though introduced less widely, have nevertheless become established far outside their native range (e.g., *Noturus gyrinus*, Tadpole Madtom). Most ictalurid introductions were deliberate, albeit some unauthorized, primarily for recreational fishing and aquaculture, but others apparently were introduced as stock contamination with other Catfishes or as discarded baitfishes (e.g., madtom species) (Fuller et al. 1999). Today, populations, often large ones, of non-native ictalurids inhabit streams, rivers, and reservoirs across the western United States (e.g., Columbia River, Rio Grande, Colorado River) (Vigg et al. 1991; Schade & Bonar 2005), including the Pacific Slope from California northward into southern Washington (Moyle 2002; Wydoski & Whitney 2003). In 12 western states, the Channel Catfish and Yellow Bullhead (*Ameiurus natalis*) are among the top 10

most common introduced fishes when present in fish-bearing streams (Schade & Bonar 2005). The Yellow Bullhead has also been introduced to British Columbia, Canada (Hanke et al. 2006). Non-native ictalurids also occur in Puerto Rico (Erdman 1984), Hawaii (Maciolek 1984), on the Pacific and Atlantic Slopes of Mexico (Miller et al. 2005; Ruiz-Campos et al. 2012), and along the Atlantic Slope of the United States from Maine to Florida (Fuller et al. 1999).

Intercontinental introductions of North American Catfishes are numerous. Outside North America, the Channel Catfish is established in South America, Japan, the Philippines, Italy, Russia, Georgia, and Uzbekistan (FishBase 2010; Goradze et al. 2011; Daga et al. 2016). The Black Bullhead (*Ameiurus melas*) is established in Chile and Great Britain, and that species, the Yellow Bullhead, and the Brown Bullhead are established throughout Europe (Wheeler 1978; Welcomme 1988; Holčík 1991; Gante & Santos 2002; Hesthagen & Sandlund 2007; Musil et al. 2008; FishBase 2010; Nowak et al. 2010). The White Catfish (*Ameiurus catus*) was introduced outside North America only to Puerto Rico and the Philippines but was discovered in a pond in Great Britain (Britton & Davies 2006), although it does not appear to have spread.

Figure 15.8. (upper) A volunteer caver prepares to ascend into Catfish Parlor Cave, Val Verde County, Texas, to assist in sampling the only known population of the Mexican Blindcat, *Prietella phreatophila*, in the United States. *(lower)* A cave researcher makes his way to a gin clear cave pool to set traps in hopes of discovering additional localities for Mexican Blindcats in the vicinity of the Catfish Parlor Cave locality (courtesy of © Jean Krejca).

Additionally, the Brown Bullhead is long established in New Zealand, where it is regarded as a pest (McDowall 1984).

Although in most cases the ecological effects of non-native ictalurids on native fishes are undocumented or poorly documented, the large species are implicated via predation in declines of native imperiled fishes as well as native sport and commercial fishes and in threatening the genetic integrity of native congeners through hybridization. Non-native Channel Catfish in the Columbia River basin are decided predators on emigrating native salmonid smolts, but their overall impact on that resource is unknown although apparently less than native piscivores (e.g., Northern Pikeminnow, *Ptychocheilus oregonensis*) (Vigg et al. 1991). In the John Day reservoir in that system, they may take a heavy toll (33% of diet by weight) on migrating salmon smolts (Poe et al. 1991). In the case of endangered fishes, state and federal management agencies in western states, such as Arizona, New Mexico, Colorado, and Utah, spend thousands of dollars and person hours each year in an effort to remove Channel Catfish (and other non-native ictalurids and fishes) by electrofishing, trapping, and liberal catch limits from western warm water streams and rivers (e.g., Colorado River, San Juan River) (Tyus & Saunders 2000; reviewed by Mueller 2005). One of the most abundant species in the Colorado River of the western United States is the Channel Catfish, a non-native that continues to alter that system for native fishes (Tyus & Nikirk 1990). Predation by non-native Channel Catfish and Flathead Catfish on stocked juveniles of the imperiled Razorback Sucker (*Xyrauchen texanus*) in the Gila River, Arizona, was deemed high enough (≤900 individuals/km) to preclude local re-establishment of the native sucker by stock-

Figure 15.9. Blue Catfish, *Ictalurus furcatus,* at night in Beaver Lake, Arkansas, October 2006 (courtesy of © Engbretson Underwater Photography).

Plate 15.1. Headwater Catfish, *Ictalurus lupus*.

Plate 15.2. Flathead Catfish, *Pylodictis olivaris* (juvenile *upper*, large adult *lower*).

Figure 15.10. The federally endangered Pygmy Madtom, *Noturus stanauli*, from the Clinch River, Tennessee (courtesy of © P. Rakes and J. R. Shute).

ing of small juveniles (Marsh & Brooks 1989; see also Marsh & Langhorst 1988). Blue Catfish introduced to Chesapeake Bay in the 1970s are implicated in the decline of native White Catfish and have filled an apex predator role in the food web, feeding on the native anadromous shads and Herrings (*Alosa* spp.; Atlantic Menhaden, *Brevoortia tyrannus*) (Schloesser et al. 2011). In the Little Colorado River, Arizona, endangered Humpback Chubs are threatened by heavy predation from non-native ictalurids, particularly Channel Catfish but also Black Bullheads (Marsh & Douglas 1997). Early reports generated concern that choking deaths

Plate 15.3. Spotted Bullhead, *Ameiurus serracanthus*.

Plate 15.4. Brindled Madtom, *Noturus miurus*.

of Colorado Pikeminnows (*Ptychocheilus lucius*) after consuming Channel Catfish could be contributing to population declines; however, flow regime changes and predation of larvae by Channel Catfish and other non-natives are more likely causes (McAda 1983; Pimental et al. 1985). In many cases, introduced Channel Catfish may be impacting native communities through competition for food rather than direct predation (Matsuzaki et al. 2011). Introduced Channel Catfish also are threatening the genetic integrity of at least one southwestern species, the Yaqui Catfish (*Ictalurus pricei*) (USFWS 1994), but hybridization between narrow range ictalurid endemics and non-native Channel Catfish and Blue Catfish is a threat to other species (Miller et al. 2005).

Introduced bullheads are also implicated in declines of native fishes. In California, the introduction of White Catfish into Clear Lake was associated with the decline of native

cyprinids (Carps and Minnows) (Dill & Cordone 1997) and the decline of the native Sacramento Perch (*Archoplites interruptus*) in Thurston Lake (McCarraher & Gregory 1970). Black Bullheads in Spain and Portugal feed on native and other exotic fishes, but the larger effects on the fish fauna are still unknown (Leunda et al. 2008). When Brown Bullheads were introduced into warm water lakes in British Columbia, populations of Threespine Sticklebacks (*Gasterosteus aculeatus*) disappeared (McPhail & Lindsey 1970). The Brown Bullhead is apparently a highly effective nest predator on the Threespine Stickleback (Wydoski & Whitney 2003). Mechanical removal may be effective for reducing non-native bullheads under certain circumstances. In the West Fork Gila River, New Mexico, a 10–12 person crew over 4–5 days annually significantly reduced abundance and biomass of bullheads over a six year period; however, gains in non-native

Table 15.2. Diversity, conservation status, and polytypy of the North American Catfishes, Ictaluridae. Numbers of species are given in parentheses after the taxonomic name. Groups are taken from Lundberg (1992; see Hardman & Page 2003 for *Ameiurus* and Grady & LeGrande 1992 for *Noturus*). Conservation status designations are followed by subscripts indicating F, United States Fish and Wildlife Service federal status; A, American Fisheries Society status (Jelks et al. 2008); and S, Southeastern Fishes Council status (Warren et al. 2000). Designations are E, Endangered; T, Threatened; V, Vulnerable; and X, Presumed Extinct.

Classification of Ictaluridae (50)	Conservation Status	Evidence of Polytypy?	Type of Evidence (references)
Ameiurus (7)			
Ameiurus natalis group (3)			
Ameiurus melas Black Bullhead		Y	mtDNA (Padhi 2010)
Ameiurus natalis Yellow Bullhead		Y	Morphology, mtDNA (Jordan 1877; Padhi 2013b)
Ameiurus nebulosus Brown Bullhead		Y?	Morphology (Hart 1952; Bailey et al. 1954)
Ameiurus catus group (4)			
Ameiurus brunneus Snail Bullhead	$V_{A,S}$	Y	mtDNA (April et al. 2011)
Ameiurus catus White Catfish		Y	mtDNA (Padhi 2012)
Ameiurus platycephalus Flat Bullhead	$V_{A,S}$	Y	mtDNA (April et al. 2011)
Ameiurus serracanthus Spotted Bullhead	$V_{A,S}$		
Ictalurus (10)			
Ictalurus furcatus group (3)			
Ictalurus balsanus Balsas Catfish	V_A		
Ictalurus furcatus Blue Catfish		Y	mtDNA (Padhi 2011)
Ictalurus meridionalis Southern Blue Catfish			
Ictalurus punctatus group (7)			
Ictalurus australis Pánuco Catfish	T_A		
Ictalurus dugesii Lerma Catfish	V_A		
Ictalurus lupus Headwater Catfish	T_A	Y	Morphology (Miller et al. 2005)
Ictalurus mexicanus Río Verde Catfish	V_A	Y	Morphology (Miller et al. 2005)
Ictalurus ochoterenai Chapala Catfish			
Ictalurus pricei Yaqui Catfish	$T_F E_A$		
Ictalurus punctatus Channel Catfish			
Pylodictus (1)			
Pylodictus olivaris Flathead Catfish		Y	mtDNA (Padhi 2014)
Noturus (29)			
Noturus flavus Stonecat		Y	Chromosomal, morphology, nuclear DNA, mtDNA (Taylor 1969; Legrande & Cavendar 1980; Burr & Warren 1986; Page & Burr 1991; Pflieger 1997; Hardman 2004; Faber et al. 2009; April et al. 2011)
Noturus exilis Slender Madtom		Y	Nuclear DNA, mtDNA (Hardy et al. 2002; Hardman 2004; April et al. 2011; Blanton et al. 2013)
Noturus funebris Black Madtom			
Noturus gilberti Orangefin Madtom	$T_{A,S}$		
Noturus gyrinus Tadpole Madtom		Y	Nuclear DNA, mtDNA (Hardman 2004)
Noturus insignis Margined Madtom		Y	Morphology, mtDNA (Bennetts et al. 1999; Hardman 2004; April et al. 2011)
Noturus lachneri Ouachita Madtom	$T_{A,S}$		
Noturus leptacanthus Speckled Madtom		Y	mtDNA (April et al. 2011)
Noturus nocturnus Freckled Madtom		Y	Nuclear DNA, mtDNA (Hardman 2004)
Noturus phaeus Brown Madtom		Y	mtDNA (April et al. 2011; Egge & Hagbo 2015)
Noturus rabida clade (18)			
Noturus albater Ozark Madtom		Y	mtDNA (April et al. 2011)
Noturus baileyi Smoky Madtom	$E_{F,A,S}$		
Noturus crypticus Chucky Madtom	$E_{F,A} T_S$		
Noturus elegans Elegant Madtom		Y	Nuclear DNA, mtDNA, morphology (Taylor 1969; Hardman 2004; April et al. 2011)
Noturus eleutherus Mountain Madtom		Y	mtDNA (Bennett 2009)
Noturus fasciatus Saddled Madtom	$V_{A,S}$		
Noturus flavater Checkered Madtom	$V_{A,S}$		
Noturus flavipinnis Yellowfin Madtom	$T_F E_{A,S}$		

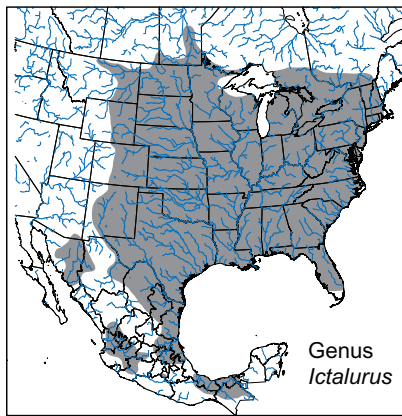| Classification of Ictaluridae (50)	Conservation Status	Evidence of Polytypy?	Type of Evidence (references)
Noturus furiosus Carolina Madtom	T_A V_S		
Noturus gladiator Piebald Madtom	V_A		
Noturus hildebrandi Least Madtom		Y	Nuclear DNA, mtDNA, morphology (Taylor 1969; Hardman 2004; Egge & Simons 2006; April et al. 2011; Egge et al. 2015)
Noturus maydeni Black River Madtom			
Noturus miurus Brindled Madtom		Y	Nuclear DNA, mtDNA (Hardman 2004; April et al. 2011; Egge & Hagbo 2015)
Noturus munitus Frecklebelly Madtom	$E\text{-}V_A$ T_S	Y	Morphology, mtDNA (Boschung & Mayden 2004; Egge & Simons 2006)
Noturus placidus Neosho Madtom	$T_{F,A,S}$		
Noturus stanauli Pygmy Madtom	$E_{F,A,S}$	Y?	mtDNA (Bennett et al. 2010)
Noturus stigmosus Northern Madtom	$V_{A,S}$		
Noturus taylori Caddo Madtom	$T_{A,S}$	Y	Allozymes (Turner & Robison 2006)
Noturus trautmani Scioto Madtom	E_F X_A		
Prietella (2)			
Prietella lundbergi Phantom Blindcat	E_A		
Prietella phreatophila Mexican Blindcat	$E_{F,A}$		
Satan (1)			
Satan eurystomus Widemouth Blindcat	$E_{A,S}$		
Trogloglanis (1)			
Trogloglanis pattersoni Toothless Blindcat	E_A		

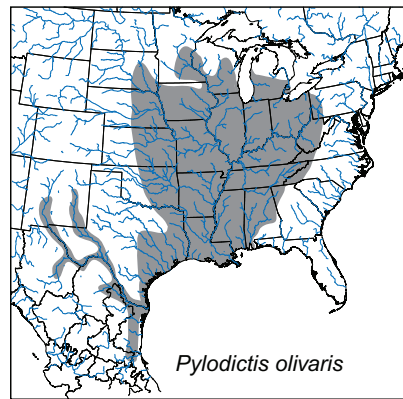*Figure 15.11.* Geographic range of *Ictalurus*.
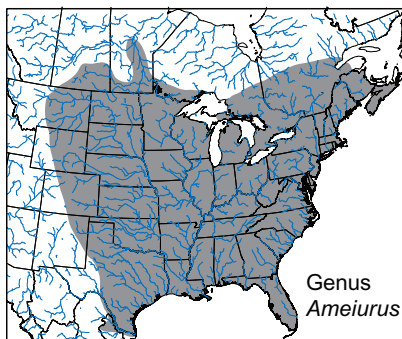

Figure 15.12. Geographic range of *Pylodictis*.
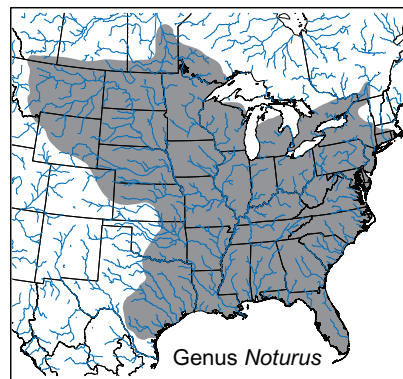

Figure 15.13. Geographic range of *Ameiurus*.
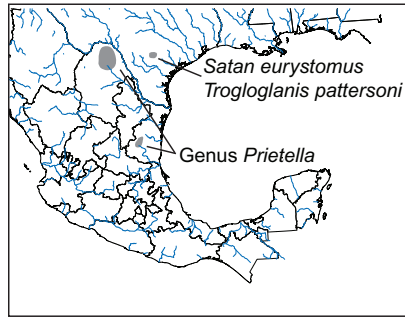

Figure 15.14. Geographic range of *Noturus*.

removal were offset by immigration of non-native Flathead Catfish from other reaches (Propst et al. 2015).

The Flathead Catfish has had measurable negative impacts on fisheries and native fishes with well-documented effects in Atlantic Slope rivers where the species was introduced and is established. A genetic study based on a single marker indicated that introduced Flathead Catfish populations in Virginia, North Carolina, and South Carolina (James, Neuse, Cape Fear, and Edisto Rivers) came from Mississippi River tributaries, and introduced populations in Georgia (Altamaha and Satilla Rivers) likely came from the Alabama River (Padhi 2014). In an attempt to control stunted fish populations, Flathead Catfish were introduced into a small Virginia reservoir in 1990 and 1994 and afterward the harvest of Brown Bullheads decreased from 2,285 in 1992 to just 25 in 1998 (Odenkirk et al. 1999). The Flathead Catfish introduced to Atlantic Slope rivers is associated with declines in a Redbreast Sunfish (*Lepomis auritus*) sport fishery as well as in populations of Channel Catfish and native bullhead species. This prompted removal efforts via liberal catch limits and persistent electrofishing of non-native Flathead Catfish in the Satilla River, Georgia (GDNR 2009; Sakaris et al. 2006), which have been effective at maintaining low Flathead Catfish biomass (Bonvechio et al. 2011). Even so, devotion of the resources to maintain such efforts in perpetuity is highly questionable. Similar declines in Redbreast Sunfish occurred with introduction of the Flathead Catfish in the Black and Lumber Rivers, North Carolina (Ashley & Rachels 2000; Sakaris et al. 2006). Likewise, native bullheads declined severely after Flathead Catfish were established in the Cape Fear River, North Carolina (Guier et al. 1981; Moser & Roberts 1999), Altamaha River, Georgia (Thomas 1995; Weller & Robbins 1999), and Choctawhatchee River, Florida (Dobbins et al. 2012). Moser & Roberts (1999) suggested that the native ictalurids had been extirpated in their study reach by Flathead Catfish. Once native bullhead populations were depressed in these

rivers, Flathead Catfish, being opportunistic predators (Pine et al. 2005), apparently shifted their diet to native Suckers (Catostomidae) and Sunfishes (Centrarchidae) (Weller & Robbins 1999), similar to patterns in other rivers (Bart et al. 1994; Thomas 1995; Walker et al. 2015). A relatively newly established, but burgeoning, population of Flathead Catfish in the Susquehanna and Delaware Rivers threatens native fishes and restoration efforts for anadromous species (Brown et al. 2005b).

Non-native Flathead Catfish can grow faster and have lower mortality rates in some Atlantic Slope rivers, relative to native populations in Gulf Slope rivers, and have potential to sustain growth for extended periods (Kwak et al. 2006; Sakaris et al. 2006), further diminishing native fishes. However, population monitoring of some of the oldest introduced populations (30+ years) in Georgia (Flint and Altamaha Rivers) revealed rapid swings in abundance and a recurring boom-and-bust cycle (Kaeser et al. 2011).

In the Gila River, New Mexico, production of non-native Flathead Catfish and Common Carp (*Cyprinus carpio*) apparently drove a 91% decrease in native fish production from 2008–2011 (Whitney et al. 2014). Consumptive demand of non-native Flathead Catfishes was equivalent to about 33–100% of the production of native fishes in some habitats, particularly where larger Catfishes were found, but was much less in other areas (Hedden et al. 2016).

Based on this evidence, concern exists among some managers that *Pylodictis* could cause declines in rare native species (e.g., Atlantic Sturgeon predation; Flowers et al. 2011); however, Flathead Catfish likely prey on fishes based on encounter rates, making rare fishes less likely to be eaten and lessening the threat to some extent (Pine et al. 2005; Baumann & Kwak 2011). Native Sunfishes and ictalurids appear to be most vulnerable to population declines from introduced Flathead Catfish, which are among the least gape-limited fishes in North America (Slaughter & Jacobson 2008). From consideration of these few examples, introduced ictalurids clearly can have detrimental effects on native fishes and fisheries.

PHYLOGENETIC RELATIONSHIPS

Before analysis of DNA or nuclear-encoded allozyme data, anatomical structures were used almost exclusively to define ictalurid taxonomic groups. As a result, much literature is available on the general morphology of ictalurids, including the features that distinguish them from other Catfish families. Living ictalurids share three derived traits:

massive jaw adductor muscles originating on the skull roof; development of a unique subpterotic process of the supracleithrum; and loss of palatal teeth (Grande & Lundberg 1988; Lundberg 1992). Two derived conditions of the pelvic structure support monophyly of the Ictaluridae, including the fossil genus †*Astephus* (Lundberg 1992): modally ≥7 pelvic-fin rays; and lack of a pelvic girdle ischiac process that is present in basal Catfishes and other Ostariophysi.

Ictaluridae are one of about 36 families of Catfishes placed in the order Siluriformes. In fact, >478 genera and 3,093 described species are placed in Siluriformes (Ferraris 2007), and their phylogenetic relationships have been studied since at least the late 1890s. Using morphology in a phylogenetic context, Fink & Fink (1996) concluded the closest living group to Siluriformes was the Gymnotiformes (American Knifefishes). A refined result emerged from extensive molecular phylogenies using multiple genes and numerous taxa of Ray-finned and Spiny-rayed Fishes (Near et al. 2012b, 2013; Betancur-R. et al. 2013ab). Those analyses resolved a close relationship between Catfishes, Characins (Characiformes), and American Knifefishes. In a well-supported tree, the siluriforms were sister to a gymnotiform + characiform clade forming the superorder Characiphysae (Betancur-R. et al. 2013ab). The siluriforms are estimated to have diverged from their most recent common ancestor in the Early Cretaceous about 106.1 mya (89.9–123.0 mya, 95% highest posterior density interval; Near et al. 2012b).

Similarly, molecular analyses, including those just mentioned, appear to be converging on the sister group to the Ictaluridae although molecular results do not necessarily agree with morphological studies. In a Wagner tree of ostariophysan fishes, including only seven siluriform taxa, the genus *Ictalurus* was sister to the genus *Bagarius* (Sisoridae, Sisorid Catfishes, of Asia) (Fuiman 1984). Lundberg (1992) suggested that elements of the Asian Bagridae (Bagrid Catfishes) were sister to Ictaluridae, although morphological synapomorphies are lacking for this clade. Numerous molecular phylogenies, however, identify the Asian Armorhead Catfishes (Cranoglanididae, single genus *Cranoglanis*) as sister to Ictaluridae with strong statistical support (Hardman 2005; Peng et al. 2005; Sullivan et al. 2006; Near et al. 2012b; Betancur-R. et al. 2013ab). The relationship of the cranoglanidid + ictalurid clade to other siluriforms is to date unresolved other than placement with a large number of other families in the well-supported Siluroidei clade (Betancur-R. et al. 2013ab).

The only reasonably modern phylogenies of Ictaluridae are those of Taylor (1969), Lundberg (1992), Hardman (2002), and Hardman & Hardman (2008). None of these include all extant taxa, and all used distinctively different data sets and methodologies. Taylor's tree (Fig. 15.16) was not phylogenetically based and was implicitly morphological. Lundberg's tree (Fig. 15.17) included fossils and was based on morphology and an explicit phylogenetic genealogical and chronological methodology.

In molecular analyses, Hardman (2002) and Hardman & Hardman (2008) used nucleotide sequences from two genes, cytochrome <u>b</u> and the nuclear recombination activation gene 2 (RAG2), combined with statistically based models to analyze gene-tree data (Fig. 15.18). Using a fossil-calibrated approach to estimate divergence times, Hardman & Hardman (2008) produced a chronology in which the modern ictalurid lineages originated early in the Eocene (roughly 50–55 mya) although confidence intervals around most nodes were wide (Fig. 15.18). The estimates indicated most of the extant species in the family originated during the Oligocene and Miocene (about 33.9–5.3 mya). Their study had good taxon sampling, excluding only four *Noturus* (Chucky Madtom, *Noturus crypticus*; Piebald Madtom, *N. gladiator*; Pygmy Madtom; Scioto Madtom, *N. trautmani*), seven *Ictalurus* species (Panuco Catfish, *I. australis*; Balsas Catfish, *I. balsanus*; Lerma Catfish, *I. dugesii*; *I. meridionalis*; Rio Verde Catfish, *I. mexicanus*; Chapala Catfish, *I. ochoterenai*; and Yaqui Catfish), and cave-dwelling species due to lack of genetic material for the two genes used.

In perhaps the most extensive phylogenetic treatment of ictalurids, Arce-H. et al. (2016) performed a combined analysis of morphological characters and molecular sequences for a total evidence set of trees that included both extant and extinct species. In total, 209 morphological traits and one nuclear and four mitochondrial genes were used in a parsimony analysis. The results contradict what was considered established knowledge as synthesized in this chapter. Major conclusions were (1) the fossil clade *Astephus* occurred outside Ictaluridae and not as a sister taxon; (2) Ictaluridae is a crown clade composed of seven living genera and ≥16 extinct species; (3) the four subterranean species formed a single clade and were the sister taxon of all ictalurids, and these results were maintained whether fossils were included or not; (4) *Ameiurus* is sister to a clade of *Ictalurus* + (the monotypic *Pylodictis* + *Noturus*); (5) Cranoglanididae is not the sister group of Ictaluridae as previously proposed; and (6) the sister group of Ictaluridae is a clade formed by extant Schilbeidae (Asian Schilbeid Catfishes), Bagridae (Bagrid Catfishes, Africa and Asia), Siluridae (Sheatfishes, Eur-
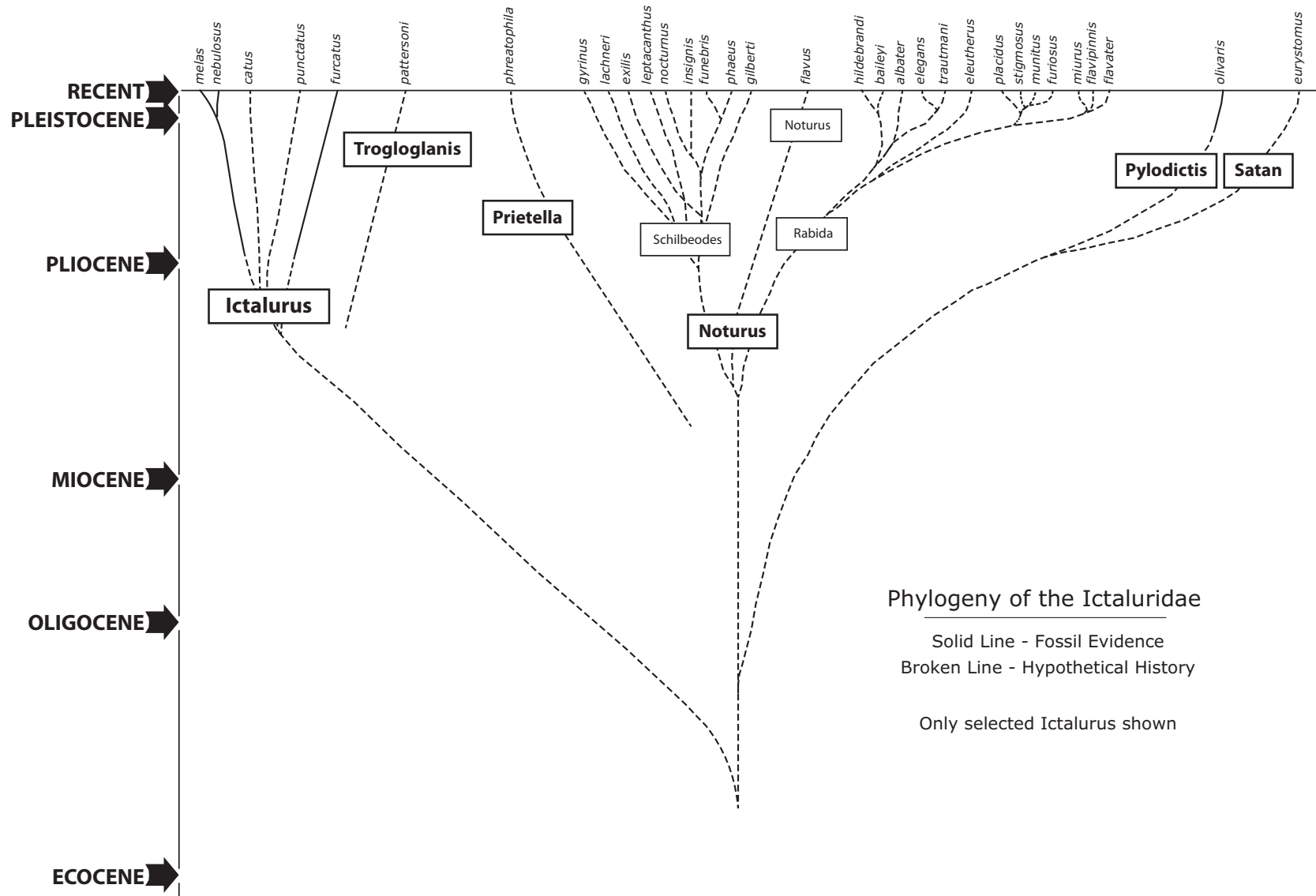
Figure 15.16. Early noncladistic phylogeny of North American Catfishes (Ictaluridae) (redrawn from Taylor 1969).
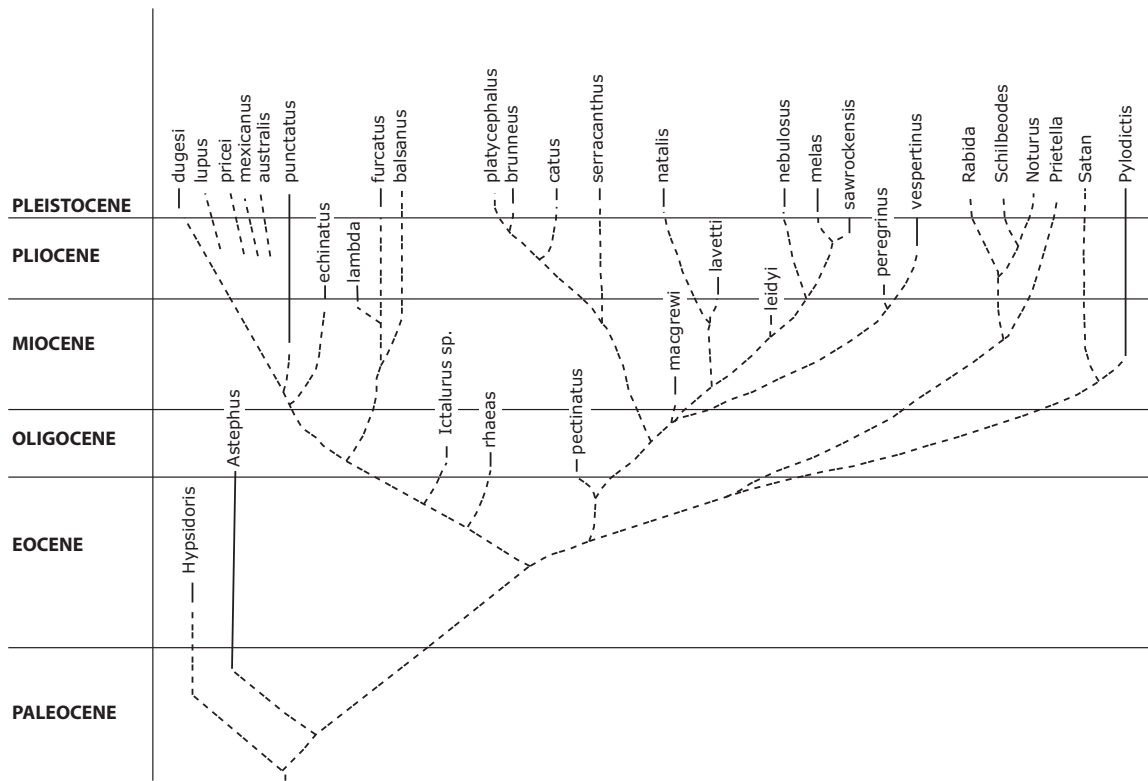
Figure 15.17. Phylogeny of North American Catfishes (Ictaluridae) (redrawn from Lundberg 1992).

asia), and Plotosidae (Eeltail Catfishes, Indian and western Pacific Oceans) (Fig. 15.18). Other findings removed the fossil genus *Astephus* from Ictaluridae and placed them in their own family, Astephidae (Arce-H. et al. 2016). In addition, a *rabida* clade of *Noturus* is maintained with *elegans* and *furiosus* groupings still recognizable (Fig. 15.18).

Fossil evidence for the timing of ictalurid diversification was examined (Fig. 15.18). Some of the previously published clock-based age estimates are close to the minimum ages of clades resolved by Arce-H. et al. (2016). The explanation for diversification times is lengthy, highly technical, and depends on several assumptions about known-age fossils, ghost lineages, molecular clocks, and other matters and as such is not covered here.

Among genera, the genus *Noturus* has received the greatest phylogenetic attention with several detailed studies (Taylor 1969; LeGrande 1981; Grady & LeGrande 1992; Bennetts et al.1999; Hardman 2004; Near & Hardman 2006; Egge & Simons 2006, 2009, 2011). The genus *Ameiurus* (Hardman & Page 2003), the cave-dwelling *Prietella* (Figs. 15.7 and 15.8), and Wilcox et al. 2004 have also received specific attention. The concern here is only with

the relationships of the genera of Ictaluridae and the reader is referred to these additional studies for details of relationships among madtoms and the other groups based on multiple data sets (i.e., morphology, chromosomes, enzyme products, nucleotide sequences).

At the familial and generic levels, the most consistent conclusions manifested in all trees, despite different data sets and methods, include (1) close affinity of North American Catfishes with the large-river, Asian endemic Armorhead Catfishes; (2) monophyly of the family Ictaluridae; (3) monophyly of the currently recognized extant genera within Ictaluridae; (4) probable sister-group relationships between *Pylodictis + Satan* and *Prietella + Noturus*; and (5) either *Ameiurus* or *Ictalurus* as basal lineages. The rarity of the blindcats has precluded their widespread inclusion into trees that use enzyme products or nucleotide sequences, except for *Prietella* (Wilcox et al. 2004). Because of this, it is difficult to adequately compare the molecular phylogenies (e.g., Hardman 2002) with the taxonomically all-inclusive morphological trees (Lundberg 1992; see Egge & Simons 2009).

Future systematic studies might concentrate on the Mexican species of *Ictalurus*, all of which are extremely

poorly known in both a descriptive and biological sense. The Brown Bullheads and Black Bullheads need better clarification of their distinctiveness throughout their broad sympatric range, and genetic work provides some indication of cryptic lineages in the Black Bullhead and other *Ameiurus* spp. (Padhi 2010; April et al. 2011; see genetics section). Many species-level taxonomic problems remain in *Noturus* (Table 15.2; see Burr & Stoeckel 1999). Egge & Simons (2009) suggest taxonomic revisions to the genus by recognizing strongly supported clades instead of subgenera. The subgenera *Noturus* (Stonecat, *N. flavus*) and *Schilbeodes* are not supported by phylogenetic work, but the *rabida* clade has strong support as do six other clades, including four within *rabida* (Egge & Simons 2009). Almost any data on the blindcats has proved beneficial, and fresh tissue samples representing the three genera are highly desirable. Little is published on the morphological variability or phylogeography of *Pylodictis*, although a recent study using a single mitochondrial gene found two to four distinct groups (Padhi 2014; see genetics section).
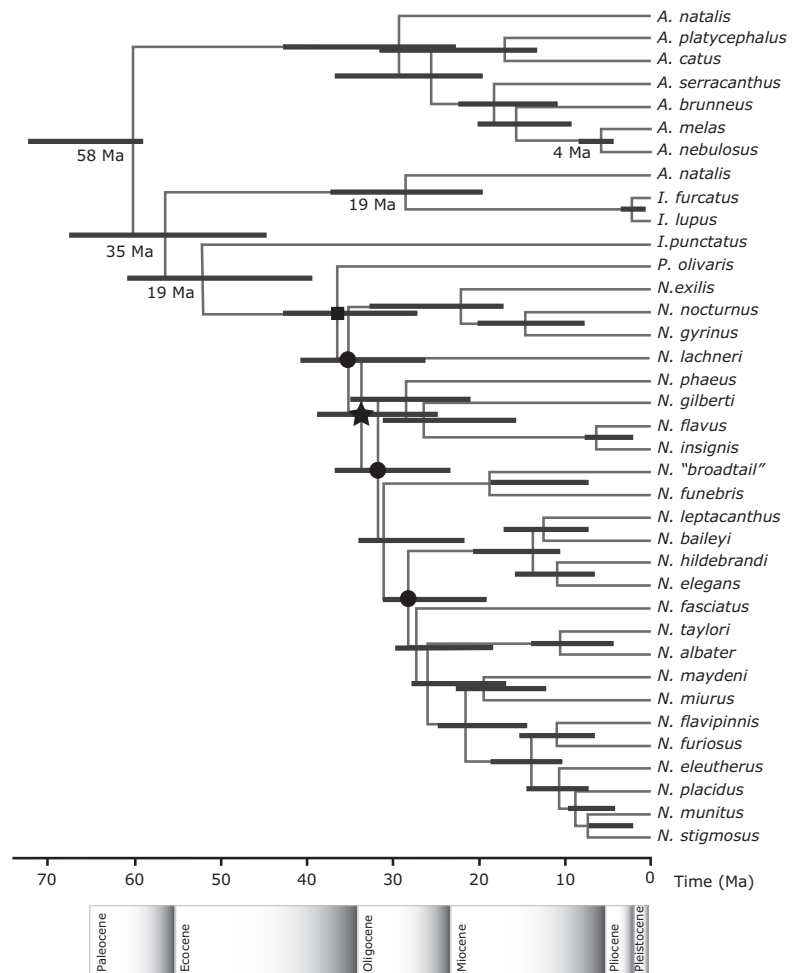
FOSSIL RECORD

Major reviews of fossil freshwater fishes in North America indicate that at least 16 extinct species of Catfishes and one extinct genus (†*Astephus*) with two species occurred on the continent (Lundberg 1975; Smith 1981; Cavender 1986; Gilbert 1998; Grande 2001; Lundberg & Luckenbill 2012; Arce-H. et al. 2016). In fact, all extant and extinct species of Ictaluridae are autochthonous to North America. Until at least the Pleistocene (1.8–0.011 mya), ictalurids were part of the fauna of the Pacific Northwest of the United States, where they no longer occur as natives (Lundberg 1992). Ictalurid history spans much of the Cenozoic era (commencing 65.5 mya) beginning by at least the Late Paleocene (37.2–33.9 mya) (Lundberg 1992). The genus †*Astephus* is known only from fossils and has a minimum age of Late Paleocene. The genus *Ictalurus* has ≥4 extinct species, and the genus *Ameiurus* has nine extinct species (e.g., Fig. 15.19) with both genera having a minimum age of Early Oligocene (33.9–28.4 mya). The genus *Pylodictis* dates to at least the Middle Miocene (20.4–11.6 mya) and younger deposits. In-

terestingly, contemporary specimens of *P. olivaris* and *I. punctatus* show no detectable osteological differences from fossil specimens of those species from the Middle Miocene (Lundberg 1992). Discovery in eastern Maryland of a Miocene species of *Ictalurus* (†*I. countermani*) extends the known native range of *Ictalurus* to the mid-Atlantic Slope and indicates extirpation of the genus from that region before the recent transplantation of *I. punctatus* and *I. furcatus* (Lundberg & Luckenbill 2012). The most diverse genus, *Noturus*, has left a meager fossil record and is known mostly from the Late Pleistocene (0.126–0.011 mya) in Kansas, Nebraska, and South Dakota. Divay & Murray (2013) assigned fossil dorsal- and pectoral-fin spines from the mid-Miocene age Wood Mountain Formation (about 16.3–13.6 mya) in Saskatchewan to *Noturus*. The site yielded 16 fish taxa, including an array of other warm water fish taxa such as the genera *Ameiurus*, *Ictalurus*, *Pomoxis*, and *Lepisosteus* as well as representative cypriniforms and an amiine. Fossils of the artesian well and cave-dwelling blindcat genera, *Satan*, *Troglo-*
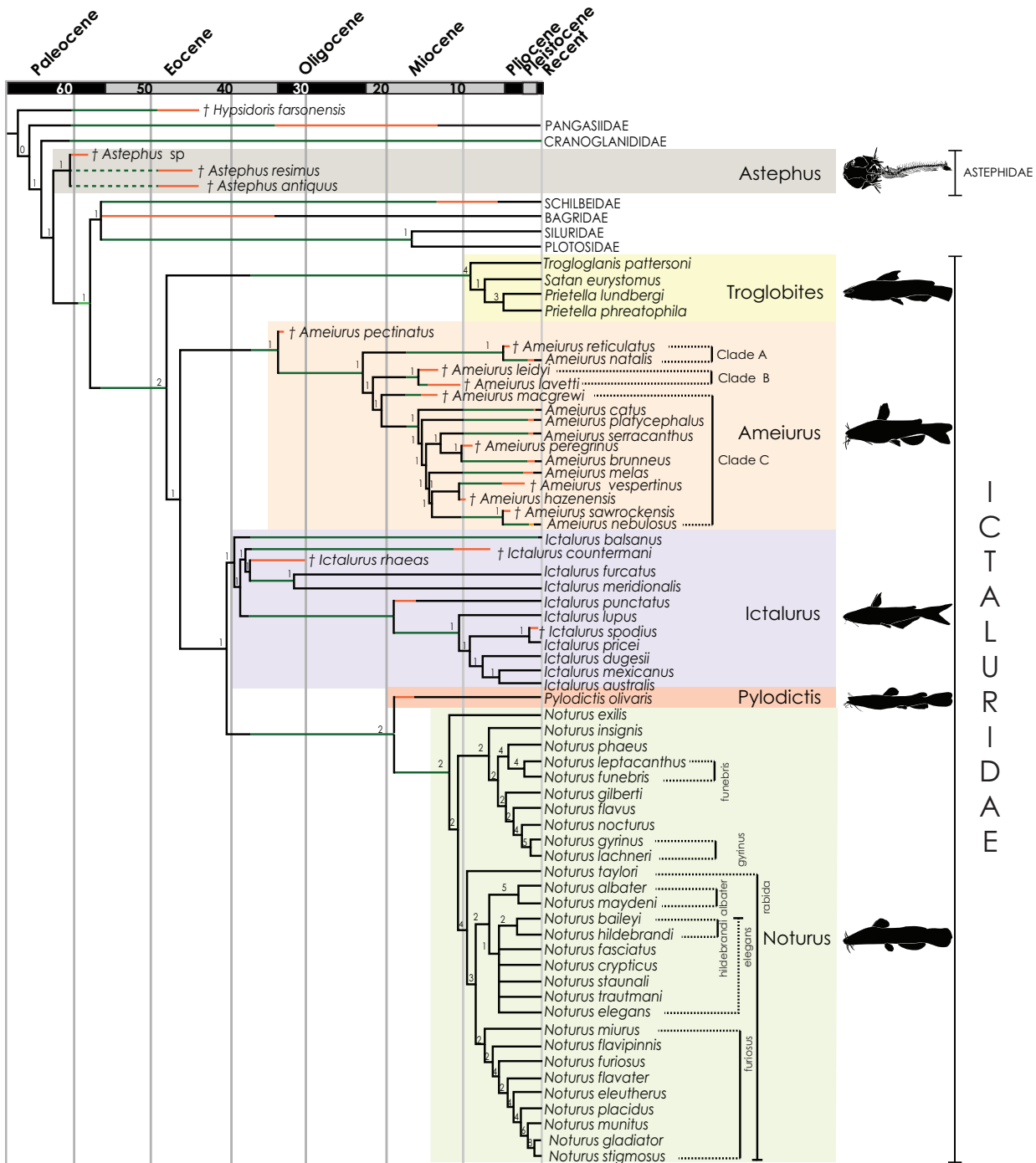
Figure 15.18. (upper) Molecular phylogeny of North American Catfishes (Ictaluridae). Maximum credibility chronogram from the combined samples of the stationary posterior distributions estimated in BEAST MCMC analysis. Branch lengths are in units of time, and error bars indicate the 95% highest posterior densities. Nodes labeled with symbols are the locations of significant (p<0.5: filled circles and star) and nearly significant (p<0.07: filled square and star) diversification rate shifts in END-EPI and SymmeTREE, respectively. Lower bounds for the five constrained nodes are labeled in million years ago (Ma) (see Hardman & Hardman 2008 for details). *(lower)* Strict consensus of 24 trees from a maximum parsimony analysis of a combined data set (CI = 0.346, RI = 0.530) mapped to geological time. Black lines indicate branching relationships, orange lines indicate known stratigraphic ranges of fossil species, green lines indicate range extensions and ghost lineages implied by the phylogenetic relationships, and dotted green lines indicate range extensions for potential ghost lineages where there is lack of phylogenetic resolution. Values on the nodes correspond to Bremer support (see Arce-H. et al. 2016 for details) *(upper,* redrawn from Hardman & Hardman 2008; *lower,* redrawn from Arce-H. et al. 2016).

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Figure 15.19. Fossil of †*Ameiurus macgrewi*, dorsal view of complete fish, 125 mm SL (modified from Lundberg 1975 as †*Ictalurus macgrewi*; used with permission of John Lundberg).

glanis, and *Prietella*, are unknown. Sites in the Tennessee River system yielded fossil evidence of *Ameiurus*, *Ictalurus*, *Noturus*, and *Pylodictis*, including species extirpated from the main channel due to impoundment (e.g., *Noturus*) and the Ozark endemic Checkered Madtom, *Noturus flavater*, suggesting a broader Pleistocene distribution with subsequent range restriction (Jacquemin et al. 2016). Grande & Lundberg (1988) provide a detailed analysis of †*Astephus* (two species), the presumed sister group to ictalurids, and its relationship to extant ictalurids. Over 200 individual specimens of that genus, representing two species, are now known, and some reached ≥600 mm TL (23.6 inches) (Grande 2001); †*Astephus* co-occurred with other living ictalurid genera. Arce-H. et al. (2016) concluded that *Astephus* is not an ictalurid, and placed the two described species in their own family, Astephidae.

MORPHOLOGY

General Morphology

Body shape in ictalurids is variable but usually is round anteriorly and laterally compressed posteriorly; the head is usually moderately to highly depressed anteriorly; and all species lack scales but are covered with thick skin (Jenkins & Burkhead 1994; Boschung & Mayden 2004).

Based on detailed comparative genome analysis of scaled and scaleless fishes, combined with scale regeneration experiments, loss of the secretory calcium-binding phosphoproteins (which are dentin, bone, milk, and salivary related proteins) may explain the evolutionary loss of scales in Catfishes (Liu et al. 2016). The mouth is usually inferior, occasionally terminal. All ictalurids possess eight barbels, two dorsally (nasal position), one each at the corner of the mouth (maxillary), and four on the chin (mental) (Figs. 15.3–15.5, 15.7, and 15.9). Possession of nasal barbels distinguishes all ictalurids from ariids (Sea Catfishes). Stout spines are the primary supporting elements at the origin of the dorsal fin (weakly developed in *Prietella*; Miller et al. 2005) and pectoral fins, the spines usually with strong serrae, sometimes developed anteriorly and posteriorly (Figs. 15.20–15.22); posterior to the spine these fins are supported by rays. The pectoral fins are jugular, and low on the body, being nearly ventral in position. The pelvic fins, positioned posteriorly on the abdomen and low on the body, and the single, usually relatively long anal fin, are supported by rays not spines. All species possess an adipose fin on the dorsal caudal peduncle (between the dorsal and caudal fins), which is fleshly and lacks rays, and may be adnate (broadly based and connected to the caudal peduncle throughout its length) or adnexed (connected to the caudal peduncle only anteriorly) (Boschung & Mayden 2004). The caudal fin varies from deeply forked (*Ictalurus* spp.) to emarginate (most *Ameiurus* spp.) to broadly rounded or truncate (*Noturus* spp.) to rounded, truncate, or slightly emarginate (*Pylodictis olivaris*).

Ictalurids are usually drab-colored or colorless (Figs. 15.2–15.5 and 15.9). Pigment patterns that do develop are in the shape of spots, saddles over the back, or strong mottling (Fig. 15.23). Intensity of pigment varied in laboratory-reared Brown Bullheads, and a process of depigmentation was observed in two individuals, probably a result of captivity (Rasquin 1949). Albinism occurs in several species, including *Noturus* (*N. gyrinus*, Stasiak & Evans 1978; *N. flavus*, Platania et al. 1986), *Ictalurus* (*I. punctatus*, Aitken 1937; Menzel 1944; *I. furcatus*, Rutherford et al. 1990), and *Ameiurus* (*A. catus*, McLane 1950; Britton & Davies 2006; *A. natalis*, Marshall 1947).

The external features of ictalurids, including color, body shape, and meristic and mensural characters, are well described (e.g., Taylor 1969; Yerger & Relyea 1968) in most state fish books (e.g., Jenkins & Burkhead 1994) and are key characters for identification schemes in field guides (e.g., Page & Burr 2011; Gilbert & Williams 2002). Devel-
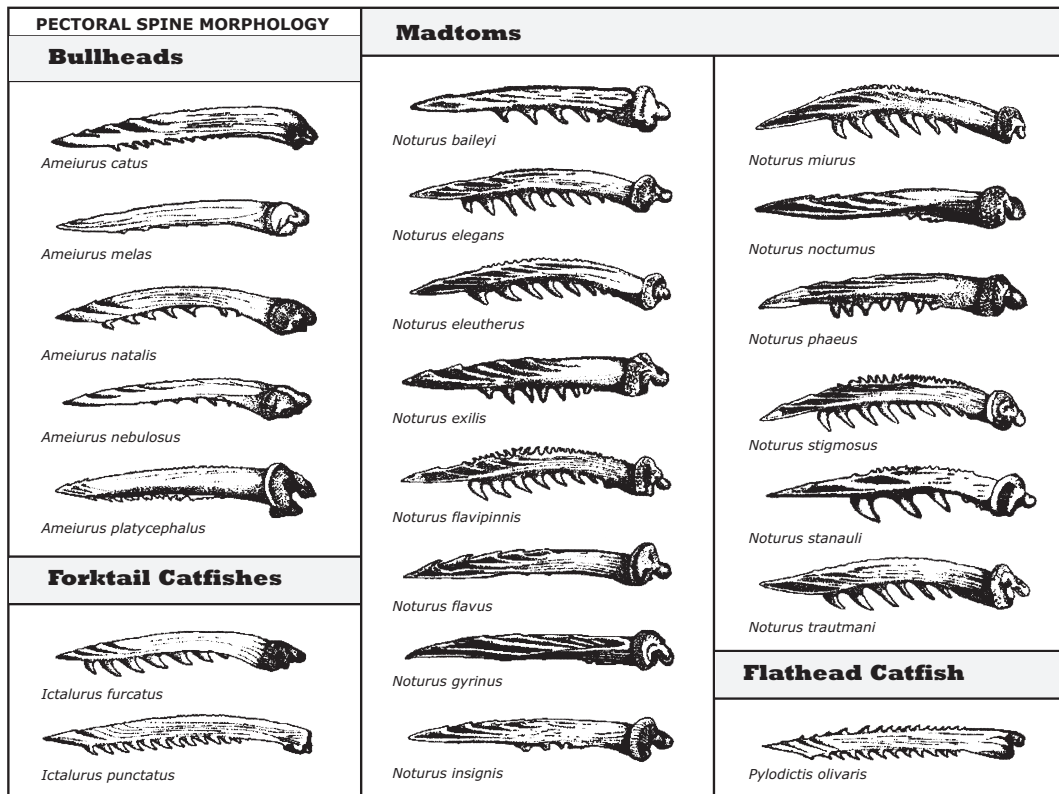
PECTORAL SPINE MORPHOLOGY

Bullheads

Ameiurus catus

Ameiurus melas

Ameiurus natalis

Ameiurus nebulosus

Ameiurus platycephalus

Forktail Catfishes

Ictalurus furcatus

Ictalurus punctatus

Madtoms

Noturus baileyi

Noturus elegans

Noturus eleutherus

Noturus exilis

Noturus flavipinnis

Noturus flavus

Noturus gyrinus

Noturus insignis

Noturus miurus

Noturus noctumus

Noturus phaeus

Noturus stigmosus

Noturus stanauli

Noturus trautmani

Flathead Catfish

Pylodictis olivaris

Figure 15.20. Representative pectoral spines from all genera of North American Catfishes (Ictaluridae) (redrawn from Simon & Wallus 2004).

opment of ictalurid larvae and their essential anatomical features are shown and discussed for *Ictalurus* (Saksena et al. 1961; Grande & Shardo 2002); *Ameiurus* (Armstrong & Child 1962); and *Noturus* (Mayden & Burr 1981). Cloutman (1979) provided a key to nine species of Catfish yolk-sac larvae, based largely on characters used to identify adults. A key to early life history stages of ictalurids in the Ohio basin is well illustrated (Simon & Wallus 2004). A thorough atlas of the anatomy and histology of the major organ systems of the Channel Catfish is available and recommended especially for details of internal organs and standard skeletal features (Grizzle & Rogers 1976).

Blindcat Morphology

The blindcats (genera *Prietella*, *Satan*, and *Trogloglanis*) are depigmented, eyeless, and apparently three species lack air bladders (Fig. 15.7); their lateral line systems are variously developed, being rather degenerate in *Prietella* (Langecker & Longley 1993; Walsh & Gilbert 1995). All four species are relatively small, ≤137 mm TL (5.4 inches), and most individuals are <80 mm TL (3.1 inches) (Longley & Karnei 1979).

Unprecedented detail is available on the external and internal anatomy of these unusual fishes (Langecker & Longley 1993; Walsh & Gilbert 1995). Weakly ossified skeletons, reduced muscles, large adipose deposits, small body size, reduction in brain centers associated with eyes, and loss of the pineal organ are some of the unusual features.

Gonad Morphology

The gonads of ictalurids are distinctive and allow for easy determination of sex on careful examination; both structures are paired. Males have a lobulate testis (Sneed & Clemens 1963; Fig. 15.24), and the ovaries of females usually have small latent oocytes even in tiny young. The genital papilla shapes of males and females are different and can be used to sex individuals externally, especially during the spawning and nesting season (Fig. 15.25).

Pectoral Myology

The rather complex pectoral muscle morphology and scaling relative to the manipulation of the pectoral spines and rays is detailed for *Ameiurus* (two species), *Ictalurus*
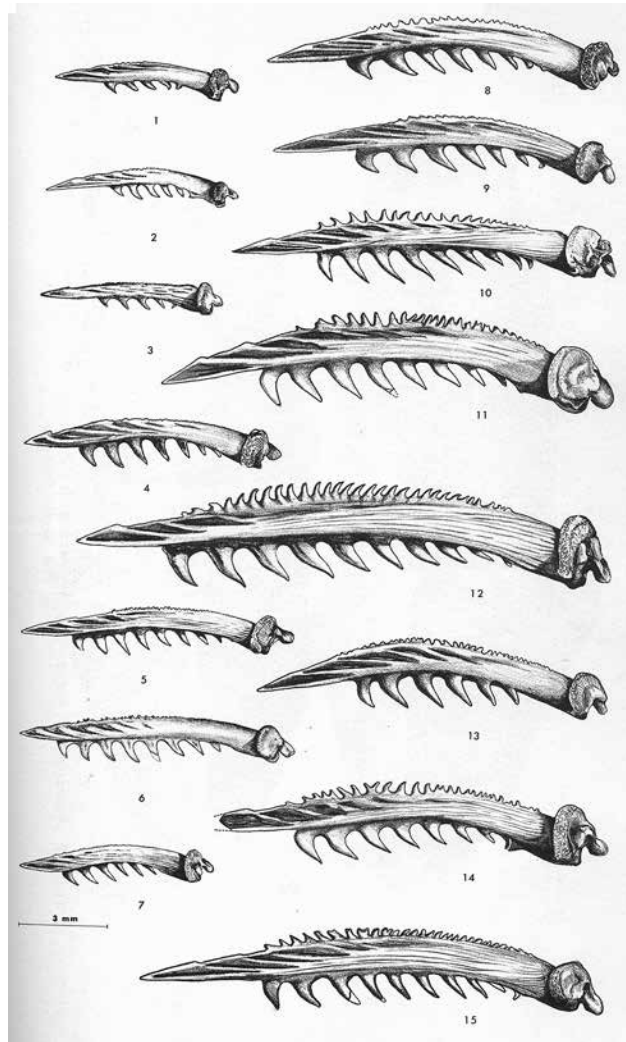
Figure 15.21. Representative pectoral spines from *Noturus* (from Taylor 1969; drawing is from a publication of the U.S. National Museum and is in the public domain).

Figure 15.22. Fossil North American Catfish (Ictaluridae) pectoral spines. *Ictalurus vespertinus*, 4 pectoral spines, 26 mm, 30 mm, 30 mm, 36 mm length from left to right (redrawn from Lundberg 1975).

(2 species), *Noturus insignis* (Margined Madtom), and the Flathead Catfish (Miano et al. 2013) (Figs. 15.26–15.31). In Catfishes the pectoral muscles of the rays appear to be evolutionarily conserved as in many teleosts, but the muscles of the first spine have changed considerably. Now a separate abductor, likely the major mediator of spine locking, and adductor muscles are present as well as arrector muscles that elevate and depress the spine, and these arrectors appear to be involved in unlocking, binding, and stridulation (see pectoral spine locking and sound production subsection, this section). Except for the Flathead Catfish, the percentage weight for total spine muscles was significantly higher than the percentage weight for ray muscles in all the species examined (Fig. 15.32). This differentia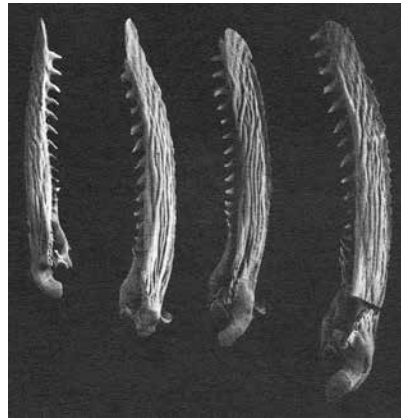l suggests selection pressure for spine abduction in ictalurids, which is not surprising given the defensive and sound production roles of the spine. The larger mass of the ray musculature relative to the spine musculature in the Flathead Catfish may be related to its living in high-flow habitats where pectoral adduction would help maintain position (Miano et al. 2013).

Pectoral Spine Locking and Sound Production

Ictalurids, like some other Catfishes, can lock the pectoral spine in place and produce stridulatory sounds with the spine. The pectoral spine can be locked into place by ventrolateral musculature torquing about its long axis and causing the spine to be bound with the pectoral girdle (reviewed by Fine et al. 1999; see also pectoral myology subsection, this section). Binding or locking occurs spontaneously when the spine is fully abducted. Wild Channel Catfish have longer and heavier pectoral spines and heavier pectoral girdles than domesticated individuals (Fine et al. 1997, 2014). This difference could result from changes in selection pressure (lower predation pressure, selection for fast growth or large size) over many generations or from epigenetic effects (phenotypic plasticity) in which genes for spine growth are turned on in the presence of predators (Fine et al. 2014). An experiment with predator exposure did not support the epigenetic hypothesis, although the experiment could not distinguish between relaxed predation pressure and inadvertent selection for smaller pectoral spines and girdles during domestication (because pectoral spine-girdle size is not considered in breeding stock selection) (Fine et al. 2014).

Stridulation sounds are produced during spine abduction when ridges on the ventrolateral surface of the spine's dorsal process contact the rough centrolateral wall of the spinal fossa. Sounds consist of short duration, wide frequency band pulses (one group/fin sweep) that vary in frequency, ampli-
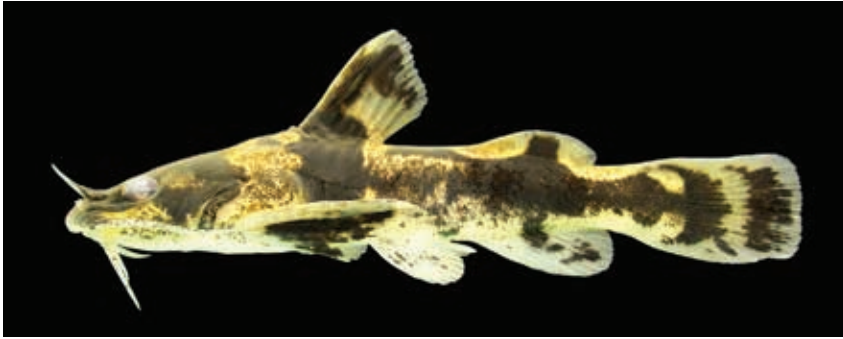
Figure 15.23. The Piebald Madtom, *Noturus gladiator*, is exemplary in illustrating an extreme mottling pattern in North American Catfishes (Ictaluridae) that presumably allows the species to lie cryptically on the bottom of lowland, upper Gulf Coastal Plain streams, like the Wolf River, Fayette County, Tennessee, where this specimen was captured (courtesy of Matt Thomas).
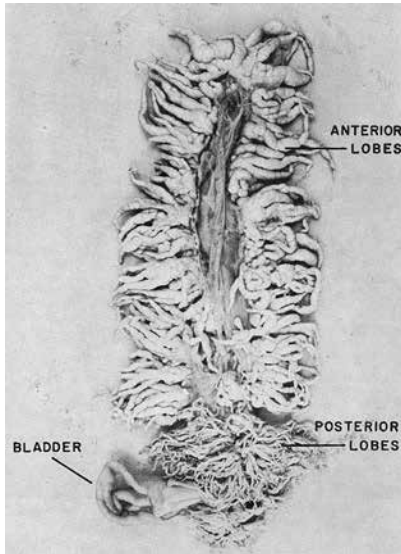

Figure 15.24. The lobulate testis of North American Catfishes (Ictaluridae) from the exemplar, Blue Catfish, *Ictalurus furcatus* (from Sneed & Clemens 1963; used with permission of the American Society of Ichthyologists and Herpetologists).

Figure 15.25. The genital papillae of both sexes (female left, male right) of the Channel Catfish, *Ictalurus punctatus*, used for sexing adults externally during the spawning season (from Grizzle & Rogers 1976; used with permission of Auburn University, Alabama Agricultural Experiment Station).

tude, duration, and repetition rate. The pectoral girdle, not the swim bladder, is the primary acoustic radiator. Until recently, the exact mechanism of sound pulse generation was not completely known. High-speed video and sound recording (Mohajer et al. 2015) revealed that in Blue Catfish sound is produced by a slip-stick mechanism with rapid jerk movements invisible to the naked eye. This is analogous to a bow playing a stringed instrument in which the bow (ridged dorsal process of pectoral spine) sticks to the string (rubbing surface of cleithrum) until the force exceeds friction causing vibration of the string and instrument (pectoral girdle). This mechanism was previously described only in invertebrates.

Catfishes are presumed to produce disturbance and stress sounds both underwater and while held in the air. Ictalurids only produce stridulatory sounds and do not have sonic swim bladder muscles as seen in other Catfish families. In Channel Catfish, stridulation sounds are probably distress signals and not warning sounds to potential predators. Evidence in the Blue Catfish, however, suggests that pectoral stridulatory sounds are optimized for transmission in water and could serve anti-predator or intraspecific communication functions (Gharamani et al. 2014). Stridulatory sounds in other Catfish clades may be associated with agonistic and courtship behaviors (e.g., Pruzsinszky & Ladich 1998; Katz et al. 2010). The Brown Bullhead is the only other ictalurid, besides the Channel and Blue Catfishes (Fine et al. 1999), that has been studied in depth for spine locking and sound production (Kleerekoper & Roggenkamp 1959; Weiss et al. 1969; Rigley & Muir 1979).

Other Skeletal Anatomy

Kindred (1919) and Gregory (1933) were among early authors that figured a skull of *Ameiurus* and *Ictalurus*, respectively, and alluded to the well-known fact that the underside of the skull of many Catfishes bears a certain resemblance to a crucifix (Figs. 15.33 and 15.34). Gregory (1933:196) stated that "the crown is formed by the opposite tripus of the Weberian apparatus. The arms of the cross are formed by the transverse processes of the complex vertebrae. The
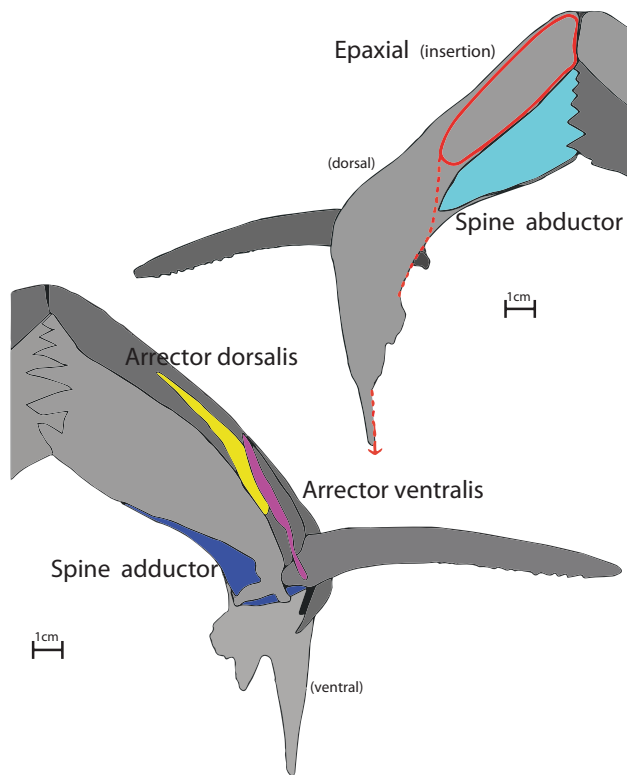
Figure 15.26. Illustration of the pectoral girdle of the Blue Catfish, *Ictalurus furcatus* (dorsal and ventral views), depicting the pectoral spine, pectoral-spine muscles, and the pathway (dashed line) and insertion of the epaxial muscle onto the dorsal cleithrum (redrawn from Miano et al. 2013).

Figure 15.27. Illustration of the ventral pectoral girdle of the Blue Catfish, *Ictalurus furcatus*, depicting the pectoral-ray muscles, the origin of the adductor superficialis, and the insertion of the hypaxial muscle (redrawn from Miano et al. 2013).

arms of the figure on the cross are the ascending processes of the parasphenoid. The 'inscription' across the base of the cross is furnished by the vomerine tooth-patch." Anglers and others often find discarded skulls of Catfishes on lake and stream banks and have noticed this phenomenon since at least the early 1900s.

Details of the skeletal anatomy of ictalurids were studied and illustrated for *Ictalurus* (Grande & Shardo 2002), *Ameiurus* (McMurrich 1884a), and *Trogloglanis* (Lundberg 1982). The pectoral anatomy (Brousseau 1978) and myology (McMurrich 1884b) of ictalurids also are illustrated (see also Miano et al. 2013 and pectoral anatomy subsection). Calovich & Branson (1964) and Paloumpis (1964) treated the supraethmoid-ethmoid complex of the skull of *Ictalurus* and *Pylodictis* and provided a key to species in these genera based on features of the skull. Experts still use skull features today to determine species-level differences among *Ictalurus* in Mexico (R. R. Miller pers. comm., now deceased). Smith (1987) described a new species of fossil *Ictalurus* from the Pleistocene of central Mexico and included drawings
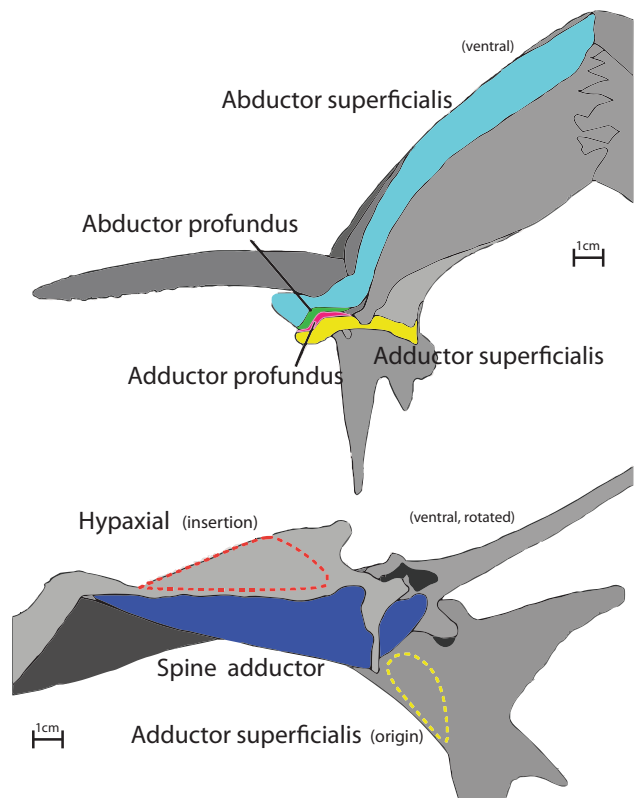
of pectoral spines and a neurocranium. The new species is similar to the living *I. dugesi*.

In a detailed study of skeletal morphology of the Stonecat, Egge (2007) discovered a previously undescribed bone (the coronomeckelian) associated with the lower jaw. Other unique anatomical features (posterior extensions of premaxillary tooth patch, unfused pectoral radials, more paired-fin rays) appear largely consistent with previous work and could be correlates of large body size or retained ancestral traits; these traits place the Stonecat at one end of a spectrum of anatomical variation among madtoms (Egge 2007).

GENETICS

Karyology

Karyotypes of ictalurid Catfishes were investigated by several workers (reviewed by LeGrande 1981; Zhang et al. 1999). The diploid (2n) chromosome numbers range from 40 in the Caddo Madtom (*Noturus taylori*) and Mountain Madtom (*Noturus eleutherus*) to 62 in Yellow Bullheads
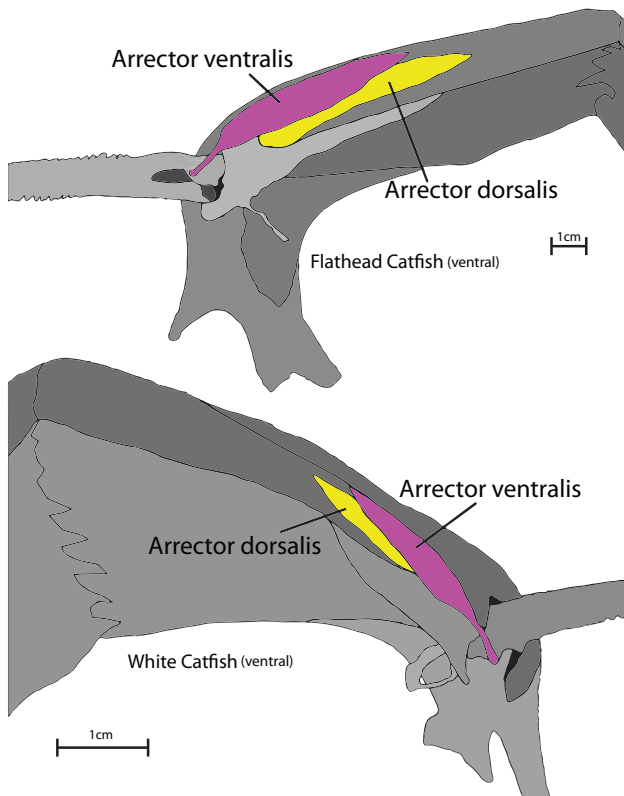
Figure 15.28. Illustration of the ventral pectoral girdle of the Flathead Catfish, *Pylodictis olivaris* (*upper*), and White Catfish, *Ameiurus catus* (*lower*), depicting the arrector ventralis and arrector dorsalis (redrawn from Miano et al. 2013).

(Table 15.3; see also Clark & Mathis 1982). The forktail Catfishes (*Ictalurus* spp.) have modally 58 chromosomes, the bullheads (*Ameiurus* spp.) have between 48 and 62, Flathead Catfish have a modal count of 56, and madtoms (*Noturus* spp.) have a range of 40–54 chromosomes. Two species, the Stonecat and Ozark Madtoms (*Noturus albater*), have either geographic variation in diploid numbers (LeGrande & Cavender 1980) or exhibit intrapopulational chromosomal polymorphism (LeGrande 1981). Karyotypes of hybrids among forktail and bullhead Catfishes showed little variability in diploid number (LeGrande et al. 1984). The one blindcat (Mexican Blindcat) karyotyped had a diploid number of 50 chromosomes (Amemiya et al. 1986). Heteromorphic sex chromosomes were identified only in the Ouachita Madtom (*Noturus taylori*), which appears to have a simple XX-XY system (LeGrande 1981). A naturally occurring triploid of the Brown Bullhead was discovered in Ohio; the phenomenon of triploidy in nature is rare and even rarer still in ictalurids (Cormier et al. 1993). The genome sizes of four species of ictalurids (genera *Ameiurus*, *Ictalurus*, and *Pylodictis*) averaged 2.11 picograms and var-

ied <2.5% within a species, much lower than in other vertebrates (Zhang et al. 1999).

Robertsian translocation, or the rearrangement of chromosomes by the fusion of the long and short arms, respectively, of two chromosomes, is often used to explain evolution of chromosome numbers in fishes and other vertebrates. LeGrande (1981) found evidence that Robertsian translocation has played a significant role in diploid chromosome number in North American Catfishes based on a significant negative correlation between large metacentric (and submetacentric) chromosomes and 2n. However, additional rearrangements involving unequal pericentric inversions and fusion of small chromosomes are superimposed on the patterns created by Robertsian translocation. Based on his conclusion that *Ictalurus* contains more ancestral characteristics than other North American Catfishes and that Bagrid Catfishes were the most likely sister to Ictaluridae (which is still not resolved; see phylogenetic relationships section), LeGrande (1981) postulated an ancestral karyotype of 2n = 58 for Ictaluridae.

Barcoding

A broad taxonomic and geographic survey using barcodes (partial sequences of cytochrome *c* oxidase subunit I, COI) of North American freshwater fishes revealed several Unconfirmed Candidate Species (>2% divergence) among North American Catfishes (April et al. 2011). Of 30 ictalurid species examined, all were distinguishable using barcodes. A total of 29 Unconfirmed Candidate Species were distributed among 11 species (2 *Ameiurus* spp. and 9 *Noturus* spp.). Most species had two Unconfirmed Candidate Species (Flat Bullhead, *Ameiurus platycephalus*; Snail Bullhead, *A. brunneus*; Ozark Madtom; Least Madtom, *Noturus hildebrandi*; Brindled Madtom, *N. miurus*; Slender Madtom, *N. exilis*; Margined Madtom; Elegant Madtom, *N. elegans*; Speckled Madtom, *N. leptacanthus*). Exceptions were the Stonecat with six and the Brown Madtom (*Noturus phaeus*) with three Unconfirmed Candidate Species. April et al. (2011) recommended that until confirmed or dispelled with supporting data (e.g., morphological or other genetic characters) each of the identified Unconfirmed Candidate Species be treated as evolutionarily significant units for conservation management purposes.

Phylogeographic Studies

Many papers on ictalurids have used enzyme product data and variation in nucleotide sequences to document introgression, to help in identifying phenotypically-similar
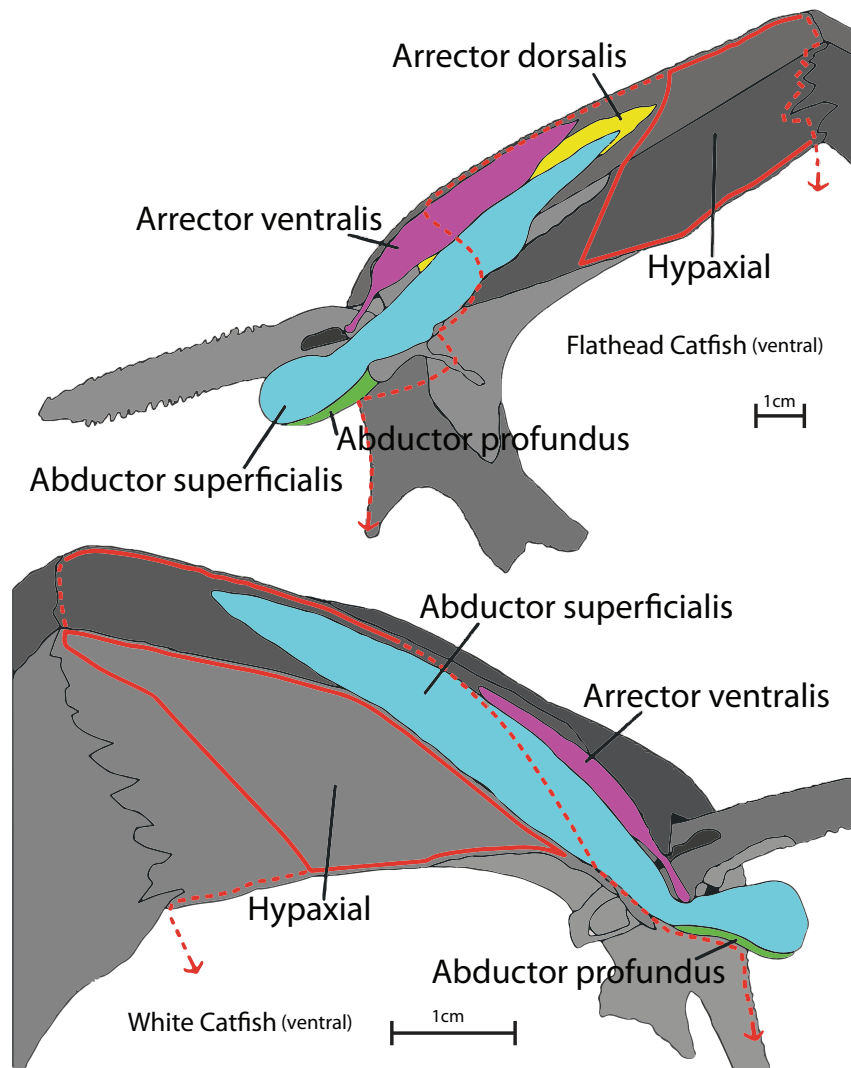
Figure 15.29. Illustration of the ventral pectoral girdle of the Flathead Catfish, *Pylodictis olivaris* (*upper*), and White Catfish, *Ameiurus catus* (*lower*), depicting the muscles of the ventral girdle and the position and insertion of the hypaxial muscle (redrawn from Miano et al. 2013).

species, to examine phylogeographic patterns, to estimate divergence times, to assess effects of historical environmental events on demography, or for phylogenetic inference (see phylogenetic relationships section). Here we summarize for each genus those studies using genetic techniques to evaluate questions other than phylogenetic relationships.

Allozymes were used to examine differences among populations of the Headwater Catfish (*Ictalurus lupus*) (Fig. 15.3) and Channel Catfish in the southwestern United States (Yates et al. 1984, Pecos River, New Mexico; Kelsch & Hendricks 1986, Devils River, Texas), and later mtDNA was analyzed (McClure-Baker et al. 2010, Rio Grande, Pecos, and Nueces Rivers; Bean et al. 2011, Rio Frio, Independence Creek of the Pecos River, Devils River). The allozyme-based Pecos River study indicated fixed differences between Headwater Catfish and Channel Catfish and little evidence of hy-

bridization or introgression (Yates et al. 1984). Allozyme analysis of the eight individuals from the Devils River provided evidence of extensive genetic interaction between the two species (Kelsch & Hendricks 1986). The mtDNA surveys indicated specimens in the Nueces River, mainstem Rio Grande, and Pecos River conformed to morphological and mtDNA characteristics of the Channel Catfish, which is believed to be non-native at least in the New Mexico portion of the Rio Grande. The native or non-native status in the Texas portion of the river is uncertain. Only two isolated populations out of 34 surveyed appeared to represent pure Headwater Catfish. Genetic evidence suggested four other populations occurring in direct tributaries to the Pecos River or Rio Grande were Headwater Catfish, but these all showed various degrees of morphological shifts toward Channel Catfish, suggested to be the result of hybridization. Individuals from the Rio Frio and Independence were iden-
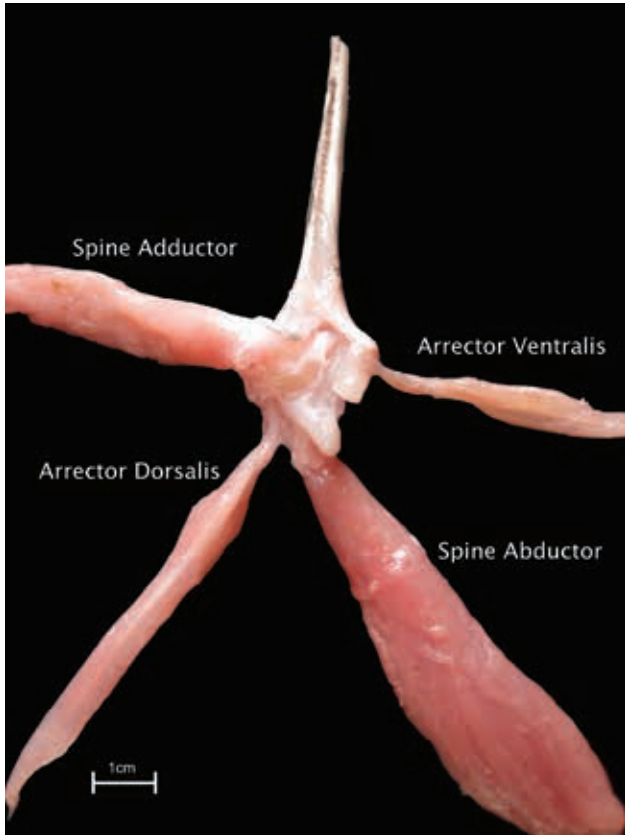
Figure 15.30. Gross dissection of the pectoral-spine and ray muscles of the Blue Catfish, *Ictalurus furcatus* (from Miano et al. 2013; courtesy of Paul Miano and courtesy of Michael L. Fine).

tified as hybrids by morphology and mtDNA haplotypes but not those from Devils River (Bean et al. 2011). The Headwater Catfish appears to persist in these river systems only in areas with reduced opportunities for contact with Channel Catfish (McClure-Baker et al. 2010).

Analysis of the COI gene in populations of the poorly understood Mexican *Ictalurus pricei* (Yaqui Catfish) complex suggested monophyly of populations from the Culiacan, San Lorenzo, Fuerte, and Tutuaca River basins. Even so, there was some support for cryptic diversity, and the Yaqui Catfish was resolved as sister to the Headwater Catfish (Castañeda-Rivera et al. 2015).

Phylogeographic analyses revealed six distinct matrilineal lineages in Channel Catfish when the mitochondrial control region was analyzed from riverine populations throughout the United States (584 individuals, 56 drainages; Padhi 2013a). A widely distributed group was discovered throughout the Mississippi-Ohio-Missouri River drainage and included western Gulf Coast populations and those introduced to Atlantic Coast rivers (South Carolina, North Carolina,
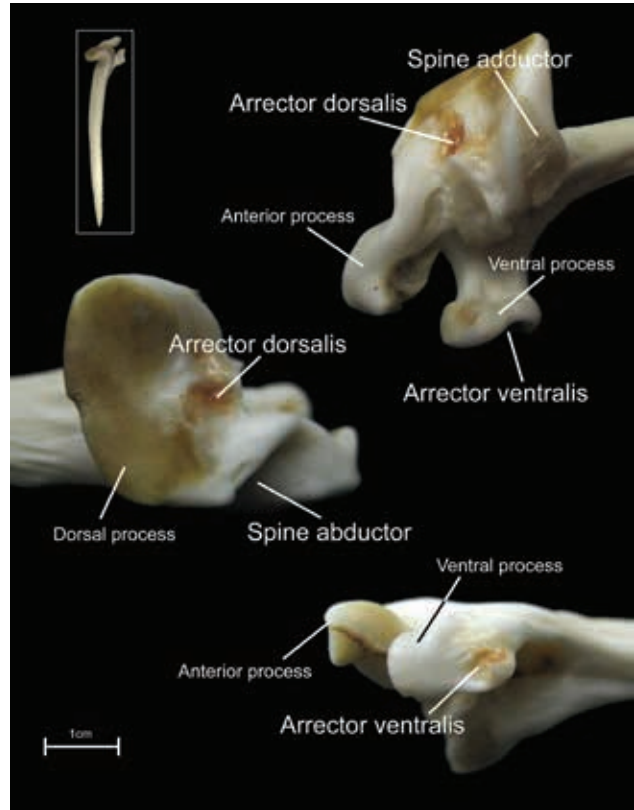
Figure 15.31. Photograph of the pectoral spine (inset) and details of the spine base (dorsal, anterior, and ventral processes) showing insertion points of the pectoral-spine muscles in the Blue Catfish, *Ictalurus furcatus*. In the inset, the dorsal process extends to the left, the anterior process is up, and the ventral process extends to the right (from Miano et al. 2013; courtesy of Paul Miano courtesy of Michael L. Fine).
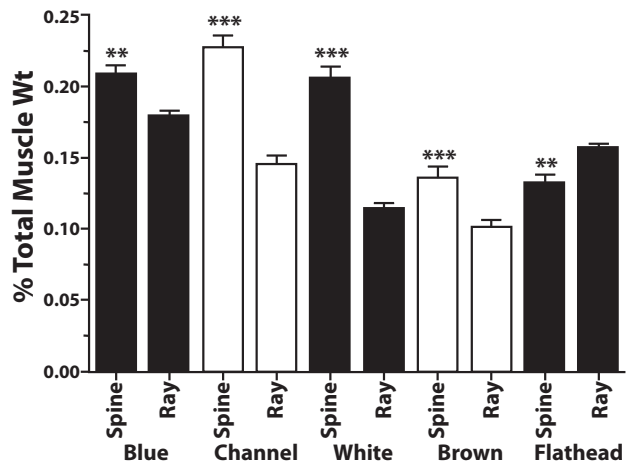
Figure 15.32. Percentage weight (mean ± SE) for total spine and ray muscles for the genera *Ictalurus* (Blue Catfish and Channel Catfish), *Ameirus* (White Catfish and Brown Bullhead), and *Pylodictis* (Flathead Catfish). Asterisks denote significant differences within a species. **P<0.01 and ***P<0.001 (redrawn from Miano et al. 2013).

Maxilla

Nasal

Lacrymal
1st suborbital

Dentary

Mesethmoid

Parethmoid

2nd Suborbital
3rd
4th
5th
6th

Frontal

Quadrate

Pterygoid

Hyomandibular

Preopercular

Opercular

Sphenotic

Subtemporal

Pterotic

Supertemporal

Posttemporal

Supraoccipital

Complex vertebra

Pectoral spine

Articular

5th Vertebra

Modified
pterygiophores

Ribs

Locking ray

Dorsal spine

Figure 15.33. Dorsal surfaces of a Channel Catfish, *Ictalurus punctatus*, skull with major bones identified (redrawn from Grizzle & Rogers 1976).

50

Premaxilla

Maxilla

Dentary

Hypohyal

Ceratohyal

Urohyal

Articular

Epihyal

Branchiostegal rays

Cleithrum

Coracoid

Basioccipital

Radials

Posttemporal

Tripus

Complex vertebra

Pectoral spine

5th Vertebra

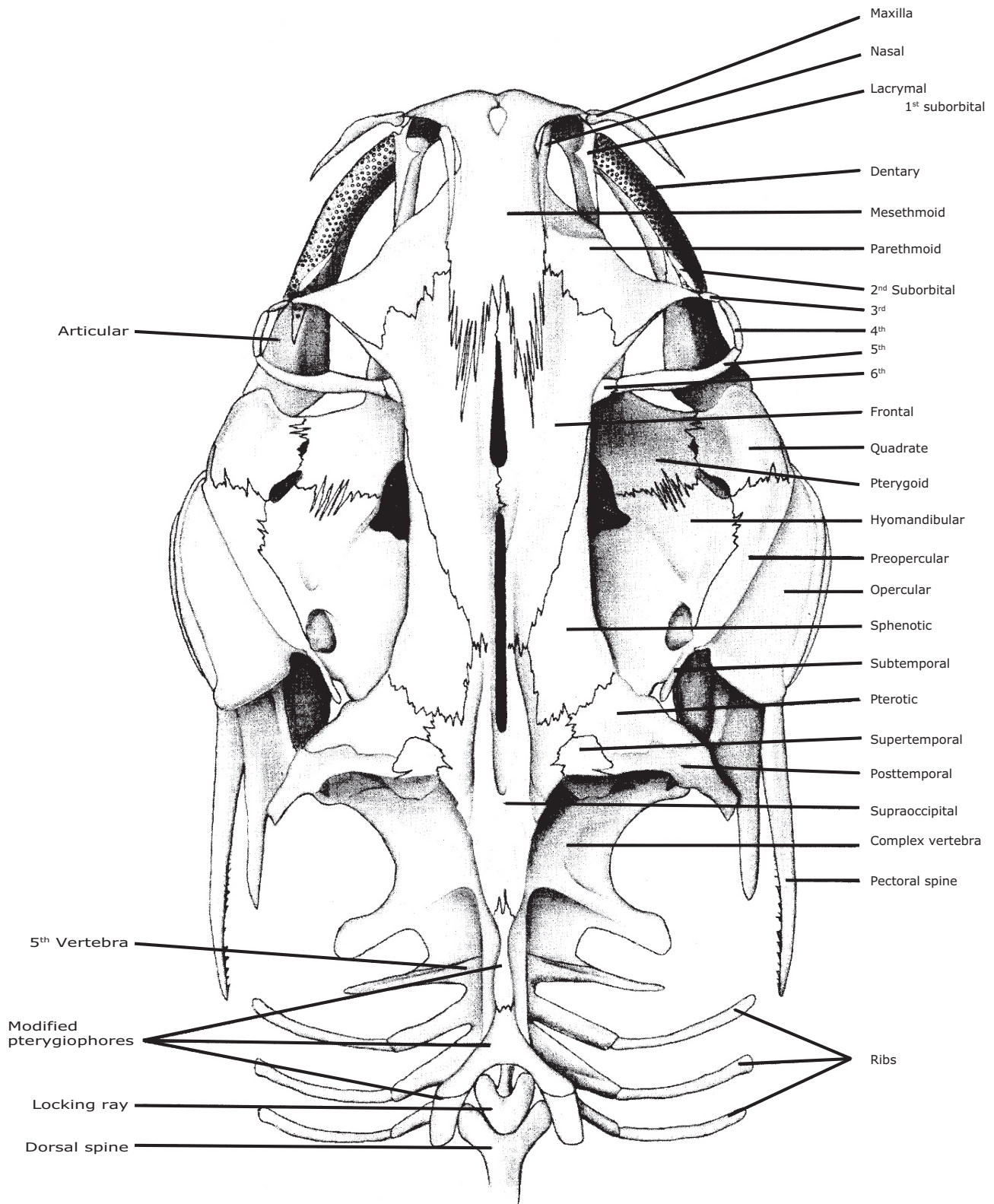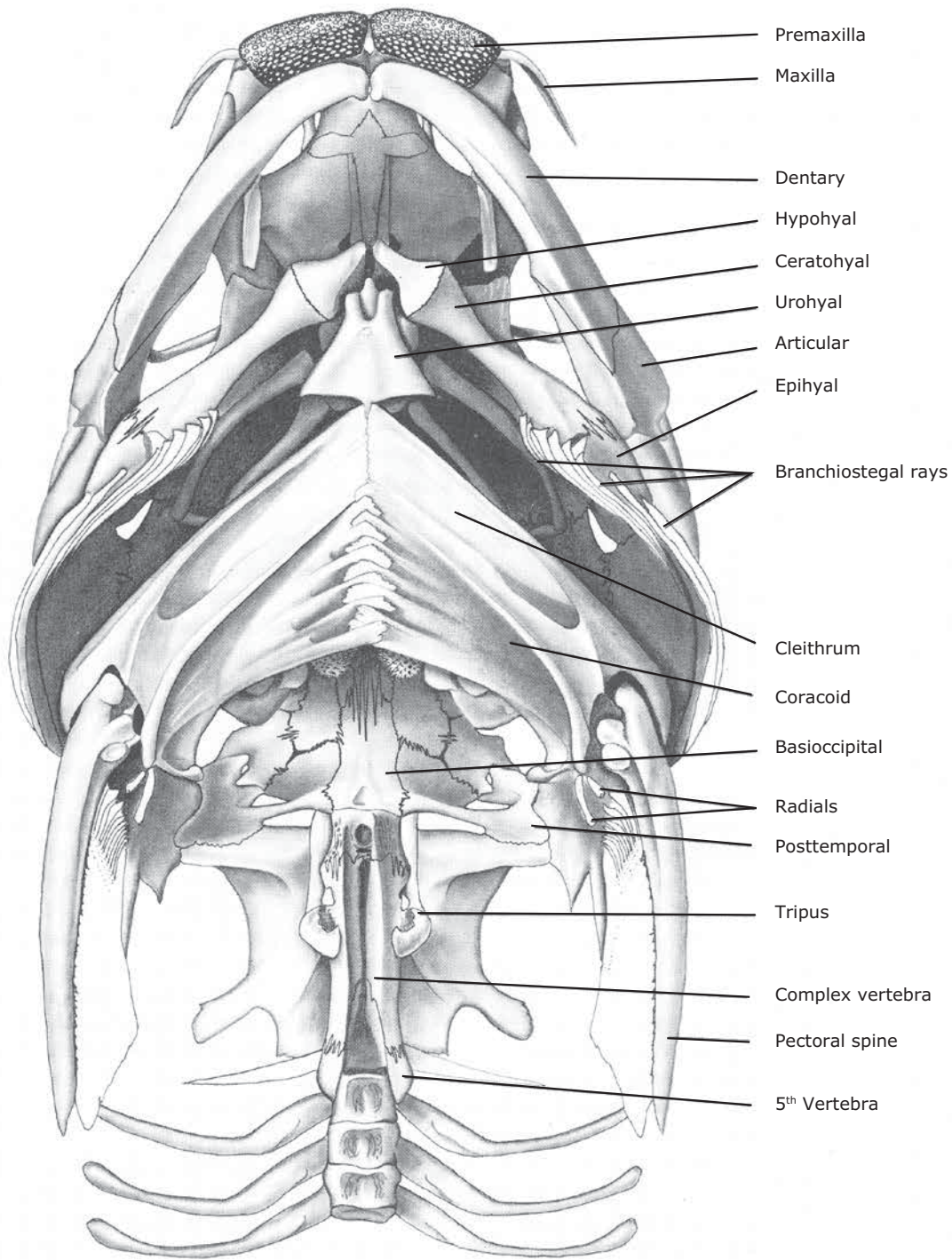*Figure 15.34*. Ventral surfaces of a Channel Catfish, *Ictalurus punctatus*, skull with major bones identified (redrawn from Grizzle & Rogers 1976).

and Virginia). A second lineage consisted of populations from southeastern Atlantic Slope drainages (St. Marys, St. Johns, Satilla, Savannah, and Altamaha Rivers). The remaining lineages occurred in Gulf Coast drainages. An eastern Gulf lineage was revealed from the Suwannee River west to the Apalachicola River. Samples from the Choc-

tawhatchee River made up another Gulf Coast lineage. Escambia and Yellow River populations made up a third Gulf lineage, and populations from the Mobile basin (Alabama River) and Pearl River composed the final Gulf Coast drainage group. Sequence divergence among the lineages was quite high, ranging from 1.2% between the Choctawhatchee

Table 15.3. Summary of karyotype data for North American Catfishes. 2n = diploid chromosome number; FN = fundamental number; LC = number of large chromosomes; LM = number of large metacentric and submetacentric chromosomes.

Species	2n	FN	LC	LM	Formula	Source
I. furcatus	58	—	—	—	—	Zhang et al. 1999
Ictalurus punctatus	56–58	92	—	—	34msm, 24stt	LeGrande 1981
A. melas	60	76	—	—	16msm, 44stt	LeGrande 1981
Ameiurus natalis	62	84	2	2	22msm, 40stt	LeGrande 1981; Zhang et al. 1999
A. nebulosus	60	76	—	—	16msm, 44stt	LeGrande 1981
Ameiurus serracanthus	52	90	8	6	38msm, 14stt	LeGrande 1981
Pylodictis olivaris	56	82	4	2	26msm, 30stt	LeGrande 1981
Noturus albater	66–72	82	4	—	—	LeGrande 1981
N. elegans	46	82	8	8	36msm, 10 stt	LeGrande 1981
N. eleutherus	40–42	66	16	10	24msm, 18stt	LeGrande 1981; Cavender 1987
N. exilis	54	68	6	—	14msm, 40stt	LeGrande 1981
N. flavater	44	64	14	10	20msm, 24stt	LeGrande 1981
N. flavipinnis	52	82	10	4	30msm, 22stt	LeGrande 1981
N. flavus	48–50	70	6–8	2	20–22msm, 26–30stt	LeGrande 1981
N. funebris	44	68	14	12	24msm, 20stt	LeGrande 1981; Zhang et al. 1999
N. gilberti	54	82	4	2	28msm, 26stt	LeGrande 1981
N. gyrinus	42	72	12	10	30msm, 12stt	LeGrande 1981
N. hildebrandi hildebrandi	46	80	12	10	34msm, 12stt	LeGrande 1981
N. h. lautus	46	80	12	10	34msm, 12stt	LeGrande 1981
N. insignis	54	74	4	—	20msm, 34stt	LeGrande 1981
N. lachneri	42	72	12	10	30msm, 12stt	LeGrande 1981
N. leptacanthus	46	72	16	12	26msm, 20stt	LeGrande 1981
N. miurus	50	74	12	8	24msm, 26stt	LeGrande 1981
N. munitus	42	62	16	10	20msm, 22stt	LeGrande 1981
N. nocturnus	48	72	10	8	24msm, 24stt	LeGrande 1981
N. phaeus	42	68	14	12	26msm, 16stt	LeGrande 1981
N. stigmosus	42	62	12	8	20msm, 22stt	LeGrande 1981
N. taylori	40	63–64	16	12	24msm, 16stt	LeGrande 1981
I. punctatus x. I. furcatus	58	—	—	—	—	LeGrande et al. 1984; Zhang et al. 1999
I. punctatus x A. catus	53	—	—	—	—	LeGrande et al. 1984; Zhang et al. 1999
I. punctatus x A. melas	59	—	—	—	—	LeGrande et al. 1984; Zhang et al. 1999
I. punctatus x P. olivaris	57	—	—	—	—	LeGrande et al. 1984; Zhang et al. 1999
Prietella phreatophila	50	—	—	—	—	Amemiya et al. 1986

River and large Mississippi River clades to 4.6% between the southeast Atlantic and eastern Gulf Slope populations. A gene network revealed some admixture among groups, likely the result of translocation or culture of non-native Channel Catfish across genetic boundaries or from incomplete sorting of ancestral haplotypes.

The genus *Ameiurus* has received little genetic attention beyond phylogenetic examination (see phylogenetic relationships section; Hardman & Page 2003), but some limited phylogeographic studies document cryptic lineages and significant divergence in some populations of the Black Bullhead (2010), Yellow Bullhead (Padhi 2013b), and White Catfish (Padhi 2012) and infer historic population characteristics in the White Catfish. Two mtDNA lineages were revealed within the Black Bullhead that could indicate past introgression with other *Ameiurus* or cryptic speciation (Padhi 2010), but geographic coverage was rather limited and geographic composition of the two lineages somewhat mixed and puzzling. A parsimony network from analysis of the mtDNA control region sequence revealed four matrilineal lineages of Yellow Bullheads separated by ≥5 mutational steps. The lineages corre-

sponded geographically to the Florida Everglades, southern Atlantic Slope, Gulf Slope, and Mississippi River basin (Padhi 2013b). The Florida Everglades lineage had greater genetic diversity than other lineages, and evidence indicates some life history traits (e.g., slower growth) are unique to the south Florida populations of Yellow Bullheads, but whether this difference is genetically linked is unknown (see ecology section). Although the mtDNA data are certainly indicative of cryptic diversity in the species, limited geographic coverage and often small sample sizes limits interpretation of the results. Two matrilineal lineages were also revealed in mtDNA analyses of the White Catfish, a southeast Gulf Coast lineage and a southeast Atlantic Coast lineage, a pattern repeatedly observed in many animal and plant taxa (Soltis et al. 2006). Estimated time of divergence of the two lineages was 0.71 mya (0.37–1.1 mya 95% highest posterior density), and a rapid divergence of haplotypes at about 0.2 mya coincided with an increase in effective population size indicative of geographic range expansion (Padhi 2012).

One of the only studies to date of geographic variation in *Pylodictis* sampled >300 individuals and 34 drainages for a portion of the mitochondrial control region and found strong and consistent evidence for two major lineages. One lineage was distributed across the Mississippi River drainage and western Gulf Coast drainages (Texas), and these two subregions formed distinct sub-lineages. The other major lineage occurred in Gulf Coast drainages with two distinct subgroups from middle (Pearl River and some lower Mississippi River tributaries) and eastern portions (east of the Pearl River in Alabama and Florida) of the Gulf Coast. Molecular clock estimates indicated divergence of the major lineages from a common ancestor sometime in the early to late Pleistocene (0.70–2.05 mya). Interestingly, the Mississippi sub-lineage showed a large negative F_{st} value (i.e., an excess of low frequency alleles), which is indicative of population expansion (Padhi 2014).

Some population-level mtDNA sequence data (sometimes with other DNA markers) generated for *Noturus exilis* (Slender Madtom; Fig. 15.35), Margined Madtom, Tadpole Madtom, Stonecat (Fig. 15.6), *Noturus stanauli* (Pygmy Madtom, Fig. 15.10), Ozark Madtom, Black River Madtom (*Noturus maydeni*), Least Madtom, and an undescribed species helped to identify unique populations or show their relationships to one another (Bennetts et al. 1999; Hardy et al. 2002; Egge et al. 2006, 2015; Bennett et al. 2009; Faber et al. 2009; Blanton et al. 2013). Detailed studies of madtom populations of several species indicate that morphological conservatism may mask sub-

Figure 15.35. Slender Madtom, *Noturus exilis* (courtesy of W. Roston).

stantial genetic diversity in the genus (e.g., Egge & Simons 2009; Blanton et al. 2013; Egge et al. 2015; Egge & Hagbo 2015), which is likely true of other ictalurids.

Allozyme studies of the Caddo Madtom and Brindled Madtom (*Noturus miurus*) in the Ouachita Mountains, Arkansas, revealed marked genetic divergence among rivers in both species and little variation within localities. The spatial genetic structuring indicated that extrinsic (large rivers with high silt loads) and intrinsic (habitat preferences) barriers to movement mediate gene flow in these species. The patterns suggested habitat specialists, especially those restricted to headwaters, might be particularly vulnerable to local extirpation because colonization from adjacent rivers is unlikely (Turner & Robison 2006). A comparative phylogeographic study of Mississippi Embayment fishes based on mtDNA (cyt <u>b</u>) confirmed these findings for madtoms, with Brindled, Brown, and Least Madtoms showing substantial isolation by drainage compared with the Bluntface Shiner (*Cyprinella camura*) (Egge & Hagbo 2015). Average percentage sequence divergence was higher within madtom species (Brindled Madtom: 3.5%; Least Madtom: 3.9%; Brown Madtom: 4.2%) than within *C. camura* (2.2%). For all three madtom species, Hatchie River populations formed a distinct clade 1–5% divergent from other clades.

Lately, genetic markers are used to assess historical population sizes and environmental events affecting demographics. This approach with an ictalurid phylogeny documented divergence times of different lineages and found some correlation of diversification with climatic changes (see phylogenetic relationships section; Hardman & Hardman 2008). Padhi (2011) used mtDNA data to infer historic population characteristics of Blue Catfish and found a strong relationship between population size and air temperatures associated with glaciation. Genetic substructuring among multiple

widely separated Blue Catfish populations was minimal. Effective population size in the Blue Catfish over the past 120,000 years as revealed by genetic analysis was inversely correlated with the increasing volume of glacial ice over that time period. Declines were relatively steep at the peak of the glaciation and effective population size only began increasing again about 5,000 years ago, several thousand years after the glaciers retreated. Genetic divergence of Slender Madtom populations coincided with a drop in sea level in the Miocene-Pleistocene, similar to other major groups of freshwater fishes. Dispersal of populations in the Ozarks up the Mississippi River facilitated colonization of formerly glaciated regions during the Pleistocene (Blanton et al. 2013). With these studies in mind, it is not surprising that a mitochondrial DNA barcoding analysis found that 11 species of Ictaluridae contained sequences that diverged >2%, making them candidates for further research and description of at least 29 potentially new species (April et al. 2011; Table 15.2).

Hybridization

Hybridization in ictalurid Catfishes is reasonably well documented (Taylor 1969; Tave & Smitherman 1982). A few apparent natural hybrids are documented in *Noturus* (Trautman 1948; Taylor 1969; Menzel & Raney 1973; Welsh & Cincotta 2004), but most hybrids were produced by human manipulation for potential use in aquaculture and propagation (Zhang & Tiersch 1997). An intergeneric hybrid between the genera *Ameiurus* and *Ictalurus* was produced, and the Blue and Channel Catfishes are hybridized for propagation purposes. Several other combinations (using either gender of the target genus) have been produced. Chromosomal inheritance patterns of hybrids are now well understood (Zhang & Tiersch 1997). Although considerable literature on this topic is available, most of it is not particularly pertinent to a general understanding of ictalurid biology.

Genetic Diversity and Environmental Stressors

A team of population biologists looked at genetic diversity in samples of Brown Bullheads from Lake Erie tributaries (Silbiger et al. 2001). Their goal was to test whether individuals from historically degraded sites displayed levels of genetic diversity different from individuals taken from reference sites. Four sites, two impacted and two reference, were the sources of samples. They found decreased genetic diversity in the samples from historically degraded sites. The degraded sites were subjected to various environmental stress-

ors for years. This is one of the first studies to examine levels of genetic diversity in multiple samples of bullheads and to relate findings to the conservation biology field.

Genetic Resources for Study

Substantial genetic resources are available for studying many Catfishes from nucleotide data to whole genome sequences. These data will play important roles in scientific studies of ecology, evolution, and taxonomy and in conservation, aquaculture, and management of ictalurids. Microsatellite loci are known for several species, including the Channel Catfish (e.g., Perales-Flores et al. 2007; Somridhivej et al. 2008), Brown Bullhead (Millard et al. 2009; Soderberg et al. 2010), Yellow Bullhead (Creer & Trexler 2006), Yellowfin Madtom, *Noturus flavipinnis*, and Smoky Madtom, *Noturus baileyi* (Williams & Moyer 2012). Other species will likely be added to this list in the future. The cytochrome b gene was sequenced for the Channel Catfish and Blue Catfish (Matsuo et al. 2001), and many species have publicly available nucleotide data for this gene. The genome of the Channel Catfish was sequenced (Waldbeiser et al. 2003; Quiniou et al. 2007), and cDNA sequences are available for Channel Catfish and Blue Catfish (Chen et al. 2010). Additionally, a growing literature exists on the genetics of toxicology (see Silbiger et al. 2001) and diseases in ictalurids (see Kucuktas & Brady 1999), topics not reviewed here.

PHYSIOLOGY

North American Catfishes occupy a broad latitudinal belt from southern Canada to the tropics of Central America. As such, many species, particularly the wide-ranging taxa, tolerate and are adapted physiologically to a broad range of environmental conditions. Some species, especially the Brown Bullhead and Channel Catfish, have a long history of use in aquatic toxicological studies (e.g., Myers & Fournie 2002; Gaunt et al. 2007; Iwanowicz et al. 2009), but here the emphasis is on physiological tolerances to extremes of critical environmental variables (e.g., dissolved oxygen, temperature, salinity, and pH), sensory capabilities, and venom production as known for each genus.

Dissolved Oxygen, Salinity, and Temperature Tolerance of *Ictalurus*

The wide-ranging genus *Ictalurus* is also tolerant of a variety of seemingly harsh environmental conditions, but

nearly all studies involve Channel Catfish and to a lesser extent Blue Catfish. Little to no information is available on most other species in the genus (e.g., species in Mexico). Channel Catfish are tolerant of hypoxic waters and oligohaline conditions. They can live in water with oxygen concentrations as low as 1–2 mg/L (Dunham et al. 1983), but they grow best at concentrations >3 mg/L and at temperatures of 24–32°C (75.2–89.6°F) (Hargreaves & Tomasso 2004) and require >4 mg/L concentrations to spawn (Hubert 1999). Metabolism is restricted at 7 mg/L, but ventilation volume does not increase until <4 mg/L, and metabolism conforms directly to ambient oxygen concentration (Hargreaves & Tomasso 2004). Embryos and larvae require ≥30% dissolved oxygen saturation to survive (Carlson et al. 1974), and high levels of turbidity (85,000 mg/L) can be fatal to larvae (Van Eeckhout 1974). They do not usually tolerate salinities >10 ppt. Eggs can tolerate 16 ppt, but they hatch only at ≤8 ppt (Allen & Avault 1970). Salinities <9–10 ppt are required for survival through the larval stage. Channel Catfish occur in the wild at salinities of 11 ppt (Perry & Avault 1968). Blue Catfish can survive salinities ≤22 ppt, occur in the wild at 11 ppt, and tolerate a broad temperature range (0–37°C, 32–98.6°F) although they grow best at temperatures around 27°C (80.6°F) and salinities <8 ppt (Perry 1968; Pelzman 1971). When acclimated at 5 ppt salinity and tested at 14 ppt, only 8.3% of Channel Catfish survived after 37 days (Allen & Avault 1970). Blue Catfish foraged on marine invertebrates in Lake Pontchartrain, Louisiana, where salinities varied between 1.2–18.5 ppt but were typically 6–9 ppt (reviewed by Peterson & Meador 1994). In a review of environmental tolerances of freshwater fishes, Channel Catfish were relatively intolerant to low dissolved oxygen (ordinal rank 4) and pH (ordinal rank 1) but moderately tolerant for water temperature (ordinal rank 6) and highly tolerant to chloride levels (ordinal rank 8; Meador & Carlisle 2007). In an aquaculture study, biomass production of Blue Catfish and Channel Catfish was lower in ponds with low dissolved oxygen (about 2.5 ppm, 32% air saturation), but Channel Catfish were more heavily affected (Torrans et al. 2012). In another aquaculture study, hybrid *Ictalurus* (female *I. punctatus*, Jubilee strain × Blue Catfish) were essentially not affected by low dissolved oxygen (25–50% air saturation), but Channel Catfish grew slower and produced less biomass (Green & Rawles 2011).

Heat tolerance of Channel Catfish is among the highest measured in North American fishes being exceeded only by some cyprinodontiforms (e.g., *Gambusia* spp., *Cyprinodon* spp.) (reviewed by Beitinger et al. 2000). In tests from multiple studies, mean critical thermal maxima

(measured as loss of equilibrium) ranged from 34.5°C (94.1°F) to 42.1°C (107.8°F; acclimation temperatures 12–35°C, 54–95°F). At acclimation temperatures of 20, 25, and 30°C (68, 77, 86°F), the critical thermal minima were 2.7, 6.5, and 9.8°C (36.9, 43.7, and 49.6°F), respectively (measured as loss of equilibrium) (Currie et al. 1998). Each 1°C (33.8°F) increase in acclimation temperature increased heat tolerance by 0.4°C (0.8°F) and decreased cold tolerance by 0.71°C (1.3°F). A cycled diel thermoperiod between 20–30°C (68–86°F) produced critical thermal minima of 6.3°C (43.3°F) and maxima of 39.0°C (102.2°F) (Currie et al. 2004). Preferred temperatures across acclimation temperatures of 6–30°C (43–86°F) ranged from 18.9 to 30.5°C (66.0 to 86.9°F; Cherry et al. 1975). Upper and lower temperatures avoided were 25 and 4°C (77 and 30°F; at 6°C, 43°F, acclimation) and 35 and 23°C (95 and 73°F; at 30°C, 86°F, acclimation).

Dissolved Oxygen, Temperature, Salinity, and pH Tolerance of *Ameiurus*

Bullheads show high tolerance to extremes of dissolved oxygen, temperature, and salinity. Some bullheads, such as the Black Bullhead and Yellow Bullhead, are quick to invade new, but highly variable environments, such as ditches, intermittent streams, and other temporary habitats. For example, Yellow Bullheads are one of the most abundant fishes in alligator ponds during summer dry-down in the Everglades of southern Florida, where hypoxic conditions can be extreme and even lethal to fishes (Kushlan 1974; Loftus & Kushlan 1987). Yellow Bullheads were part of a hypoxia-tolerant group in Mercer Bayou, Arkansas, found at oxygen concentrations <1 mg/L (Killgore & Hoover 2001). Bullheads (*Ameiurus melas*, *A. natalis*, and *A. nebulosus*) were ranked as more tolerant of low dissolved oxygen than other Catfishes in a review (ordinal ranks of 6, 7, and 7, respectively; Meador & Carlisle 2007). During the spring flood pulse in the Atchafalaya basin, Louisiana, the Black Bullhead was part of a distinctive fish assemblage of black-water sites that included the Warmouth (*Lepomis gulosus*), Spotted Gar (*Lepisosteus oculatus*), Pirate Perch (*Aphredoderus sayanus*), and Flier (*Centrarchus macropterus*) in their greatest abundances. Black-water sites characteristically were warm (28°C, 78.8°F), hypoxic, often with <2 mg/L of dissolved oxygen throughout the water column, and surface saturations of about 28% (Rutherford et al. 2001). In the laboratory, Yellow Bullheads and Black Bullheads had mean critical dissolved oxygen values of 0.49 mg/L (0.46–0.52, 95% confidence limits) and 1.13 mg/L (1.00–1.27), respectively (at

26°C, 78.8°F; measured as cessation of ventilation and opercular movements) (Smale & Rabeni 1995). Species of *Ameiurus* can tolerate low dissolved oxygen levels because their hemoglobin can efficiently load oxygen at low concentrations even under conditions of high levels of carbon dioxide (Haws & Goodnight 1962; Lodge 1974; Lagler et al. 1977). Behavioral adaptations during hypoxia, such as rapid opercle movement at the surface and air-gulping, may also increase tolerance (Kushlan 1974; Becker 1983; Rutherford et al. 2001). Standard metabolic rate was higher in Brown Bullheads from contaminated (higher sediment PCBs, pesticides, heavy metals, etc.) compared to uncontaminated sites in the Detroit River, Michigan, with differences persisting both immediate (<10 days post-capture) and long-term (1 year post-capture) trials; however, differences were not found in F1 offspring, suggesting that difference in metabolic rate were due to acclimation and not from maternal effects or adaptation (Leadley et al. 2016).

The bullheads also show tolerance to heat and have broad temperature tolerances in general. Both the Yellow Bullhead and Black Bullhead can survive temperatures of 35°C (95°F) in nature and 37–38°C (99–100°F) in laboratory experiments (acclimated at 26°C, 79°F) (Smale & Rabeni 1995). In tests of 21 fish species, another member of the genus, the Brown Bullhead, the only ictalurid represented, had the largest thermal niche (i.e., temperature polygon = 1162°C^2) of any fishes tested except the highly eurythermal Goldfish (*Carassius auratus*) and Sheepshead Minnow (*Cyprinodon variegatus*) (Beitinger & Bennett 2000). In a review of environmental tolerances of freshwater fishes, Yellow Bullheads were ranked highly tolerant of high-water temperature (ordinal rank 7), but Black Bullheads and Brown Bullheads were relatively intolerant (ordinal ranks 2 and 4, respectively; Meador & Carlisle 2007). Laboratory temperature preferences of Brown Bullheads varied from about 12°C (53.6°F) in winter temperature regimes to 27°C (80.6°F) in summer regimes (acclimation temperatures 3.5 and 28.0°C, 38.3 and 82.4°F, respectively) (Richards & Ibara 1978; see also Coutant 1977 and references therein). Individuals ceased feeding at acclimation temperatures of 3.5°C (38.3°F; Richards & Ibara 1978). Similarly, under winter ice in an Ontario lake (water temperature 4°C, 39.2°F) feeding of adult and young Brown Bullheads was minimal, but in early spring fish were actively feeding at water temperatures of 6.5°C (43.7°F; Keast 1968). When temperatures become too low, bullheads can burrow into loose substrates and become torpid (Loeb 1964). Using a lab-validated bioenergetics model for Brown Bullhead, Hartman (2017) predicted increases in growth

days for northern latitudes (between 8 and 43% for sites >38 degrees N) and substantial declines in growth days at southern latitudes of upwards of two months for adult fish south of about 33 degrees N. These projections were based on adding 4°C to daily water temperatures at 10 sites from across the range of Brown Bullhead and suggest significant population impacts, including extirpation and potentially greater metabolism and accumulation of contaminants such as polynuclear aromatic hydrocarbons (PAHs).

Bullheads appear relatively tolerant to oligohaline, and even mesohaline, conditions. Experimentally, White Catfish had a 60-h median lethal concentration (LC$_{50}$) of 14 ppt in diluted seawater (Kendall & Schwartz 1968), which is consistent with field salinity values observed for the species (4–14 ppt) in trawl catches in Mullica River, New Jersey (Martino & Able 2003). The species was not captured at downriver sites with salinities >15 ppt. White Catfish also move into oligohaline marshes (usually <5 ppt) (Rozas & Hackney 1984), where they feed on marine invertebrates (e.g., crabs, polychaetes) (Heard 1975). The Black Bullhead displays similar salinity tolerance; in brine pond water, their LC$_{50}$ ranged from 10.0 to 13.8 ppt (Clemens & Jones 1955; Chipman 1959). In Suisan Marsh, California, non-native Black Bullheads occur in salinities ≤13 ppt (Moyle 2002), and they are abundant in the oligohaline Guadalquivir Estuary, southern Spain, where salinities are <5 ppt (Garcia-de-Lomas et al. 2009). Bullheads (*Ameiurus melas*, *A. natalis*, and *A. nebulosus*) have high chloride tolerances compared with other fishes and Catfishes (ordinal ranks of 7–9; Meador & Carlisle 2007).

Field studies suggest *Ameiurus* have different preferences if not tolerances for pH. Across a gradient of naturally acidic New Jersey lakes, the Brown Bullhead occurred across a broad range of pH from 4.1 to 9.0, but the median pH was near 7.0. Its probability of occurrence increased from 20% at lake pH of 4.1 to ≥80% in lakes with pH ≥6.5. Likewise, White Catfish were associated with a slightly higher range of pH (6.0–8.5) but had a circumneutral median. In contrast, the Yellow Bullhead occurred across a lower range of pH (4–6.6) with a median pH of 5. Its probability of occurrence dropped from >80% in lakes with pH<5.5 to 0% in lakes with pH ≥7 (Graham 1993; see also Rahel 1984). In acidic Wisconsin lakes, Yellow Bullheads and Black Bullheads occurred in lakes spanning a pH range of about 4.5–7.0 (Rahel & Magnuson 1983). Experimentally, adult Black Bullheads were among the most acid-tolerant fishes studied from those lakes. Median survival occurred at 240 h at a pH of 3.05 (starting pH 5.5, dropped 0.5 units/24 h); the young were somewhat more sensitive. Black Bullheads and Brown Bull-

heads also tolerate relatively high alkalinities (pH 8.0–8.5), but a pH >9 is apparently ultimately lethal (McCarraher 1971; Moyle 2002). A review of environmental tolerances found Brown Bullheads to be among the most pH tolerant of all fishes studied (ordinal rank 10), but Black Bullheads and Yellow Bullheads had lower tolerances (ordinal rank 5 and 7, respectively; Meador & Carlisle 2007).

Physiological Tolerances of Other Genera

Little in the way of quantitative tolerance information is available for any other genera of ictalurids. In metabolic trials from 3–32°C (37.4–89.6°F), juvenile Flathead Catfish ate more food with increasing water temperatures, particularly between 19–32°C (66.2–89.6°F). Fish rarely fed at <15°C (59°F), most stopped eating at 11°C (51.8°F), and no fish fed at <7°C (44.6°F; Bourret et al. 2008). Salinity tolerance in the species is relatively high. Juvenile Flathead Catfish had a 96-h median lethal concentration (LC_{50}) at 14.5 ppt salinity (synthetic seawater at 18°C, 64.4°F). Acclimation tests with fish exposed to daily increases in salinity of 4 ppt produced an LC_{50} of 15.8 ppt. To assess transition success from fresh water to salt water, fish were transferred from fresh water (at 18°C, 64.4°F) to salinities of 8, 11, or 14 ppt for 24 h and then returned to fresh water for 48 h. Fish exposed to salinities of 8 or 11 ppt for 24 h had >95% survival. Fish exposed to the 14 ppt level did not survive the 24-h exposure. The results suggest dispersal of this species likely is not limited by seasonally low estuarine salinities on the Atlantic Coast (e.g., Chesapeake Bay) (Bringolf et al. 2005). A review of environmental tolerances of freshwater fishes found Flathead Catfish to be highly tolerant of high chloride levels (ordinal rank 8) and temperature (ordinal rank 9) but only moderately tolerant of low dissolved oxygen (ordinal rank 5) and intolerant of low pH (ordinal rank 2; Meador & Carlisle 2007).

Most species of *Noturus* (madtoms) live in flowing waters, often in uplands or shaded reaches, where dissolved oxygen levels and temperature extremes likely are not limiting (Burr & Stoeckel 1999; Banks & DiStefano 2002; see Gagen et al. 1998). One species, the Tadpole Madtom, occupies diverse habitats, which include static water situations, such as lakes, swamps, and oxbows. That species is apparently adapted behaviorally or physiologically to withstand at least moderately hypoxic conditions and the high summer water temperatures of many southeastern wetlands. In the laboratory, an upland species, the Slender Madtom, had a mean critical dissolved oxygen

concentration of 0.60 mg/L (loss of equilibrium as the end point) (Smale & Rabeni 1995) and a mean critical thermal maxima of 36.6°C (97.9°F, acclimated at 26°C, 78.8°F). The one blindcat studied (*Prietella phreatophila*) lives in water with temperatures of 27–31.5°C (80.6–88.7°F) and a pH of 7.45–7.92 (Hendrickson et al. 2001). A review of environmental tolerances of freshwater fishes that included three madtoms (*Noturus flavus*, *N. gyrinus*, and *N. insignis*) revealed some variability in tolerances of pH, chloride, dissolved oxygen, and water temperature. All were relatively intolerant of low dissolved oxygen (ordinal ranks 3–5) and moderately tolerant of high water temperature (ordinal ranks 4–6). However, *N. insignis* was less tolerant of chloride levels (ordinal rank 3) compared with the others (ordinal ranks 8–10), and *N. flavus* was intolerant of low pH (ordinal rank 3) compared with the others (ordinal ranks 6–7; Meador & Carlisle 2007).

Swimming Performance

Swimming performance has rarely been investigated in North American Catfishes with only a few studies available for Blue Catfish and Channel Catfish. Fingerling Blue Catfish fatigued more quickly than Channel Catfish after being forced to swim at 60 cm/s (23.6 inches/s); however, there was no difference in recovery time (judged by cortisol, glucose, and lactate concentrations) between species or between still or flowing water (Beecham et al. 2009). Mean relative (13.7 body lengths / s) and absolute (70 cm/s, 27.6 inches/s) swimming speeds were relatively high for Blue Catfish compared with many other fishes from Texas and Louisiana streams (Leavy & Bonner 2009). Burst-swimming speed (fatigued in <20 s) for Blue Catfish was 110 cm/s (43.2 inches/s), and maximum sustained swimming speed (not fatigued in >200 min) was 30 cm/s (11.8 inches/s), but these were less than values for a hybrid *Ictalurus* (female *I. punctatus* × male Blue Catfish; Beecham et al. 2009).

Vision

Ictalurid eyes contain both rod and cone photoreceptors with the rods being slightly more numerous than cones (Walls 1942; Arnott et al. 1974; Ali & Anctil 1976; Sillman et al. 1993). Photoreceptors appear in larvae 5 days after hatching, and no ontogenetic changes occur in visual pigments or photoreceptor structure or arrangement. The rod and cone outer segments are often embedded in a granular tapetal material thought to enhance the ability of the receptor to trap photons and increase vision in dim

light (Levine & MacNichol 1979; Sillman et al. 1993). Although Liebman (1973) reported double cones in Black Bullheads, subsequent workers on *Ameiurus* and *Ictalurus* observed only single cones (Arnott et al. 1974; Sillman et al. 1993). Rods absorb maximally near 540 nm, and the cones contain either a red-sensitive visual pigment ($\lambda_{max} = 608$ nm, near 625 nm in Yellow Bullheads) or a green-sensitive visual pigment ($\lambda_{max} = 535$ nm, near 512 nm in Yellow Bullheads) (Liebman 1973; Levine & MacNichol 1979; Sillman et al. 1993). Blue or ultraviolet sensitive cones are lacking. The visual system is consistent with species that live where the amount of blue light is low or lacking altogether (Sillman et al. 1993).

The eyes of *Ameiurus* are probably of little importance in feeding, but they may be the controlling sense organs in the negative reactions to light and in the orientation to light (Schiche 1921). Blinded fish show a marked thigmotactic reaction resulting in resting positions that bring as many parts of the body as possible in contact with solid objects. When blinded fish are subjected to conflicting stimuli, the chemical stimulus is the strongest. Eddy (1925) first reported that blinded fish do not aggregate, and Parr (1927) strongly suggested that the densely packed schools of young bullheads are controlled primarily by tactile stimulations. Experimentally, Bowen (1931) confirmed Eddy's work by showing Catfishes do not aggregate in the dark, and aggregations are broken up in about 1 min after light is removed. She concluded that the eyes are important for integration and that without them the aggregations cannot form.

Electroreception

The fact that Catfishes detect and orient to weak electric fields was known soon after the turn of the twentieth century. Research on electroreception over the past several decades has added greatly to our understanding of the anatomy, physiology, and behavioral significance of this unusual capability (reviewed by New 1999). Ictalurids produce weak electrical fields through muscle contractions and nerve impulses, as is true of other fishes; however, they apparently do not actively generate electric fields, even weak ones, via an electric organ as in African Electric Catfishes (Malapteridae) and some other Catfish families (e.g., Bagridae, Clariidae), but they can detect weak bioelectric fields. Electrosensitivity is used by Catfishes to detect prey, for social interactions among conspecifics, and to help in navigation and orientation in turbid water environments. The organs of electroreception, the ampullary electroreceptor organs, are specializations of

the mechanosensory lateral-line system of the skin. In the Brown Bullhead, the density of receptors is greatest on the dorsum of the head and tail and lowest near the mouth, gills, and anus (Peters et al. 1974). The ampullary organ consists of an ampullary pore in the epidermis that leads to a short canal that terminates in a bulbous chamber, the alveolus. These organs are filled with a highly conductive gelatinous material. The receptor cells are located in the base of the alveolus and typically number 7–8. The electroreceptor organs detect weak electric fields emitted by animate or inanimate objects, providing information about the properties of nearby objects (Tong & Bullock 1982; New 1999 and references therein). This sensory system is particularly important in aquatic systems in which visibility may be reduced because of high turbidity. In a laboratory study of Brown Bullheads, fish generally responded more to the intensity of electrical signal than the specific frequency but demonstrated some plasticity in prey detection behavior by using both the frequency and intensity of signal in deciding which source to pursue in food detection (Eeuwes et al. 2008). In the laboratory, the electroreceptor organs of Brown Bullheads detected potential prey fish at a distance of 5–10 cm (2–4 inches; Roth 1972), but since electroreceptors in the central nervous system are even more sensitive, the actual detection distance might be greater (New 1999). Surprisingly, electrosensitivity has been investigated in only two ictalurids, Channel Catfish and Brown Bullheads. In addition, the ear, skin, and lateral-line systems are all sensitive to vibrations (Parker & Van Heusen 1917).

Taste Reception

Catfishes are particularly acute at gustatory sensation. Taste buds are apparently present on the skin over the whole body in *Ameiurus*, being especially dense on the barbels, and nearly the entire surface of the skin is sensitive to both tactile and gustatory stimuli (Herrick 1903). Individual taste receptor cells (or solitary chemosensory cells) on the body surface ranged from 1,000–2,000/mm^2 in *Ameiurus* (similar for cichlids, Zander, and most European cyprinids examined; compared to the highest of about 4,000/mm^2 in the cyprinid *Rutilus rutilus*, Roach) (Kotrschal 1991). Additionally, branches of cranial nerves are distributed on the head, on the flanks to the tail, and on the fins and barbels. Olfactory organs of *Ameiurus* (studied in *A. nebulosus*) are distance receptors of chemical stimuli and are distinct from the taste organs of the skin (Parker 1910). Species of *Ictalurus* and *Ameiurus* can

identify and locate complex amino acids in the laboratory (Caprio 1975; Dolensek & Valentincic 2010; Valentincic 2011); however, bullheads were studied in much greater detail. Neurons in oral and extraoral taste receptors show complex responses to chemical and tactile stimulation in ictalurids (Kanwal et al. 1988). In bullheads taste alone can guide individuals to sources of chemical stimuli ≥25 fish lengths away (the limits of aquaria used in the experiments) (Bardach et al. 1967). This sort of discrimination can be done in the absence of any current; that is, they perform a true gradient search by means of taste. Interestingly, neither unilateral nor bilateral deprivation of the olfactory sense impaired their searching ability, but unilateral deprivation of taste receptors on skin and barbels caused pronounced circling behavior toward the side where the taste buds were intact. The presence of flow reduced the ability of Brown Bullheads to find the source of an odor in a controlled experiment (Sherman & Moore 2001). Olfactory and gustatory sensation may diminish as a stress response from capture or confinement (Channel Catfish; Tucker 1973). The gustatory acuity of bullheads and probably other ictalurids may approach the olfactory acuity of many other fish species.

When a piece of meat is brought into contact with the barbel of a bullhead, the fish will immediately seize and consume the morsel. The same behavior occurs when the meat is brought into contact with the side of a bullhead. Herrick (1903) referred to this quick capture and swallowing of a prey item as the gustatory response. The same form of response can also be produced by discharging meat juice from a pipette against the side of a bullhead. When the branch of cranial nerve 7 that innervates the taste buds on the flank of the fish is severed, the gustatory response no longer occurs (Parker 1912). Olmsted (1918:448) found that bullheads responded even to human saliva with a biting response. He observed, "But since human saliva proved fairly stimulating to the fish (bullhead), the time-honored custom of 'spitting on one's bait' does seem to be more than superstition and perhaps for this reason may receive the sanction of science."

Auditory Reception

In Brown Bullheads, auditory sensitivity ranged from 100 to 4,000 Hz, reaching a maximum around 600–700 Hz (at 28 db below 1 dyne/cm^2), much higher than that of Goldfish (*Carassius auratus*) (Weiss et al. 1969). Other aspects of auditory reception, including neural pathways have been studied, mostly in Channel Catfish (e.g., Moeng & Popper 1984; McCormick & Bradford 1993; New & He 1998). As in other fishes, sensory information from several modalities (e.g., auditory, electrosensation) travels along the same neural pathways (Striedter 1991), although there is some separation of lateral-line and auditory neural paths and receptors in the brain (Knudsen 1977).

Hypogean Species

The hypogean genus *Prietella*, being blind and living in total darkness, evidences some unusual physiological adaptations (Figs. 15.7 and 15.8). Individuals are apparently incapable of perceiving light but are sensitive to sound. Odors and tastes of prepared foods are detected quickly. Several individuals had low condition factors in the wild, and one was kept for 44 months without food in an aquarium (Hendrickson et al. 2001).

Venom Apparatus

Statements alluding to the sting and probable venom of ictalurid Catfishes date back to the late nineteenth century (Jordan & Gilbert 1882b). Nearly everyone that angles or handles Catfish is aware of the localized pain of being spined or stung by a Catfish species, especially so if it is a madtom Catfish (genus *Noturus*). Severe inflammation, infection, and even limb or digit amputation can result from envenomation or if the spine lodges and breaks off in flesh or bone (Fig. 15.1), and several papers in the medical literature describe these effects (Murphey et al. 1992; McKinstry 1993; Shepherd et al. 1994; Baker 1997; Blomkalns & Otten 1999). Early workers pioneered the anatomical and descriptive accounts of the venom glands of the Brown Bullhead and 10 species of madtoms (Reed 1907, 1924) and investigated the venom apparatus of the White Catfish (Citterio 1925). All species possessed an axillary venom gland, two madtom species possessed venom in ductless glands that lay encased in the integumentary sheath along the entire length of the pectoral and dorsal spines, and rudimentary glands occurred at the tip of the sting (spine and integumentary sheath as a unit) in the Brown Bullhead or were limited to the distal portions of the sting in the White Catfish. Detailed work in madtoms revealed parallels in morphology (Egge & Simons 2011). Four basic sting morphologies exist with respect to the venom glands and spine: (1) smooth spine with no venom gland (found in *Prietella*, Orangefin Madtom, *Noturus gilberti*); (2) smooth spine with venom gland along spine shaft (Stonecat; Black Madtom, *Noturus funebris*; Tadpole

Madtom; Ouachita Madtom, *Noturus lachneri*; Freckled Madtom, *Noturus nocturnus*; Speckled Madtom, *Noturus leptacanthus*; and Yellow Bullhead); (3) serrated spine with venom gland along spine shaft (Brown Madtom, *Noturus phaeus*; *N. exilis*; *N. insignis*; Least Madtom, *Noturus hildebrandi*; Channel Catfish; and Flathead Catfish) and; (4) serrated spine with venom glands along spine shaft and posterior serrations (found in all of the *rabida* clade
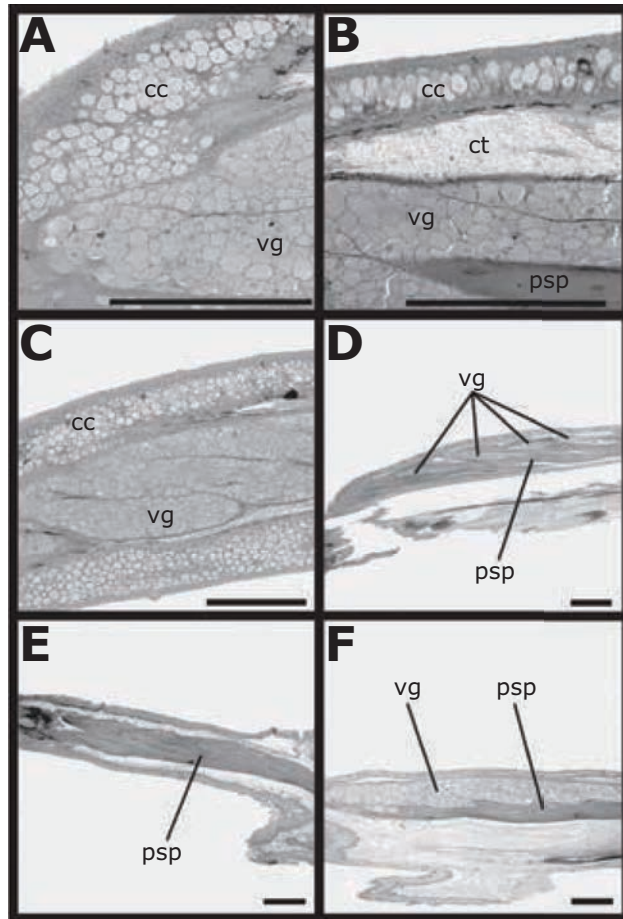
sensu, Egge & Simons 2011, except *N. hildebrandi*). In most species, the venom glands were restricted to less than half the length of the spine, but *Noturus gyrinus* and *N. lachneri* had especially large glands that reached nearly to the spine base (Egge & Simons 2011; Figs. 15.36 and 15.37). Although general morphology of madtom stings is similar to previous reports for other ictalurids, Egge & Simons' (2011) work has contradicted the previous claim
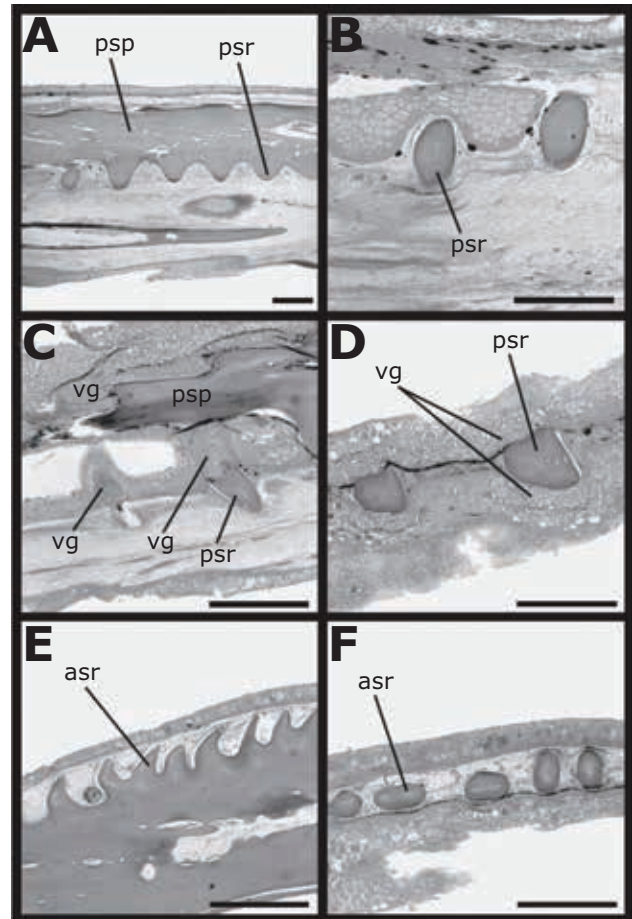

Figure 15.36. Histological sections of *Noturus* pectoral venom glands. (A) Margined Madtom, *Noturus insignis*, frontal section through tip of venom gland. (B) Margined Madtom, frontal section through venom gland tissue on spine shaft. (C) Freckled Madtom, *Noturus nocturnus*, frontal section through venom gland lateral of pectoral spine. (D) Least Madtom, *Noturus hildebrandi*, frontal section through entire pectoral sting, illustrating venom gland tissue in spine grooves. (E) Orangefin Madtom, *Noturus gilberti*, frontal section through entire sting, illustrating smooth pectoral spine with no venom gland tissue. (F) Ouachita Madtom, *Noturus lachneri*, frontal section illustrating smooth pectoral spine and venom gland with large venom cells. Key: cc = club cells; ct = connective tissue; psp = pectoral spine; vg = venom gland. Distal tip of spine on left. Scale bars = 1 mm (redrawn from Egge & Simons 2011).

Figure 15.37. Histological sections of *Noturus* pectoral spine serrations. (A) Brown Madtom, *Noturus phaeus*, frontal section through posterior serrations, showing lack of venom gland tissue. (B) Brown Madtom, transverse section through posterior serrations, showing lack of venom gland tissue. (C) Elegant Madtom, *Noturus elegans*, frontal section through posterior serrations, showing venom gland tissue association with spine shaft and posterior serrations. (D) Yellowfin Madtom, *Noturus flavipinnis*, transverse section through posterior serrations, showing associated venom gland tissue. (E) Piebald Madtom, *Noturus gladiator*, frontal section through anterior serrations, showing lack of venom gland tissue. (F) Yellowfin Madtom, transverse section through anterior serrations, showing lack of venom gland tissue. Key: asr = anterior serrations; psp = pectoral spine; psr = posterior serrations; vg = venom gland. Distal tip of spine on left. Scale bars = 1 mm (redrawn from Egge & Simons 2011).

that species with serrated spines have no venom glands (Reed 1907). Phylogenetic analysis revealed that the common ancestor of madtoms likely had pectoral spines with a venom gland and serrations, although most madtoms do not express this specific morphology, and several transitions occur among these character states (Egge & Simons 2011).

Experimental work with 14 ictalurids, which involved injection of extracts of Catfish stings into Western Mosquitofish (*Gambusia affinis*) suggested that madtom stings were not necessarily more toxic than some of the other ictalurids; it was doubtful if secretions from the axillary gland reached the pectoral sting; and pectoral and dorsal stings did not differ in their toxicity (Birkhead 1967, 1972). Sting extracts from the Black Bullhead and Slender Madtom were lethal to *Gambusia*, and extracts from the stings of Yellow Bullheads and several other madtom species were quite virulent. Stings of the Channel Catfish, Brown Bullhead, and Ozark Madtom were essentially innocuous, and those from the Speckled Madtom and Flathead Catfish were not considered toxic. In trials with Largemouth Bass (*Micropterus salmoides*), Channel Catfish with intact spines were initially attacked just as frequently as those with spines removed. Bass also repeatedly attacked fish with intact spines, suggesting that sensitization may occur over time. The pectoral spine thus functions as a defense against a gape-limited predator by increasing handling time but not by deterring predation (Bosher et al. 2006).

Work comparing sting toxicity of Tadpole Madtoms and Yellow Bullheads shows higher toxicity of the madtom venom, likely due to the presence of a single protein not found in Yellow Bullhead. The madtom sting may be adapted for predatory defense, because handling time of Largemouth Bass was higher for intact Tadpole Madtoms as opposed to other prey items (*N. gyrinus* with flesh stripped from the spine; *N. gyrinus* with spine removed; Yellow Bullhead; Bullhead Minnow, *Pimephales vigilax*; Wright 2012). Despite increased handling time with Tadpole Madtoms, Largemouth Bass were equally likely to consume Tadpole Madtoms and Fathead Minnows (*Pimephales promelas*). Although they showed signs of discomfort, the Largemouth Bass displayed no long-term effects from consuming Tadpole Madtoms and readily consumed additional madtoms. Future comparative analyses should yield insight into the generality of these findings because the Tadpole Madtom has one of the largest venom glands of all madtoms (Egge & Simons 2011).

BEHAVIOR

Movement

North American Catfishes exhibit a diversity of movement behaviors from the relatively stationary madtoms to the highly vagile Blue Catfish (Table 15.4). Seasonality and reproduction play major roles in the timing and distances of movement. Distances and directions moved and percentage of stationary versus mobile Catfishes apparently varies in different stream systems (e.g., Funk 1955). However, as is usual in such studies, most marked individuals are never recaptured, potentially indicating a highly mobile population (e.g., Greenback 1956; Fausch & Young 1995; Albanese et al. 2003). This is true even for the less-studied madtoms, which limits generalizations about maximum or average movements.

The use of stable isotopes and trace elements to identify natal habitats, stock sources, and long-distance movements in ictalurid Catfishes is in its infancy, but it was successfully applied to Flathead Catfish and Blue Catfish. Stable carbon and oxygen isotopes of spines and otoliths and strontium:calcium ratios of otoliths distinguished populations of Catfishes from the Mississippi-Missouri watershed except for similarities between lower and middle Mississippi River individuals, indicating a high potential for such markers in elucidating movement and migration of Catfishes (Smith & Whitledge 2011).

Channel Catfish are mobile animals in streams because they require different habitats for spawning, recruitment, general growth, and overwintering. Tagging and tracking studies indicate both upstream and downstream movements, high activity, and low residency (about 10%) (Cooke & McKinley 1999; Hubert 1999). Although recaptures >100 km (62 miles) from initial tagging sites are infrequent, movements >400km (248.5 miles; e.g., Dames et al. 1989) and extremely low recapture rates for Channel Catfish and Blue Catfish indicate high mobility (Pugh & Schramm 1999; Table 15.4). In one study, a Missouri River-resident Channel Catfish moved 469 km (291.4 miles) in only 72 days (Dames et al. 1989). In introduced populations of Channel Catfish in the middle-upper San Juan River, New Mexico-Utah, although recapture rates were low (≤3%), some marked fish each year consistently moved >161 km (100 miles) and ≤217 km (134.8 miles) from the initial capture site with variation among size classes in distance traveled (J. E. Davis pers. comm.; Davis et al. 2010; Duran et al. 2011, 2012; Table 15.4). Channel Catfish in the lower Wisconsin and Mississippi Rivers moved ≤280 km (174 miles) during

Table 15.4. Summary of movement studies for North American Catfishes (Ictaluridae).

Species	Method	Number of Fish Tracked or Recaptured (% recaptured)	Time Period Tracked	Mean Distance, km (miles)	Maximum Distance, km (miles)	Relative Seasonal Distance-frequency	Location	Reference
Ictalurus furcatus	Radio and acoustic tag telemetry	80	2 years	—	347.6 (216)	Spring > Summer > Autumn > Winter	Missouri River	Garrett & Rabeni 2011
	Acoustic receiver telemetry	92	4 years	—	689 (428)	Spring = Summer = Autumn = Winter	Upper Mississippi River	Tripp et al. 2011
	Mark-recapture	334 (tagged)	6 years	24 (15)	79 (49)	—	Kentucky Lake	Timmons 1999
	Mark-recapture	3 (1.4%)	2 years	—	12 (7.5)	—	Lower Mississippi River	Pugh & Schramm 1999
Ictalurus punctatus	Telemetry	134	3 years	—	280.4 (174)	Autumn > Spring > Winter > Summer	Lower Wisconsin and upper Mississippi Rivers	Fago 1999
	Mark-recapture	356 (tagged)	6 years	11 (6.8)	58 (36)	—	Kentucky Lake	Timmons 1999
	Mark-recapture	3 (1.6%)	2 years	—	52 (32.3)	—	Lower Mississippi River	Pugh & Schramm 1999
	Radio telemetry	38	2 summers	5.7 (3.5)	44.5 (27.7)	—	Red River, Minnesota-South Dakota	Wendel & Kelsch 1999
	Mark-recapture	128	2 years	About 78 (48.5)	216.9 (134.8)	—	San Juan River, New Mexico-Colorado-Utah	J.Davis pers. comm.
	Mark-recapture	21 (3%)	About 1 year	85.1 (52.9)	217.3 (135)	—	San Juan River, New Mexico-Colorado-Utah	Davis et al. 2010
	Mark-recapture	32 (3.2%)	About 1 year	53.9 (33.5)	202.8 (126)	—	San Juan River, New Mexico-Colorado-Utah	Duran et al. 2011
Ameiurus brunneus	Mark-recapture	34 (36%)	3 years	0	1 fish captured outside original site; no distance given	—	Nickajack Creek, Georgia	Sakaris et al. 2011b

Ameiurus natalis	Mark-recapture	19 (4.3%)	1 year	3.7 (2.3)		Spring = Summer > Autumn = Winter	Duke Swamp, North Carolina	Whitehurst 1981
Ameiurus nebulosus	Mark-recapture	19 (1.8%)	1 year	5.2 (3.2)		Spring = Summer > Autumn = Winter	Duke Swamp, North Carolina	Whitehurst 1981
	Radio telemetry	10 (summer); 12 (spring); 18 (fall-winter)	About 1 year		3.5 (2.2)	Spring > Autumn Winter > Summer		Sakaris et al. 2005
Pylodictis olivaris	Radio telemetry	56	92–1,554 days	42.4 (26.3)	120 (74.6)	—	Iowa River, Iowa	Gelwicks & Simmons 2011
	Radio telemetry	24	3 years	32.1 (20)	77.4 (48.1)	Spring, Summer, Autumn > Winter	Fox River, Wisconsin	Piette & Niebur 2011
	Radio telemetry	20	3 years	57.6 (35.8)	158.5 (98.5)	Spring, Summer, Autumn > Winter	Wolf River, Wisconsin	Piette & Niebur 2011
	Radio and acoustic tag telemetry	18	Late summer-fall of 2 years	—	124 (77.1)	—	Minnesota River, Minnesota	Shroyer 2011
	Radio and acoustic tag telemetry	77	2 years	—	751.9 (467.2)	Spring > Summer > Autumn, Winter	Missouri River	Garrett & Rabeni 2011
	Radio telemetry	6	24 hours	0.712 (0.442)	1.55 (0.96)	—	Grand and Cuivre Rivers, Missouri	Vokoun & Rabeni 2006
	Mark-recapture	370 (12.6%)	2 years	6.5 (4.0)	161 (100)	—	Missouri River	Travnichek 2004
	Mark-recapture	18 (7%)	2 years	About 1.3 (0.81)	6 (3.7)	—	Lower Mississippi River	Pugh & Schramm 1999
	Mark-recapture	265 (31%)	3 months	—	8 (5.0)	—	Apalachicola River, Florida	Dobbins et al. 1999
Noturus lachneri	Sampling after defaunation	—	About 1 year	—	0.034 (0.02)	—	Three creeks, Saline River, Arkansas	Gagen et al. 1998
Noturus placidus	Mark-recapture	12 (4.7%)	About 1 year	0.018 (0.011)	0.225 (0.140) (1 fish)	—	Cottonwood River, Kansas	Fuselier & Edds 1994

autumn, but movement decreased in winter (maximum 49 km, 30.4 miles), spring (maximum 39 km, 24.2 miles), and summer (maximum 32 km, 19.9 miles) (Fago 1999). In the Red River, North Dakota-Minnesota, Channel Catfish moved <6 km (3.7 miles) on average (maximum 15.45 km, 9.6 miles) (Wendel & Kelsch 1999). In telemetry studies, adults moved from wintering areas to spawning sites and then to summer feeding areas in river systems. Often this involves movement from a major river (Missouri River) into a tributary stream and then back (Hubert 1999; see also Dames et al. 1989). Reservoir populations move into tributaries to spawn and return to reservoirs during summer and over winter. Adults may move to more optimum sites because their original reach of habitat is degraded or access to spawning grounds are blocked by dams. In the Ohio and Wabash Rivers, Channel Catfish exhibited a pattern of genetic isolation-by-distance, based on 10 microsatellite loci, supporting previous field observations of natal homing or smaller ranges in summer with long-range movements occurring frequently. Additionally, for some populations in the region, impoundments decreased genetic diversity and produced more genetic differentiation than expected based on geographic distance alone (Sotola et al. 2017).

Blue Catfish may be the most migratory of the ictalurids (Graham 1999), moving both upstream and downstream for some distance in response to seasonal changes in water temperature (Table 15.4). Of 75 Blue Catfish that were detected multiple times with ultrasonic receivers, maximum movement averaged just 6.1 km (3.8 miles); however, maximum movement varied from 1.3 to 689 km (0.8–428.1 miles), a staggering range (Tripp et al. 2011). Some 40% of nearly 3,000 tagged Blue Catfish moved >16 km (9.9 miles) from their original point of capture in Lake of the Ozarks, Missouri. In Kentucky Lake, the mean distance traveled during an eight-year study was 23.6 km (14.7 miles), more than twice that of Channel Catfish (Timmons 1999). Several studies document downstream movement coinciding with autumn temperature decreases in rivers (Lagler 1961; Pflieger 1997; Tripp et al. 2011) and extensive up- and downstream movement as fish seek overwintering habitat and spring spawning sites (Graham 1999; Tripp et al. 2011).

Home range in a Missouri reservoir was somewhat larger for Blue Catfish than Channel Catfish in some seasons but not others. In spring Blue Catfish home range was 79.3 ha (0.30 mi^2) versus 72.1 ha (0.28 mi^2) in Channel Catfish. In summer home ranges were larger for Blue Catfish (48.1 ha, 0.19 mi^2, versus 40.6 ha, 0.16 mi^2) but were smaller in autumn (26.1 ha, 0.10 mi^2, versus 37.7 ha,

0.15 mi^2) and similar in winter (21.5 ha, 0.083 mi^2, versus 20.3 ha, 0.078 mi^2) (Fischer et al. 1999).

Bullheads appear to have high site fidelity, although studies are limited (Table 15.4). Marked Yellow Bullheads and Brown Bullheads in a lowland North Carolina stream were recaptured at the original point of marking and upstream and downstream of the marking location. For Brown Bullheads, 47% did not move, 21% moved downstream, and 32% moved upstream; Yellow Bullheads showed a slightly different pattern with 36% not moving, 8% traveling downstream, and 52% moving upstream. For those that moved, the average distance traveled ranged between 2.6 and 5.2 km (1.6–3.2 miles) over periods of 11–131 days. The longest distance traveled was 178.2 km (110.7 miles) upstream by a White Catfish (Whitehurst 1981). In Lake Erie, fixed-station telemetry (49 fish) and genetic studies (112 fish) suggested Brown Bullheads rarely left the study area of Presque Isle Bay (Millard et al. 2009). Similarly, Brown Bullheads in the Anacostia River, Washington, DC, were located via telemetry ≤1 km (0.6 miles) from the initial capture location by the end of spring (linear home range 2.1 km, 1.3 miles) but traveled less in summer, being found ≤500 m from the initial capture location (linear home range 0.5 km, 0.3 miles). During autumn and winter, fish dispersed more extensively, remaining ≤4.2 km (2.6 miles) upstream and ≤3.1 km (1.9 miles) downstream of the initial capture location (linear home range 2.1 km, 1.3 miles). No tagged fish were located outside of the Anacostia River (Sakaris et al. 2005). During winter ice cover in a shallow, Wisconsin backwater lake of the Mississippi River, directional trapping revealed relatively large numbers of Yellow Bullheads moving under the ice from the river to the lake, but the stimulus for the apparent waves of movement was unclear (Greenbank 1956).

Only one of 34 recaptures for Snail Bullheads (*Ameiurus brunneus*) were outside the initial tagging area in Nickajack Creek, Georgia, although recapture rates were relatively low (26%) (Sakaris et al. 2011b). Evidence of flow-mediated movements is apparent in some studies. In a Minnesota stream with beaver impoundments, Black Bullheads and two other species accounted for 80% of fish movement, usually in a downstream direction and associated with elevated discharge (Schlosser 1995).

Flathead Catfish are often sedentary and may establish preferred use areas (Jackson 1999; Pugh & Schramm 1999). After nocturnal forays, individual adults will return to specific locations, which are often large piles of instream wood (Vokoun & Rabeni 2006). From the little information available, introduced Flathead Catfish

populations maintain their generally small home ranges (Dobbins et al. 1999). Nevertheless, the species can move relatively great distances. For example, six fish traveled >100 km (62.1 miles) and two fish traveled >650 km (403.9 miles) in the Missouri River (Garrett & Rabeni 2011; Table 15.4). Most movement is at night and often into shallows; direction of movement is apparently random but probably related to local habitat conditions (e.g., Vokoun & Rabeni 2005b). Linear ranges determined by radiotelemetry were between 0.75–1.04 km (0.47–0.65 miles) in two southern rivers (Jackson 1999), indicating that much of the life of an adult is spent in a single, long reach. Home range and movement distances varied seasonally in the St. Joseph River, Michigan, and were greatest in the spring (1,045 and 1,513 m; 0.65 and 0.94 miles, respectively) and autumn (1,146 and 1,296 m; 0.71 and 0.81 miles, respectively), lower in summer (218 m and 596 m; 0.14 and 0.37 miles, respectively), and nonexistent in winter (Daugherty & Sutton 2005). Other studies support the finding of little or no winter movement (Weller & Winter 2001; Vokoun & Rabeni 2005b; Piette & Niebur 2011). In two rivers in Missouri, Flathead Catfish movement could be characterized by three main periods separated by short migrations. An overwintering period was followed by outmigration in spring; next was the spawning period, characterized by greater activity and longer movements, followed by another migration, a late summer-autumn restricted movement period, and an autumn migration to overwintering areas (Vokoun & Rabeni 2005ab). The general pattern is confirmed by other studies (Garrett & Rabeni 2011; Piette & Niebur 2011). Within this framework, individual fish varied significantly with some fish remaining in a reach throughout the year and some fish traveling >180 km (111.8 miles; Vokoun & Rabeni 2005ab). In the nearby, but larger, Missouri River, >80% of recaptures were ≤5 km (3.1 miles) and 94% were ≤20 km (12.4 miles) from the tagging location; however, maximum movement was 160 km (99.4 miles), and average movement distances varied with size classes. Large individuals (>508 mm TL, 20 inches) moved about three times (12.6 km, 7.8 miles) the distance of the small fish (305–380 mm TL, 12–15 inches; 4.5 km, 2.8 miles) (Travnichek 2004). In Wisconsin, similar patterns were found in the Iowa River with mean and maximum linear movements of 42 and 120 km (26 and 74.6 miles), respectively (Gelwicks & Simmons 2011), the Fox River (mean 32.1 km, 19.1 miles; maximum 77.4 km, 48.1 miles), and Wolf River (57.6 km, 35.8 miles; 158.5 km, 98.5 miles) (Piette & Niebur 2011). Fish tracked for multiple years

show high fidelity to particular locations, especially during summer, autumn, and the overwintering period (Gelwicks & Simmons 2011; Piette & Niebur 2011). Although Flathead Catfish may have fairly restricted or consistent home ranges, seasonally varying and infrequent long-distance movements suggest that management over larger spatial scales may be necessary (Vokoun & Rabeni 2005ab; Gelwicks & Simmons 2011).

Madtoms apparently do not make long-distance movements or migrations, although there are studies of only a few species. In tagging studies, most species are recaptured in the same reach where they were originally tagged (Dinkins & Shute 1996; Case 1970; Fuselier & Edds 1994; Puchala et al. 2016). For instance, Dinkins & Shute (1996) recaptured seven of 45 tagged Yellowfin Madtoms in the same pool where they were originally tagged. Of 693 adult Tadpole Madtoms tagged, only five were recaptured at a site other than the original tagging location (Case 1970). Even for the largest madtom, the Stonecat, only 7% of recaptures were outside the original capture site (Puchala et al. 2016). Some seasonal shifts in habitat from riffles to pools may occur (Mayden & Burr 1981; Dinkins & Shute 1996), but the distances moved, even for a small fish, are not great (Burr & Stoeckel 1999). Despite these generalities, Ouachita Madtoms rapidly recolonized formerly dry reaches after resumption of flow, moving a minimum of 2–35 m (6.6–114.8 feet) to the defaunated reaches (Gagen et al. 1998). Also, one Neosho Madtom (*Noturus placidus*) moved a maximum of 225 m (0.14 miles) while all others remained in the riffle where they were originally captured (Fuselier & Edds 1994). In another study (Manny et al. 2014), two Northern Madtoms (*N. stigmosus*) were recaptured almost 2 km (1.2 miles) from their marking location in the Detroit River over 15 and 45 day periods (Michigan and Ontario, Canada) having traveled through a 8–11 m (26.2- 36.1 feet) deep and >0.8 km (0.5 miles) wide channel. Movement of Margined Madtoms through weirs in a tributary of the James River, Virginia, was not related to flow events, day length, temperature, or water level, unlike some of the cyprinids studied (Albanese et al. 2004). Margined Madtoms moved ≥130 m (426.5 feet) to recolonize a defaunated reach of a tributary to the upper James River, Virginia, where they reached >30% of original abundance in ≤4 weeks of removal and about 100% of original abundance in ≤50 weeks of removal (Albanese et al. 2009). These data suggest that, as in other small-bodied stream fishes, restricted movement with occasional long-distance treks is the norm for madtoms (Smithson & Johnston 1999; Petty & Grossman 2004).

Diel Activity

North American Catfishes may be active during both the day and night, generally more so at night. Diel studies of stomach contents indicate that much feeding activity is crepuscular (e.g., Darnell & Meierotto 1965; Mayden & Burr 1981; see ecology section). Highest feeding rates in Channel Catfish young coincided with peaks in invertebrate drift after sunset; however, actual stomach contents (chironomid larvae) suggested that the fish were not heavily using the drift (Armstrong & Brown 1983). Introduced Brown Bullheads in a New Zealand lake were more active at night and moved to shallow water, especially during winter (Dedual 2002), and diel activity of Yellow Bullheads measured in the laboratory indicated 80% of activity occurred during the dark period (Reynolds & Casterlin 1978). Although adult Black Bullheads were consistent with this pattern, moving extensively at night, juveniles swam actively in schools during the day and remained relatively inactive at night in a Wisconsin study (Darnell & Meierotto 1965). Flathead Catfish are more active during dusk, night, and early morning hours when they use a wider variety of habitats (gravel, sand, open water) than during the day (Daugherty & Sutton 2005; Vokoun & Rabeni 2006). In one study, fish remained stationary >90% of the time with limited movement during the day, when they made discrete movements to habitat structures (e.g., instream wood, undercut banks) (Vokoun & Rabeni 2006). This general pattern is confirmed by other investigators for Flathead Catfish (Daugherty & Sutton 2005). Channel Catfish and Flathead Catfish occurred at higher densities at night during summer, but Stonecat had similar densities during diurnal and nocturnal sampling (Brewer & Rabeni 2008). Brown Madtoms appeared to feed most actively (judged by presence of undigested gut contents) just after sunset and again a few hours before sunrise; total prey in stomachs matched this pattern before sunset but had a second peak in the late morning instead of before sunrise (Chan & Parsons 2000). This is consistent with knowledge of other madtoms (Mayden & Burr 1981; Burr & Stoeckel 1999).

Sociality

The young of ictalurids aggregate in densely packed schools, especially in the bullheads (*Ameiurus* spp.), and the role that the sense organs play in these social aggregations has intrigued researchers since the early 1900s. In normal aggregations there is a constant pushing through-out the cluster. Individuals on the outside push in toward the center, pushing out others, which immediately push back into the group. The reciprocal pushing of individuals apparently gives a much greater thigmotactic as well as gustatory stimulus and may produce a social appetite, which results in the tendency toward group formation (Bowen 1931). Laboratory-held stocks of Brown Bullhead juveniles showed antagonistic behavior and territoriality (Carr et al. 1987). Bullhead aggregations are an excellent example of a simple type of vertebrate society (Fig. 15.38).

Experimentally blinded or olfactory deprived Brown Bullheads and Yellow Bullheads kept in large aquaria exhibited complex behaviors, including territory establishment, dominance hierarchies, intricate agonistic displays, and outright fights (Bardach et al. 1967; Todd et al. 1967). Blinded fish exposed to water in which another bullhead resided recognized individuals of their own spe-
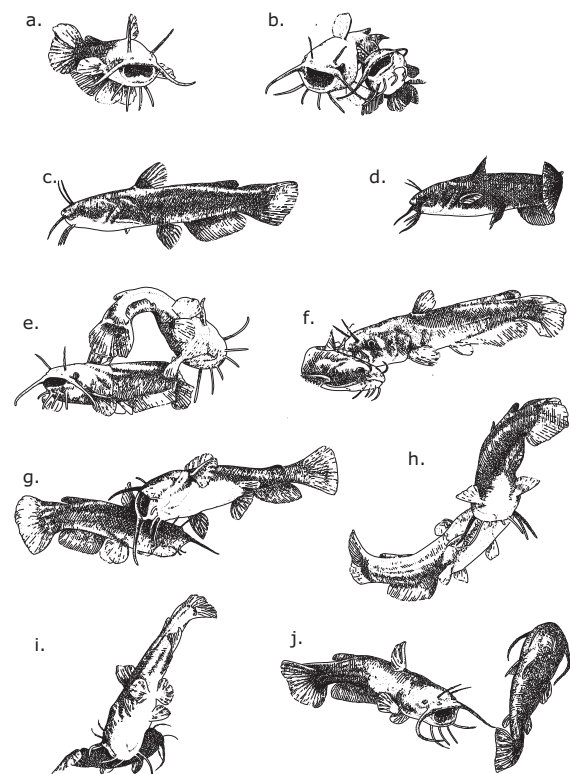

Figure 15.38. Agonistic behaviors of bullheads (genus *Ameiurus*). A low-key form (a) contrasts with more extreme displays (b, left, and j). Both approaching (c) and circling (d) occur in interactions of various intensities. Intermediate in intensity are the tail thrust (e, top), lateral display (b, right), and nip (f), all common actions among equals. The head thrust (g) and mouth fight (h) and bite (i) are actions of greater intensity. Encounters between territorial fish usually end in a chase (j) with the dominant fish pursuing (redrawn from Todd 1971).

cies by means of pheromones. In a series of experiments in which blinded bullheads had their nares cauterized, fish deprived of the olfactory sense could not discriminate between two other fish of their own species. The main source of the ability of one bullhead to recognize another of its own kind was a chemical stimulus produced in the skin mucus (Todd et al. 1967). Natural stressors (e.g., fighting) alter the pheromone system of bullheads (i.e., a previously submissive individual will attack a previously dominant individual that has just lost an agonistic encounter). This change in status might be due to altered slime or perhaps chemical changes in the urine. Research to date indicates that at least among bullheads and probably madtoms, individual chemosensory recognition is a vital part of communication outside the breeding season (Todd 1971). Because the large ictalurids (i.e., non-madtoms) lack bold external markings and often live in dimly lit environments, chemical recognition is a solution to the need for individual recognition. A bullhead not only identifies but also remembers the identification of a particular individual. Outside the nesting season, both males and females occupy individual territories. Aggressive actions include nipping, chasing, tail thrusts, mouth fights, and actual fighting involving vicious biting and occasionally death for one of the contestants (Carr & Carr 1985). Experiments suggest such dominance and aggression behavior is not directly related to food availability, although large fish grew faster than small fish (Keen 1982).

Noturus Ethogram

The first behavioral catalog or ethogram for any madtom was published for the Neosho Madtom (Bulger et al. 2002ab; Fig. 15.39; Table 15.5). Fourteen active and nine inactive behaviors were categorized into six specific behavioral types: resting, swimming, feeding, aggression, cavity enhancement, and courtship. The terminology of the ethogram helps in standardizing earlier terms used to describe the same behaviors. For example, their term carousel refers to mutual caudal embrace and tail curl to male-only caudal embrace, two sets of terms used to describe fundamental aspects of courtship and spawning (Fig. 15.39; Table 15.5).

Care-giving Behavior

A most dramatic example of care-giving behavior in an ictalurid is the field experiment of C. C. Abbott related in
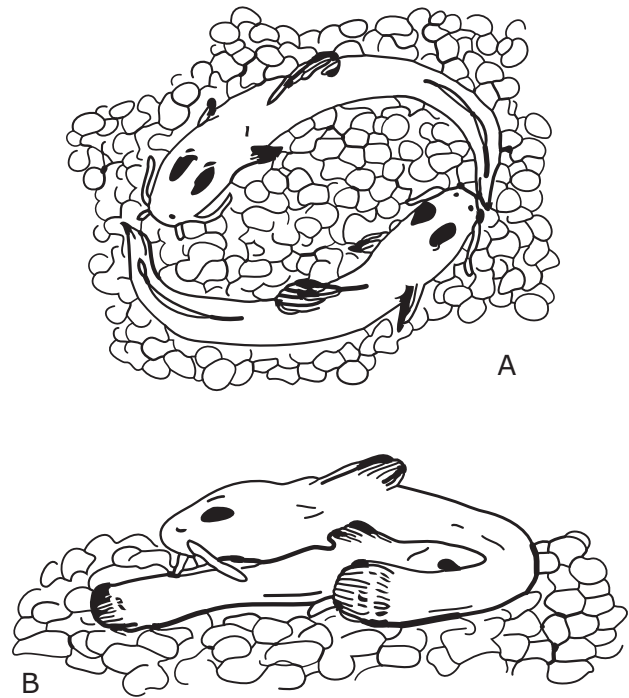

Figure 15.39. Courtship behavior of the Neosho Madtom, *Noturus placidus*. (A) Carousel behavior: male and female swim in circles head to tail near substrate. (B) Tail curl behavior: male and female lie above substrate with tail of male wrapped around head of female while both quiver (redrawn from Bulger et al. 2002b).

Breder & Rosen (1966:258; see also reproduction section). Abbott told of catching a whole family of young *Ameiurus catus* in a small transparent globe, covering it with a fine screen and placing it in the water near the parent fish (gender not indicated). "The parent 'recognized' its offspring and tried to get at them. When the young were released, they and the parent immediately swam away 'in compact ranks.'" This is now old news (Fig. 15.2). Abbott's second experiment is the most fascinating. The globe was placed on the bank of the stream from which the young were taken, in full view of the parent fish. "This fish at once recognized that her young were not in the creek although they were swimming in water . . . its curiosity overcame its discretion; and it left the creek . . . made its way to the base of the globe containing her [not gender identification] young, a distance of about two feet. Here she remained for 9 min . . . and then returned to the water. In a few moments she returned . . . I now liberated the young catfish and they immediately clustered about their parent and followed her into deep water." We agree with Breder & Rosen (1966) that this experiment needs to be repeated.

Table 15.5. Ethogram of behaviors of Neosho Madtom, *Noturus placidus*. Behavior labeled as I = inactive (resting) or A = active, and categorized as type: resting, swimming, feeding, cavity enhancement, aggression, and courtship (from Bulger et al. 2002a).

Behavior	Description	Activity	Type
Performed by either fish:			
Upside down	Resting upside down under structure	I	Resting
Quiet in	Resting quietly under structure	I	Resting
Quiet out	Resting quietly out of structure	I	Resting
Restless in	Moving slightly about under structure	I	Resting
Restless out	Moving slightly about outside of structure	I	Resting
Circle alone	Swimming in circles against glass at front, back, or side of tank	A	Swimming
Swim	Swimming in no particular pattern	A	Swimming
Feeding	Feeding	A	Feeding
Headstand	Vertical in water nudging rocks with head	A	Cavity enhancement
Rock move	Moving a rock in its mouth (picks up rock and drops it in another place)	A	Cavity enhancement
Spin	Swimming in circular pattern under structure	A	Cavity enhancement
Fanning	Fanning tail while resting under structure	A	Courtship
Performed by both fish:			
Quiet in both	Both fish resting quietly under structure	I	Resting
Quiet out both	Both fish resting quietly out of structure	I	Resting
Restless in both	Both fish slightly moving about under structure	I	Resting
Restless out both	Both fish slightly moving about out of structure	I	Resting
Circle chase	One fish chases other in circular pattern in front, back, or side of tank; individuals periodically meet at and have some sort of physical contact (rub, bite, or nudge)	A	Swimming
Bite	One fish bites at body of other fish	A	Aggression
Chase	One fish chases other in no particular pattern	A	Aggression
Nudge	One fish nudges resting individual and swims away or rests next to it; nudged individual may swim or remain resting	A	Aggression
Jostle	Fish switch positions back and forth under structure between short periods of rest	A	Courtship
Carousel	Fish swim together head to tail in small circular pattern under structure	A	Courtship
Tail curl	Fish lay side by side, head to tail; male tail wrapped around head of female and both fish quiver; this behavior only seen following carousel	A	Courtship

Hypogean Species

Among the hypogean ictalurids, behavioral observations are available only for *Prietella* (Fig. 15.7). Jaw locking (two individuals mutually grasping jaws) occurred in *Prietella* especially when new individuals were introduced into an aquarium. Jaw locking lasted for several hours, and probably involved males establishing social dominance hierarchies. Individuals also rested on their sides (common in other ictalurids in aquaria), and possible courtship behaviors occurred, but no eggs or larvae were ever found (Hendrickson et al. 2001).

REPRODUCTION

Overviews of the reproductive biology of North American Catfishes in natural settings (i.e., not in a culture pond) are summarized for Channel Catfish (Hubert 1999), Blue Catfish (Graham 1999), Flathead Catfish (Jackson 1999), and the entire genus *Noturus* (Burr & Stoeckel 1999). No synthesis of this information is available for bullheads (*Ameiurus*), but major papers are summarized here. In fact, *Ameiurus*, in several fundamental ways, is different from the remainder of the ictalurids as presently understood. Few data exist on any of the four species of blindcats (Table 15.1). Stoeckel & Burr (1999) reviewed >120

papers on reproductive traits and methods used to spawn ictalurids, which are not covered here.

Despite the huge range in size of adults, broad generalizations are possible about reproduction in ictalurids without sacrificing accuracy. Some of these include (1) a largely summer (i.e., June, July, August) nesting season (in some regions, May is often the beginning of the nesting season and September the ending); (2) head-to-tail spawning positions; (3) cavity nesting (i.e., speleophilic; Balon 1975); (4) possible polygamy; (5) production of relatively large embryos and hatchlings in a precocial state or the mesolarval stage (sensu Snyder 1976); (6) parental care-giving behaviors primarily by the male (Blumer 1979); (7) oral manipulation of the egg mass and fanning of eggs and larvae; (8) filial cannibalism (Clemens & Sneed 1957; Breder & Rosen 1966; Wallace 1967, 1972; Burr & Stoeckel 1999; Phillips 2003); (9) tight schools of young with care-giving parent(s) in *Ameiurus* continuing for weeks post-hatching (Fig. 15.2); and (10) biparental care more frequent in *Ameiurus* (Blumer 1985b). Even with these shared generalizations, consideration of life history information (i.e., fecundity, generation time, and offspring investment), places genera in surprisingly disparate positions in trilateral life history (see next paragraph). One of the most striking shortcomings of the data on reproduction in ictalurids is how little is published on the large species (i.e., Blue Catfishes and Flathead Catfishes), and how poorly known the Channel Catfish is in natural (i.e., non-culture settings) or wild settings. Little substantive reproductive data exists on Snail Bullhead, Spotted

Bullhead, *Ameiurus serracanthus*, and Flat Bullhead, *Ameiurus platycephalus* (see Olmstead & Cloutman 1979). Also, despite the relatively large literature on North American Catfish life history, surprisingly little information is available across multiple populations of the same species, which would be useful in considering population variability and environmental effects (Baker & Heins 1994).

Winemiller & Rose (1992) developed a trilateral life history model that provides a useful framework for comparing North American Catfishes. The model, created from life history data from many fishes, proposes trade-offs between fecundity, offspring investment (parental care and egg size and nutrition), and generation time, which defined the three major axes of the model and the three major life history strategies: periodic (maximizing fecundity), equilibrium (maximizing offspring investment), and opportunistic (minimizing generation time) (Fig. 15.40). When compared with other fishes, North American Catfishes are generally all classified as equilibrium strategists or intermediate between strategies for many madtoms (opportunistic-equilibrium) and bullheads (equilibrium-periodic) (Winemiller & Rose 1992; Mims et al. 2010). Here, however, Catfish genera are compared among each other using the same trilateral framework (Fig. 15.40) and information in Table 15.2. *Ictalurus* spp. with their high fecundity and relatively low parental care, are shifted more toward the periodic strategy. The genera *Ameiurus* and *Noturus* with their extreme parental care and shorter generation time are more equilibrium-opportunistic than the other genera. The genus *Pylodictis* is intermediate among the other genera with relatively high fecundity and
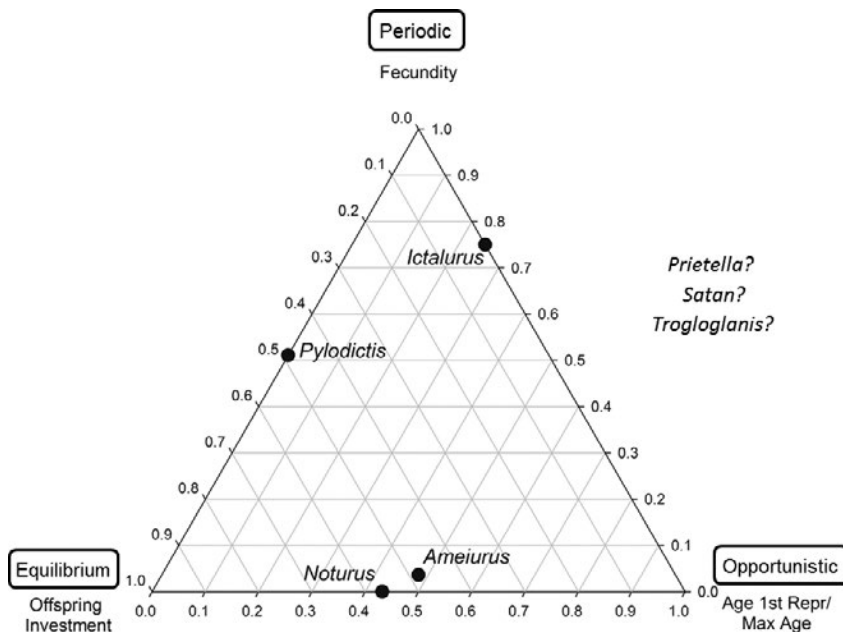

Figure 15.40. Genera of North American Catfishes (Ictaluridae) placed in trilateral life-history space (see Winemiller & Rose 1992). Genera were ranked based on fecundity (right axis), generation time (bottom axis), and offspring investment (left axis) using life-history information (Table 15.1). Traits were scaled between 0 and 1 for ternary plots. Age at first reproduction relative to maximum age (similar results for minimum size at maturity relative to maximum size) was used as a proxy for generation time. Information on the cave Catfishes (genera *Prietella*, *Satan*, *Trogloglanis*) was too scant to place them in the model.

intermediate offspring investment but short generation time relative to maximum age. The relative life history strategies of North American Catfishes also generally follow the predictions of Winemiller & Rose (1992) with respect to environmental conditions promoting investment in certain traits. Periodic strategists, for instance, should be favored under predictable and seasonal conditions, and indeed *Ictalurus* species are well-documented to take advantage of seasonal floodplain inundation, perhaps more extensively and to more benefit than Flathead Catfish (Mayo & Schramm 1999; Schramm et al. 2000; Schramm & Eggleton 2006). Opportunistic strategists should be favored under more variable environmental conditions, and many *Ameiurus* species and most *Noturus*, the more opportunistic-shifted genera, occur in small to medium size streams that are characterized by more temporally variable flows and environmental conditions (Schlosser 1987). Habitats that have increased competition for resources, greater resource stability, and low disturbance levels promote the equilibrium strategy, and some *Ameiurus* prefer small impounded waters that may have these conditions (although based on combined data within genera, see Table 15.2, *Ameiurus* and *Noturus* are similarly situated between opportunistic and equilibrium endpoints).

Here, major aspects of reproduction are described for all major genera when known. First, sexual dimorphism among all genera is described and then age and size at maturity; spawning season, spawning habitat, and spawning behavior; fecundity; and embryo and larval development are summarized for *Ictalurus* (forktail Catfishes), *Ameiurus* (bullheads), Flathead Catfish, and *Noturus* (madtoms). Finally, the scant information on reproduction in the blindcats is presented.

Sexual Dimorphism

Ictalurids do not undergo dramatic external changes in color or fin size during the breeding season as is characteristic of many fishes in eastern North America (e.g., darters, Percidae; minnows, Cyprinidae; see Page & Burr 2011). During spring and summer months (about April to September), adult males develop enlarged dorsal cephalic muscles, swollen lips, and swollen genital papillae (Figs. 15.25 and 15.41). Both sexes of Channel Catfish and some of the bullhead species develop enlarged heads and lips. As the nesting season progresses, males often have scratches on their dorsal surfaces and napes, presumably related to spawning activities, rubbing against nesting materials, or preparing nests. Requiring verification is the intriguing suggestion that males have longer tails than females, especially during the nesting season, a possible adaptation for head clasping of the female during quivering and egg deposition (Chan 1995).

The sexes are easily determined internally by examination of gonads. Mature male testes of ictalurid Catfishes are all similar and are elongate, whitish, and opaque with long, villiform projections (i.e., lobulate testes) of varied sizes (Clugston & Cooper 1960; Sneed & Clemens 1963; Fig. 15.24). Mature females have easily discernible eggs of varying sizes, and ripe eggs are huge (Table 15.1) compared with most other North American fishes.

Maturity in *Ictalurus* (forktail Catfishes)

Age at sexual maturity of Channel Catfish, the exemplar for the genus *Ictalurus*, varies tremendously (2–12 years) depending on geographic location and other environmen-
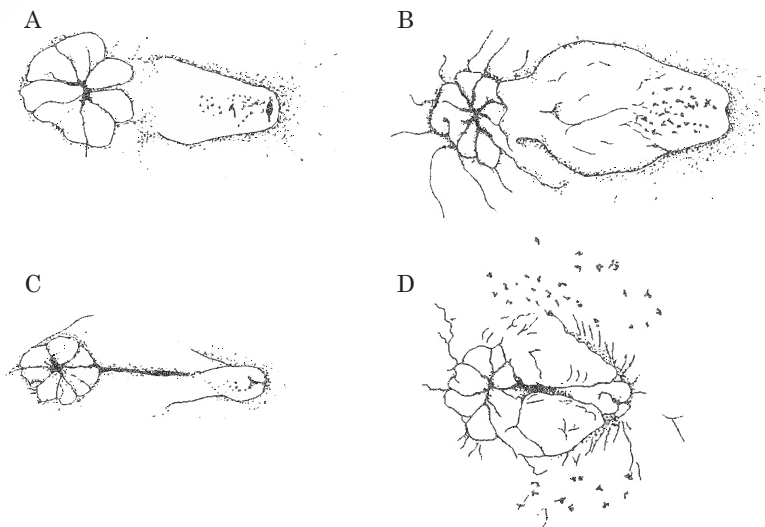

Figure 15.41. Genital papillae of Slender Madtoms, *Noturus exilis*, from Green Creek, Illinois. (A) Non-breeding male, 70.0 mm SL, captured 7 January 1978. (B) Breeding male, 92.0 mm SL, captured 25 May 1979. (C) Non-breeding female, 78.0 mm SL, captured 7 January 1978. (D) Breeding female, 71.5 mm SL, captured 27 June 1979. Left is anterior (redrawn from Mayden & Burr 1981).

tal factors (i.e., length of growing season, watershed fertility; Shephard & Jackson 2005), but modal age of maturity is about 4–5 years (Hubert 1999; Table 15.1). Adults from southern states mature at about 2–3 years, those from colder waters at 6–12 years. Even within a given population, age at maturity varies widely; a range of ≤7 years can exist between youngest and oldest fish at sexual maturity (Hubert 1999). Within a population, ≤250-mm (9.8 inches) difference in length at sexual maturity can exist. Size at sexual maturity ranges from 170 to 550 mm TL (6.7–21.7 inches), but modal lengths are 300–375 mm TL (11.8–14.8 inches). Fish apparently are mature at shorter lengths in southern areas. Males reportedly mature at lengths 25–50 mm (1–2 inches) shorter than females, but the reverse occurs in other populations (Hubert 1999).

Spawning Season, Spawning Habitat, and Spawning Behavior in *Ictalurus* (forktail Catfishes)

Channel Catfish normally spawn once a year in late spring (as early as March or April in South Carolina) to early summer (mid-June to July in South Dakota and Wyoming) at water temperatures of 21–29°C (69.8–84.2°F); optimal spawning temperature appears to be 27°C (26–28°C) (78.8–82.4°F; Table 15.1). Numerous studies in riverine and lacustrine habitats support such generalizations (Hubert 1999). Manipulation with Common Carp (*Cyprinus carpio*) pituitary extract can bring about autumn spawning (November) in cultured Channel Catfish (Brauhn 1971), and the pheromone prostaglandin F-2alpha injected into females attracted male Channel Catfish and Blue Catfish most strongly compared with other hormonal injections (Broach & Phelps 2011). Most nesting, with embryos in the nest, occurs in June and July throughout the natural and naturalized range of the Channel Catfish (Hubert 1999). Flooding and reduced water temperature after the onset of spawning may lead to cessation or intermittency of spawning, especially at <15°C (59°F; Deacon 1961).

Habitat for nesting and spawning are secluded and semidarkened areas provide visual cover and protection from strong currents. A few instances of spawning on the bottom at sites with no nearby cover are known (Geibel & Murray 1961; Becker 1983; Table 15.1). Males apparently select the nesting site, which can be crevices in woody debris, cavities between roots of undercut trees, burrows in banks, and spaces between and under rocks. Few studies have actually identified and described a nest in the wild. One nest in a Kansas stream was in a hole (12–15 cm, 4.7–5.9 inches, diameter) at the base of a clay bank extending into a chamber

(75 × 30 cm, 29.5 × 11.8 inches) with a floor of clean gravel and a small mound of gravel at the entrance (Deacon 1961). In a Wyoming river system, one spawning site was a cavity under a large boulder, and 12 others were in the main channel associated with cover formed by large boulders or submerged woody debris over a gravel-rubble substrate in water 1.2–1.8 m (3.9–5.9 feet) deep (Gerhardt & Hubert 1990). Spawning occurred among rubble and boulders in water 2.5–3.0 m (8.2–9.8 feet) deep in a New Mexico reservoir (Jester 1971). Channel Catfish also may leave lacustrine settings and move to riverine habitats to spawn (Hubert 1999; see behavior section).

Before spawning, mature males select a nest site, clean it, and then spawn with a female in the prepared nest. Courtship behavior has only been observed in aquaria but involves a period of biting and nudging followed by head-to-tail orientation and tail wrapping around the head of the partner before actual spawning. The entire process can last 4–6 h (Clemens & Sneed 1957; Wydoski & Whitney 2003; Tatarenkov et al. 2006). Both observational (Clemens & Sneed 1957) and genetic (Tatarenkov et al. 2006) information support the tendency of serial monogamy in Channel Catfish. Males may spawn multiple times per season but with only one female per event, who apparently spawns only once a season (Clemens & Sneed 1957; Sigler & Sigler 1987; Tatarenkov et al. 2006). Once eggs are laid, the male chases the female off the nest and begins guarding and caring for the developing embryos. During the 6–10 day period before hatching, males fan and manipulate the eggs with fins and body, possibly to aerate them or to remove flocculent material from the egg surface (Brown 1942; Clemens & Sneed 1957; Davis 1959). Males cease guarding after the young leave the nest or shortly thereafter (about 7–10 days; see fecundity in *Ictalurus* [forktail Catfishes] subsection). They apparently do not travel with the school as in *Ameiurus*. A few fish may spawn more than once in a season (Dill 1944; Carlander 1969).

Fecundity in *Ictalurus* (forktail Catfishes)

Total annual fecundity of Channel Catfish (estimate of number of eggs in ovaries) ranges from about 1,000 to 60,000 eggs (Jerald 1970; Fig. 15.42; Table 15.1). The number of eggs produced generally increases with age and TL. Fish weighing 0.45–1.8 kg (1.8–4.0 pounds) produce about 8,800 eggs/kg, but for larger fish (>1.8 kg, 4.0 pounds) egg production decreases to 6,600 eggs/kg (3,000 eggs/pound) (Clemens & Sneed 1957). Mean fecundity varies among different populations, but this is probably an artifact of variation

Figure 15.42. Egg mass of a Channel Catfish, *Ictalurus punctatus*, recently removed from a spawning container in a culture pond (courtesy of © David Cline, Auburn University).

in ages and lengths of females in the samples (Hubert 1999). Eggs of mature females compose about 15% of total body weight shortly before spawning occurs (Muncy 1959).

Embryo and Larval Development in *Ictalurus* (forktail Catfishes)

In *Ictalurus* (Channel Catfish), embryos (3.5–4.3 mm, 0.1–0.2 inches, in diameter) require 9–10 days at 16–18°C (60.8–64.4°F), 9–12 days at 19–21°C (66.2–69.8°F), and 6–7 days at 24–26°C (75.2–78.8°F) to hatch (Brown 1942; Clemens & Sneed 1957; Reyes 2010). Eggs are spherical, adhesive, demersal, and yellow when first laid; they are deposited in a large mass (Fig. 15.42). Eggs become darker (brown) as development progresses. Hatchling size is variable, but modally ranges from 9.8 to 10.1mm TL (0.39–0.40 inches; Fig. 15.43; Simon & Wallus 2004; Reyes 2010). Young actively swim 1–2 days after hatching and leave the nest after about seven days. Young may stay in a shoal of siblings for 1–2 weeks before dispersing into shallow flowing water at about 25 mm TL (0.98 inches). Blue Catfish eggs hatch in 7–10 days at 24–26°C (75.2–78.8°F); hatchlings are 8.5–9.5 mm TL (0.33–0.37 inches; Simon & Wallus 2004).

Maturity in *Ameiurus* (bullheads)

Maturity in White Catfish occurs in the third or fourth year of life at 178–203 mm TL (7–8 inches); females were mature at 208 mm TL (8.2 inches) in South Carolina (Stevens 1959), 211 mm FL (8.3 inches) in California (Murphy 1951), and 1–2 years and about 152–211 mm FL (6.0–8.3 inches; Jones et al. 1978) on the Atlantic Slope (Table 15.1). Black Bull-
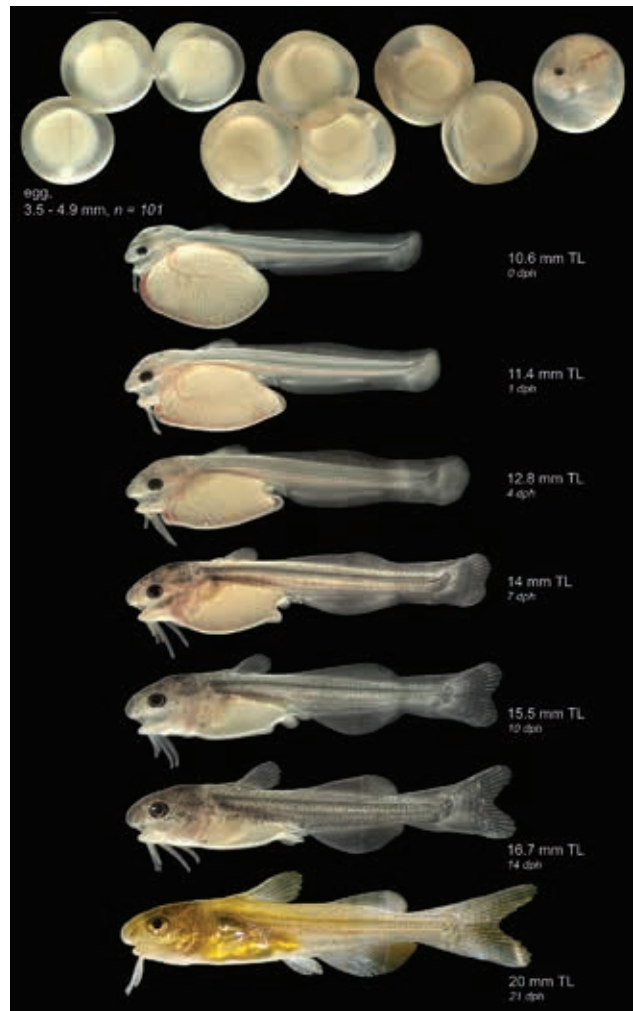

Figure 15.43. Channel Catfish, *Ictalurus punctatus*, life stage developmental series of eggs and larvae raised at 19–21°C (dph = days post hatching) (courtesy of René Reyes, Tracy Fish Collection Facility, U.S. Department of the Interior, Bureau of Reclamation; photograph is in the public domain).

heads have a modal maturity of 2–3 years and about 180–250 mm TL (7.1–9.8 inches; Simon & Wallus 2004). Brown Bullheads are mature by ages 2–3 at about 200 mm TL (7.9 inches). Mature female Snail Bullheads are 3–4 years old and 127–172 mm TL (5.0–6.8 inches; Sakaris et al. 2011b). The sex ratio in species of *Ameiurus* is near 1F:1M (Brooks et al. 1982) with slight biases toward each gender depending on sampling gear.

Spawning Season, Spawning Habitat, and Spawning Behavior in *Ameiurus* (bullheads)

Reasonable reproductive data exists for five of the seven species of *Ameiurus* (e.g., Ryder 1883; Eycleshymer 1901;

Smith & Harron 1904; Kendall 1902, 1910; Richardson 1913; Ulrey et al. 1938; Breder 1935, 1939; Borgeson & McCammon 1967; Carlander 1969; Dennison & Bulkley 1972; Wallace 1967, 1972; Campbell & Branson 1978; Phillips 2003). The primary data are for four species common in the eastern United States or on the Atlantic Slope: *A. catus*, *A. melas*, *A. natalis*, and *A. nebulosus*.

Summer spawning periods are the rule throughout the native range of the bullhead species; peak months are June and July, some nesting may occur in late May at lower latitudes and extend into late August at more northern latitudes (Table 15.1). Spawning and nesting occurred in late May in a southern Michigan lake population of Brown Bullheads (Blumer 1985a). Spawning temperatures are >20°C (68°F) and ≤30°C (86°F) (the latter probably recorded during the actual nesting period). Averages are in the range of 23–27°C (73.4–80.6°F). In Black Bullheads, testosterone and estradiol increased with increasing GSI in the spring for both sexes, dropping just before spawning but with estradiol peaking during spawning (Rosenblum et al. 1987). Treatment with gonadotropin-releasing hormone can cause an increase in sex hormone production, but the fish are not sensitive to this treatment in summer following spawning (Rosenblum & Callard 1987).

Bullheads build saucer-shaped nests, sometimes in open water, often in shaded areas, but in riverine environments we find them in typical cavity nests under flat rocks, near undercut banks with root wads, or in anthropogenic structures, including large coffee cans, under boards, and inside automobile tires (Table 15.1). Saucer-shaped nests are often in still or slow-moving water; the nests are 300–914 mm (11.8–36.0 inches) in diameter and 305–457 mm (12–18 inches) deep (Jones et al. 1978). Most bullheads apparently nest in shallow water but Brown Bullheads in lakes make nests in water >1 m (3.3 feet) deep (Blumer 1986). In White Catfish, both sexes reportedly excavate a single saucer-shaped nest. Pebbles are removed with the mouth or by fanning them aside with fins and body. The spawning act is part of the typical repertoire for ictalurids, a lateral head-to-tail orientation with the male's caudal fin curved around the female's head (Jenkins & Burkhead 1994). Once the large mass of eggs (Fig. 15.44) is deposited in the nest, the male guards and fans the eggs (Fig. 15.45). In some instances, eggs may be cared for by both parents (well known in Brown Bullheads; Blumer 1986). After hatching, the male usually cares for the young (Fowler 1917). In Brown Bullheads one or both sexes may guard the eggs for the 6–9 day incubation period and then through 7–10 days until larvae leave the nest. After this the male guards the school of lar-
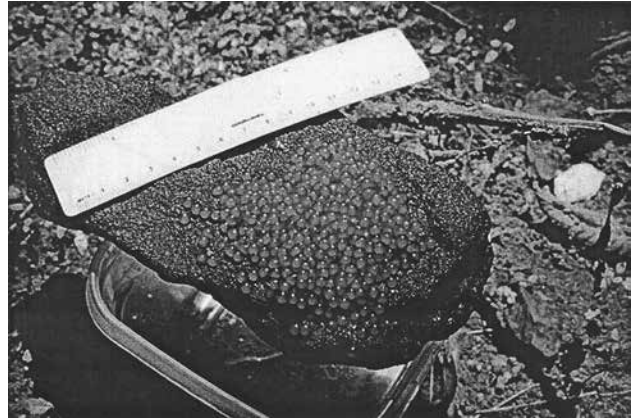

Figure 15.44. Clutch of Yellow Bullhead, *Ameiurus natalis*, eggs from Little Kinkaid Creek, Illinois (courtesy of BMB).

vae for an unknown duration (see next paragraph). Female Black Bullheads reportedly construct a nest about equal in diameter to her length, although both sexes may participate in construction (Boschung & Mayden 2004). She fans away objects and moves them with her snout. The spawning pair embraces head to tail with a clasp of the female's head by the male's tail. The female quivers for about 1 s and eggs are released; about 200 eggs / spawning episode are released. Spawning is repeated about five times in 1 h (Wallace 1967). Spawning and nesting in Yellow Bullheads is similar to that of the Black Bullhead (Wallace 1972); 300–700 eggs are laid during a spawning clasp.

Adult Bullheads care for their young brood long after hatching. Schools of small black fish can be seen in lakes and streams during the summer and are accompanied by at least one adult, sometimes both parents. The lengthy parental care exemplified in bullheads is not exhibited by other ictalurid genera. The literature is not precise in terms of how long parents remain with the young school, but guarding of young probably continues until the end of their first summer (certainly late August in many locations) and abandonment may occur when young reach about 25 mm TL (1 inch; Black Bullhead; Scott & Crossman 1973) or in Yellow Bullheads at about 50 mm TL (2 inches; Mansueti & Hardy 1967). The young without the parent(s) may persist in schooling during the day (Darnell & Meierotto 1965) throughout the summer. Two schooling Brown Bullhead broods in Lake Danford, Quebec, contained 610 and 778 young (Scott & Crossman 1973).

Fecundity in *Ameiurus* (bullheads)

Fecundity estimates for *Ameiurus* have sometimes been over-generalized. Various studies report 1,000–4,000

Figure 15.45. A Black Bullhead, *Ameiurus melas*, male guarding a clutch of eggs (photograph taken in Lake Metonga, Crandon, Wisconsin, July 2005, by and used with permission of © Engbretson Underwater Photography).

presumably mature eggs in ovaries (Menzel 1945; Prather & Swingle 1960). In the Black Bullhead, fecundity ranges were 2,500–5,500 eggs/female (Dennison & Bulkley 1972). Three female Black Bullheads (176–322 mm TL, 6.9–12.7 inches) from Louisiana had 176–812 ripe eggs, 2–3 mm (0.08–0.12 inches) in diameter (Simon & Wallus 2004). Female Brown Bullheads (227–347 mm TL, 8.9–13.7 inches) had 1,797–9,870 mature eggs (Harvey & Fortin 1982). Mature ovarian oocytes for three gravid Snail Bullheads were 200–280 (mean diameter 3.25–4.65 mm, 0.13–0.18 inches) for females 127–172 mm TL (5.0–6.8 inches; Sakaris et al. 2011b). Five female Brown Bullheads (159–423 mm TL, 6.3–16.7 inches) from different geographic locations had ripe egg counts from 73 to 2,856; eggs were 2.0 mm (0.08 inches) in diameter (Simon & Wallus 2004). The literature contains fecundity estimates as high as 13,000 for a single female, but we doubt the accuracy of the count and that the number represents ripe eggs. Brown Bullhead egg clutches in a Michigan lake averaged 1,163 ± 95 eggs (Blumer 1982, 1985a). Egg clutches (i.e., the egg masses found in nests) of White Catfish are deposited in large masses, one of which was 203 mm (8.0 inches) long, 102 mm (4.0 inches) wide, and 12.7–19.5 mm (0.5–0.8 inches) thick; it contained 2,000 embryos (Jones et al. 1978). Age-2 White Catfish produced 2,500–4,000 fry/spawn (Prather & Swingle 1960). Eggs from mature

females captured in June were 4.0–4.5 mm (0.16–0.18 inches) in diameter (Menzel 1945). Fecundity in Black Bullheads may be more related to length than to age, and pond populations appear to have lower mean fecundity than stream populations (Campbell & Branson 1978).

Embryo and Larval Development in *Ameiurus* (bullheads)

In *Ameiurus*, eggs hatch in 6–7 days at water temperatures averaging 26.5°C (79.7°F) (White Catfish; Miller 1966), 6–8 days at 21–22°C (69.8–71.6°F) (White Catfish; Reyes 2010), and 8–9 days at 19–21°C (66.2–71.6°F) (Black Bullhead; Reyes 2010). The fry become progressively darker after hatching. After four days they are dark brown, except on the belly (Prather & Swingle 1960). Embryos (fertilized eggs) are spherical, demersal, adhesive, and 3.2–5.5 mm (0.13–0.22 inches) in diameter; pale yellow in color; each egg has a large yolk mass and a perivitelline space about 10–20% of egg diameter (summarized by Simon & Wallus 2004; Reyes 2010; Fig. 15.46). Hatchlings (as mesolarvae) are 9–9.8 mm TL (0.35–0.39 inches); yolk absorption is complete at 12 mm (0.47 inches; Fig. 15.46). Brown Bullhead embryos hatch in 6–9 days at 20.6–23.3°C (69.1–73.9°F); 5 days at 25°C (77°F); and 8 days at 20–21°C (68–69.8°F) (Simon & Wallus 2004). Brown Bullheads took a maximum
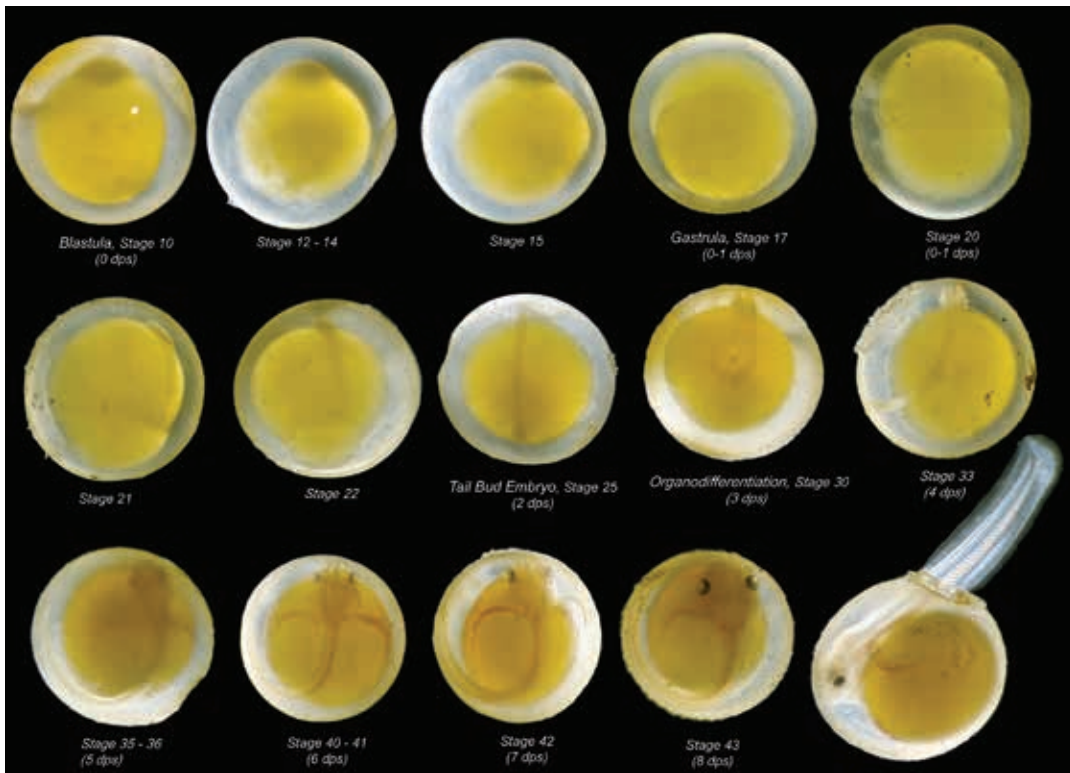
Figure 15.46. (*upper*) White Catfish, *Ameiurus catus*, life stage developmental series of eggs. Stages are based on Armstrong & Child (1962); cleavage stages (Stages 1–7) are not shown. (*lower*) White Catfish life stage development of series of eggs and larvae. All eggs and larvae raised at 19–21°C (dps = days post spawning) (photographs by and used courtesy of René Reyes, Tracy Fish Collection Facility, U.S. Department of the Interior, Bureau of Reclamation; photograph is in the public domain).

of 13 days to hatch during May in Michigan with temperatures varying between 14 and 29°C (57.2–84.2°F) (Blumer 1985a). The most complete description and detailed illustrations of the development of any species of *Ameiurus* is that of the Brown Bullhead (Armstrong & Child 1962; see also White Catfish and Black Bullhead in Reyes 2010). Embryos of that species are positively geotropic and hatchlings are negatively phototactic.

Maturity in *Pylodictis olivaris* (Flathead Catfish)

Estimates of maturity in Flathead Catfish vary, but males generally mature somewhat earlier than females. In a Kansas study, males matured at 3–5 years and were >38 cm TL (15.0 inches); females matured at 4–6 years and were >46 cm TL (18.1 inches; Minckley & Deacon 1959). In a Texas population, maturity occurred between ages 2–5 and 290–635 mm TL (11.4–25.0 inches; Munger et al. 1994). In

Nebraska, males were mature in 3–4 years at 356–432 mm TL (14–17 inches), females in 3–5 years at 356–508 mm TL (14–20 inches; Simon & Wallus 2004). Texas individuals <356 mm TL (14 inches) did not spawn, and few <432 mm TL (17 inches) spawned. Most Flathead Catfish mature between 50 and 75 cm TL (19.7–29.5 inches); lengths that generally correspond to weights of about 1.5–4.0 kg (3.3–8.8 pounds), respectively (Munger et al. 1994; Jackson 1999).

Spawning Season, Spawning Habitat, and Spawning Behavior in *Pylodictis olivaris* (Flathead Catfish)

Similar to other ictalurids, Flathead Catfish spawn in cavities during summer months at temperatures around 19–24°C (66.2–75.2°F) (Snow 1959; Turner & Summerfelt 1971ab; Jackson 1999), probably peaking at 24–28°C (66.2–82.4°F) (Simon & Wallus 2004). Adults (probably males) select protected and darkened nesting sites, including large hollow logs, root masses from downed trees, excavated chambers in clay banks, and anthropogenic structures (old tires, car bodies, metal drums, hot water heaters, prepared nesting boxes). In observations of a single male and female in a large glass tank (11,356 L; 3,000 gallon), a saucer-shaped depression was excavated (apparently by both sexes) in a cavity or under a large submerged object. As noted, the spawning act was observed in an aquarium, and the fish had been propagated in a hatchery (Fontaine 1944; Henderson 1965; Breder & Rosen 1966). Adults were about 1.2 m TL (4 feet) and chose a corner of the aquarium in which to nest. Both sexes used their tails and mouths to clear an area of sand down to the rocky material. The completed nest was about 1.5 m (5 feet) in diameter. The male moved over and beside the female, gently rubbing his belly on her back and sides. The male barbels play some role because they touched the female during the period he rubbed up against her. The male eventually came to rest on the substrate with his caudal peduncle and caudal fin encircling the head of the female. The male quivered noticeably. These courtship behaviors were repeated regularly over a two-week period. When ready, the female began depositing eggs in a depression in the gravel; she expelled eggs in masses of 30–50 that were then fertilized by the male. The pair lay in the same direction, side by side, turning their bellies together. The female then left the nest, and the male fluffed and arranged the eggs. The adhesive, compact, golden-yellow mass can consist of 100,000 embryos (and probably more) (Breder 1935; Fontaine 1944; Fig. 15.47). Actual spawning oc-

curred over a 4.5-h period. The female was then removed from the aquarium, and the male began guarding the egg mass. After spawning in nature, the female apparently leaves or is aggressively chased away, and the male remains to guard, fan, and clean the egg mass. Males in Texas hatchery pens behaved viciously while guarding eggs (Henderson 1965:175). A male would "tear the female to pieces" when she attempted to enter the spawning jar that contained eggs. A number of females that had spawned were killed by the male, in spite of efforts to remove the female from the area as soon as possible.

In the aquarium, the male used fin movements and agitations to aerate eggs and flush away silt, and he turned the egg mass several times a day (Fontaine 1944; Boschung & Mayden 2004). After the young have hatched and begun to swim, they remain for several days in a compact school near the nest but soon disperse and take up their solitary life. The male guards the mesolarvae for about seven days after hatching. To our knowledge, no one has reported in a peer-reviewed paper the observation in nature of a spawning act of a pair of Flathead Catfish, and no reports exist of wild-caught egg masses, descriptions of egg masses, or numbers of eggs and their weights.

Fecundity in *Pylodictis olivaris* (Flathead Catfish)

The Flathead Catfish is the second largest Catfish in North America. In part because of its size in both length and weight, egg production is impressive. Fecundity increases with size. Both ovaries in a female contain eggs, and the numbers that follow are estimates based on ma-

Figure 15.47. Egg mass from propagated female Flathead Catfish, *Pylodictis olivaris*, at Lost Valley Hatchery, Missouri (courtesy of Missouri Department of Conservation).

ture ova. In Kansas, mature females, 305–610 mm TL (12–24 inches), had 6,900–11,300 eggs in their ovaries (Minckley & Deacon 1959). Females weighing 1.04–11.66 kg (2.3–25.6 pounds) had 4,076–31,579 eggs (Turner & Summerfelt 1971b). The mean number of eggs per fish in Arkansas was 13,250 (range 7,961–26,923) for females weighing 1.7–8.2 kg (3.7–18.0 pounds); the number of eggs/kg ranged from 2,397 to 5,749 (1,087 to 2,613 eggs/pound) (Summerville & Crawley 1970). In Nebraska, females 485–930 mm TL (19.1–36.6 inches) had about 3,307 eggs/kg (1,500 eggs/pound) (Simon & Wallus 2004).

Embryo and Larval Development in *Pylodictis olivaris* (Flathead Catfish)

The fertilized embryos (eggs) of *Pylodictis* are demersal, adhesive, and cream to yellow (custard) in color. Mature chorion diameter is about 5 mm (0.2 inches), the yolk may be dark (Snow 1959); eggs adhere to one another in a mass, sometimes described as looking like boiled tapioca pudding (Breder & Rosen 1966). The one egg mass reported in an aquarium was 40.6 cm (16 inches) in diameter, 15.24 cm (6 inches) thick in the center tapering to the thickness of one egg on the outside edge of the mass (Breder & Rosen 1966). A local television program in the Midwest featured hand grapplers on the Wabash River removing adult males from hollow logs and then removing the egg clutches in large handfuls and discarding them (BMB pers. obs.). We do not know of a single clutch mass in a research collection anywhere. Eggs hatch in 6–7 days at 23.9–27.8°C (75.0–82.0°F) or 9 days at 24–25.9°C (75.2–78.6°F) (Snow 1959; Giudice 1965). Fontaine (1944) reported that hatchlings were about 5 mm (0.2 inches) long; we think this is too small and must be a rough estimate of TL at hatching. Hatching size is reported to be about 11–15 mm TL (0.4–0.6 inches; Snow 1959; Simon & Wallus 2004). We are unaware of accurate measurements of hatchlings in peer-reviewed publications or elsewhere, and we are quite certain that 15 mm (0.6 inches) is too large. Simon & Wallus (2004) illustrated young that are 13–19 mm TL (0.5–0.7 inches).

Maturity in *Noturus* (madtoms)

In madtoms, smaller species tend to mature earlier than larger species, and females tend to be smaller than males. In the 18 species in which age or size at maturity is known, eight species reach maturity at 1-year-old or during their second summer of life. The majority of these species do not attain 100 mm SL (3.9 inches), and the female is usually the

one reaching reproductive age in the second summer. Smaller species of *Noturus* maturing by one year include *Noturus leptacanthus*, *N. albater*, *N. hildebrandi*, and *N. baileyi*. The larger species of *Noturus* (i.e., *N. flavus*, Fig. 15.6; *N. flavater*, Fig. 15.48; *N. flavipinnis*, Yellowfin Madtom; *N. furiosus*, Carolina Madtom; *N. gilberti*, Orangefin Madtom; Tadpole Madtom; Margined Madtom; Brown Madtom) do not reach maturity until they are age 2+ (i.e., third summer of life) (Burr & Stoeckel 1999). Species in between these size extremes reach maturity at 1–2 years (Burr & Stoeckel 1999). Females in most species do not grow as large as males (many do not live as long), a consequence of a trade-off between reproductive output and somatic growth.

Spawning Season, Spawning Habitat, and Spawning Behavior in *Noturus* (madtoms)

Breeding pairs or guardian adult males tending eggs or young occur in *Noturus* from about the first week of May to about the third week of September (Table 15.1). The rather broad span of dates is caused by one species, *N. gyrinus*, studied in Lake Waccamaw, North Carolina, a mid-southerly latitude for this wide-ranging species. With only two exceptions (*N. h. hildebrandi* and Orangefin Madtom) all of the remaining species have nesting seasons from about mid-June through mid-August, and >90% of the species studied are nesting at temperatures in the range of 24–30°C (75.2–86°F). Increasing photoperiod is an apparent environmental cue that at least in part triggers courtship and nest-building behaviors (Bulger et al. 2002a). All species nest in a cavity, either under natural stream substrates (i.e., rocks, logs, empty bivalve shells, crayfish burrows, under roots of vegetation; Figs. 15.49 and 15.50) or in human refuse (inside cans and bottles, under boards,

Figure 15.48. Checkered Madtom, *Noturus flavater*, Swan Creek, Missouri (courtesy of W. Roston).

under a tin sheet). Nest cavities can be made solely by the male (Mayden & Burr 1981) or females can also participate in nest construction (Fitzpatrick 1981; Chan 1995; Bulger et al. 2002b). Tank-held Neosho Madtoms under a long-day, short-night photoperiod performed nearly all their cavity enhancement activities in the dark, being relatively inactive during daylight hours (Bulger et al. 2002b). Cavity enhancement in this species was reduced in aquaria with water flow, suggesting negative impacts of heightened flow during the spawning season (Bryan et al. 2006).

Nests with egg clutches are guarded by males only (Fig. 15.49). Guardian males may stay with their brood for ≥2 weeks and maybe ≤3 weeks during which time the guardian male apparently feeds little, if any. Brown Madtom males may spend a minimum of 10–21 days with the nest after egg laying (Chan 1995). A Neosho Madtom male spent >1 week with an aggregation of yolk-sac larvae (Wilkinson & Edds 1997), and Smoky Madtom males may spend three weeks with their brood (Dinkins & Shute 1996). Some evidence of female preference for larger males exists in that large males guard large clutches, but this is not widely documented across species (Burr & Stoeckel 1999).

Fecundity in *Noturus* (madtoms)

As a group, madtoms are among the least fecund of North American freshwater, oviparous fishes. Counts of annual oocyte production, based on mature or ripe oocytes only, range from a minimum of six in *Noturus lachneri* to a maximum of 570 in *N. flavus* (Figs. 15.49 and 15.50). The average annual fecundity across all species studied is 100 in females that average 58 mm SL (2.3 inches). Relatively small species such as *Noturus leptacanthus*, *N. hildebrandi lautus* (Least Madtom, northern subspecies), Elegant Madtom (*N. elegans*), and Ouachita Madtom represent the low extreme in the continuum with mean annual fecundity estimates of 24, 30, 31, and 33, respectively. The Stonecat, with an average fecundity of 378, is more fecund than congeners in number of progeny per female, but mature females are larger and produce slightly fewer oocytes per gram of body weight (Burr & Stoeckel 1999). A few studies since Burr & Stoeckel's (1999) review filled in data on fecundity and other life history traits of some species (*Noturus funebris*, Bennett & Kuhajda 2008; Frecklebelly Madtom, *N. munitus* Bennett et al. 2010; *N. phaeus* Chan & Parsons 2000) but have not significantly changed how the general pattern is framed. Relative fecundity, expressed as mature oocytes / g body weight, allows for standardized comparison of fecundity among
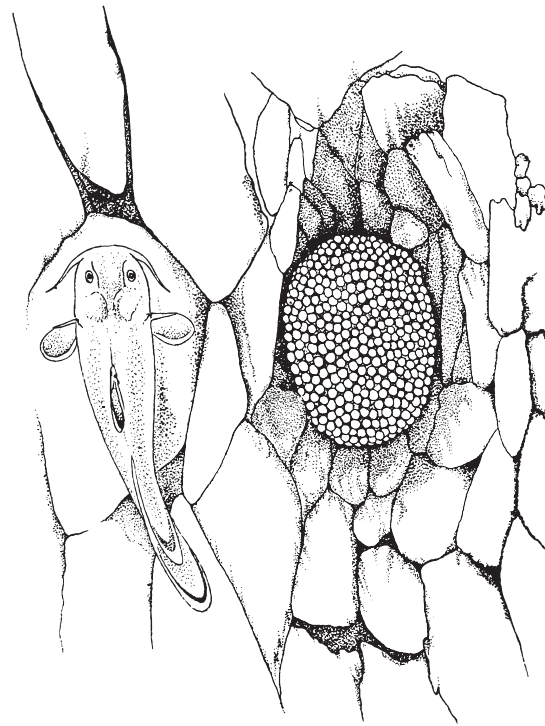

Figure 15.49. (upper) A male Slender Madtom, *Noturus exilis*, with his clutch of eggs after a large rock (254 × 101 mm, 10 × 4 inches) protecting the nest was removed in Green Creek, Illinois (courtesy of © R. Mayden and B. Burr). (*lower*) Composite illustration of a nesting male Margined Madtom, *Noturus insignis*, and his clutch of exposed eggs (scale slightly reduced) in July 1916 in Tohickon Creek (Delaware River tributary), Pennsylvania (10 nests observed). The nests of madtoms are typically in shallow excavations under flat rocks, and in this case, the nests were excavated to a depth of about 51–76 mm (2–3 inches), the egg masses about 55 mm (2.2 inches) in length or diameter, and the usually flattened cover rocks about 30–61 cm (1–2 feet) in diameter (redrawn from Fowler 1917).

madtom species (Mayden & Walsh 1984; Burr & Stoeckel 1999) but is not known for all species.

Relative to other eastern North American fishes, and given their low fecundity, female *Noturus* lay a small clutch of large eggs or embryos. Clutches found in nests are in a single mass in >98% of case studies. Clutches lie free in the nest and are not attached to other surfaces (Figs. 15.49 and 15.50); eggs adhere only to one another (Burr & Stoeckel 1999). Across 20 species for which nest-clutch information is known, the grand mean of annual clutch production is 101 eggs or embryos. Nest clutch sizes (eggs or embryos) range from ≤25 in *Noturus leptacanthus* (range 13–25, mean 17.6) and *N. hildebrandi lautus* (11–22, mean 19.2) to numbers >200 in Checkered Madtom, *Noturus flavater* (304+) and *N. flavus* (104–208, mean 174).
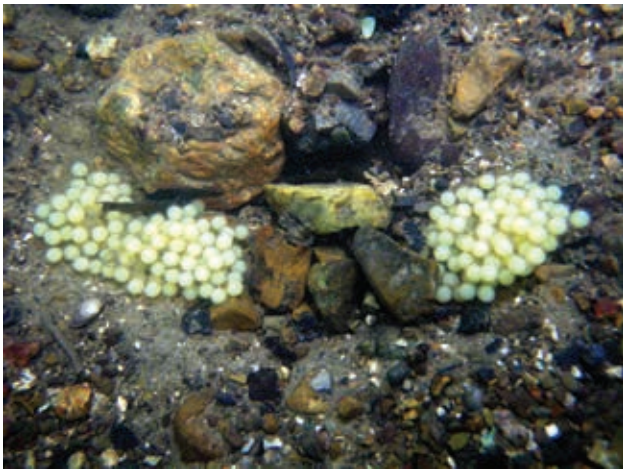

Figure 15.50. Clutch of a male Yellowfin Madtom, *Noturus flavipinnis*, in Copper Creek, Virginia (courtesy of © P. Rakes and J. R. Shute).

Mature ovarian and fertilized eggs of *Noturus* are large, both in absolute terms and relative to their body size. Mean mature oocyte diameter ranges from 2.0 to 3.8 mm (0.08–0.15 inches; mean 2.5 mm, 0.1 inches) in *Noturus* (Table 15.1). Few North American freshwater fishes produce eggs >3.0 mm (0.1 inches) in diameter, and in most cases, the eggs range from 1.0 to 2.0 mm (0.04–0.08 inches) in diameter. Only ictalurids and salmonids have relatively large eggs, >4.0 mm (0.16 inches) in diameter in some species and populations.

Embryo and Larval Development in *Noturus* (madtoms)

Fertilized, developing eggs of *Noturus* are among the largest for North American fishes. Mean chorion diameters ranging from 2.6 to 5.0 mm (0.10–0.20 inches), and yolk diameters ranging from 2.6 to 4.0 mm (0.10–0.16 inches; excluding *Noturus baileyi*). The perivitelline space is large. They range in color from whitish or light cream to deep amber, most being deep yellow. Clutches removed from nest sites and incubated in the laboratory hatch in 5.8–9.0 days at 24–26°C (75.2–78.8°F) (Table 15.1). The few species incubated at cooler temperatures (i.e., 20°C, 68°F) hatched in about 11–12 days. In the 17 species in which considerable detail of hatching or development is described, all embryos hatch as mesolarvae (following definitions of Snyder 1976; Fig. 15.51). All break through the chorion tail first. Hatchlings range in size from the tiny *N. baileyi* at 3.4 mm TL (0.13 inches) to the largest described at 10.0 mm TL (0.39 inches) for *N. insignis* (Table 15.1). Mean size at hatching is 7.0 mm TL (0.28 inches). The Stonecat, the largest species of *Noturus*, hatches at only
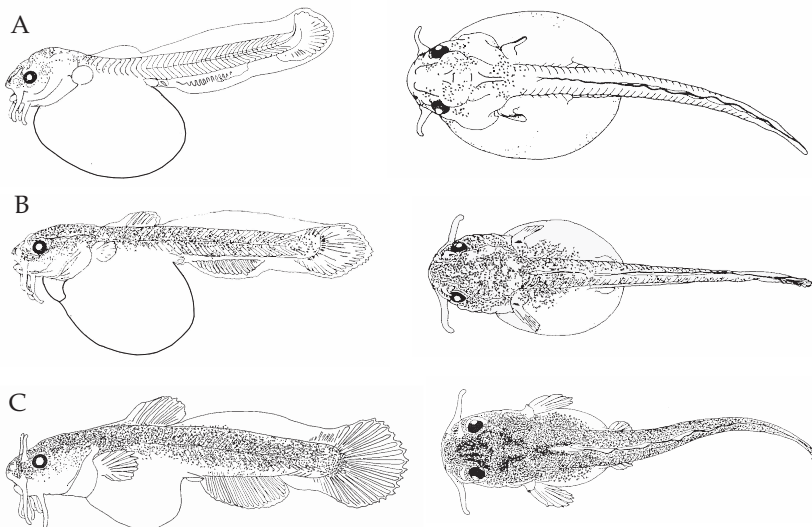

Figure 15.51. Development of the Slender Madtom, *Noturus exilis*, from Green Creek, Illinois (lateral view left, dorsal view right): (A) 1-day-old (197 h) larva, 8.1 mm TL; (B) 3-day-old larva, 10.0 mm TL; (C) 6-day-old larva, 12.2 mm TL (redrawn from Mayden & Burr 1981).

6.7–7.5 mm TL (0.26–0.30 inches), and several species that do not approach its maximum adult size have much larger larvae (e.g., *Noturus nocturnus*, *N. insignis*, and Mountain Madtom, *Noturus eleutherus*). Although the data are limited, relatively small yolk diameters of fertilized eggs appear to be correlated positively with relatively small propagule size (Burr & Stoeckel 1999).

Hatchlings all have large intact yolk sacs; some melanophore development on the dorsum; the barbels, nostrils, and eyes well developed; and precocious development of fins and fin rays. Schooling behavior of hatchlings is well developed, although remaining upright with a large yolk sac is difficult. Larvae are negatively phototaxic and positively geotropic (staying on or close to the substrate). The yolk is absorbed in 7–15 days at 24–26°C (75.2–78.8°F), averaging 7.7 days. Larvae leave the nest by at least 10 days post-hatching (Wilkinson & Edds 1997).

Reproduction in Blindcats

As might be obvious by now, little is known about the blindcats in general, and even less is known about their life histories. Hidden in an eternal lightless environment in artesian wells and caves has made their study difficult, expensive, dangerous, and frustrating. In *Satan* and *Trogloglanis* the morphology of the gonads corresponds to the basic pattern in the family. The ovaries are tubular shaped, and the testes are lobulated. Ovaries of the largest *Trogloglanis* (Langecker & Longley 1993) contained about 200 oocytes at different stages of maturation (largest 0.5 mm, 0.02 inches, in diameter).

ECOLOGY

Habitat

North American Catfishes are a vital part of lentic and lotic fish communities east of the Western Continental Divide in the United States and have been successfully introduced west of the Divide, especially in California. Because they are primarily warm-water fishes, they are only a minor part of the fauna of southern Canada. One species, the Flathead Catfish, has been introduced into Atlantic Slope waters and has had a tremendous negative impact on native Catfishes (*Ameiurus* spp.), which it apparently consumes in massive quantities (Moser & Roberts 1999; see diversity and distribution section). During the day Catfishes reside under cover or structure, in log jams, holes in the bank, and almost any hiding place

imaginable in whatever major environment (i.e., lotic or lentic) they inhabit. They are primarily benthic fishes locating food by touch-taste, electroreception, and olfaction. As a group they occupy a wide variety of environments, including reservoirs, farm ponds, large rivers, montane streams, tidal fresh water, and many places in between these extremes. Some species occur in mesohaline zones, but no ictalurid carries out its reproductive cycle in salinity >2.0 ppt (Perry 1968; see physiology section). Most of the species occur in quiet, warm water. A few madtoms are restricted entirely to pools or only in riffles of clear streams. The blindcats are captured only in artesian wells or karst systems and are rarely seen alive by humans. The three largest species, Channel Catfish, Blue Catfish, and Flathead Catfish, characteristically occupy large rivers but are also successful in lake or reservoir habitats. At the continental scale, climate and elevation are the best predictors of North American Catfish species richness. High species richness of ictalurids is associated with higher precipitation and temperature and with lower heterogeneity in elevation (Knouft & Page 2011).

Habitat of *Ictalurus*

Ictalurus species undergo substantial ontogenetic and seasonal changes in habitat use. In streams and rivers in Alabama, juvenile Channel Catfish (<150 mm TL, 5.9 inches) occupied nearshore shallow habitats with slow velocities at night and occurred in the main channel with variable depths and velocities during the day. As individuals grew, they began occupying deep, fast habitats (Irwin et al. 1999b). In a flow-regulated river in Missouri, juvenile Channel Catfish (9–245 mm SL, 0.4–9.6 inches) selected habitats with 0–0.4 m/s (1.3 feet/s) velocity and low cobble (0–19%) in summer and habitats with moderate silt (30–59%) and gravel (30–39%) and depths of 0.2–0.4 m in autumn (0.66–1.31 feet; Brewer & Rabeni 2008).

Studies have also examined coarse habitat use at broader scales across large sections of rivers. In the middle Mississippi River, juveniles (10–180 mm TL, 0.4–7.1 inches) were found mostly in off-channel and island habitats with only a few juveniles occurring in the main channel (Phelps et al. 2011); off-channel habitats were identified as the most suitable habitats for Channel Catfish regardless of size, and species presence was positively associated with current velocity and negatively associated with depth (Braun & Phelps 2016). Adult Channel Catfish in the unimpounded Mississippi River (from its mouth upstream to the confluence with the Missouri River) were

most abundant at upstream and downstream sections, which had longer areas of dikes and also gravel bars; Blue Catfish decreased in upstream sections and was most abundant along natural banks (Miranda & Killgore 2011). Flooding may increase Channel Catfish abundance in floodplain rivers with a lag period of 1–2 years (Jackson & Ye 2000). In the unimpounded Mississippi River, Blue Catfish decreased in upstream sections and was most abundant along natural banks (Miranda & Killgore 2011).

Habitat of *Ameiurus*

Bullheads occupy a great variety of lentic and lotic environments. They generally frequent smaller water bodies than forktail Catfishes and often thrive in ditches, impoundments, oxbows, river edges, and small farm ponds; the Yellow Bullhead and Spotted Bullhead are occasional in caves or cave entrances. Native White Catfish appeared to be less flexible in habitat use than introduced Channel Catfish in the lower section of the Hudson River, New York. Higher catch-per-effort was observed in upstream reaches and in shoal habitats, but Channel Catfish had higher abundance in different habitats in upstream (shoals) and downstream (near-shore, tributary mouths) reaches. White Catfish condition was also lower in downstream reaches, but Channel Catfish condition did not differ among reaches (Jordan et al. 2004). Yellow Bullheads, however, showed no consistent preference for any of three vegetated habitat types in the Atchafalaya River, Louisiana (Troutman et al. 2007). Non-native adult Black Bullheads in France preferentially used reed-bed habitats instead of marsh meadows during flooding, and range expansion of the species is linked to reduced agricultural activity and subsequent expansion of reed beds in the region. Young-of-the-year abundance did not follow this pattern but was negatively related to water depth, unlike adult abundance (Cucherousset et al. 2006). Non-native Brown Bullheads in a New Zealand lake were located on average within 1–3 m (3.3–9.8 feet) of the surface in early summer but deeper (3–9 m, 9.8–29.5 feet) in winter, compared with the maximum lake depth of >40 m (131.2 feet; Dedual 2002). There is less evidence of floodplain habitat use in *Ameiurus*; however, Black Bullhead abundance was positively associated with spatial and temporal channel connectivity in floodplain ponds of a Utah lake tributary (Landress 2016).

Habitat of *Pylodictis*

As in *Ictalurus*, Flathead Catfish undergo ontogenetic changes in habitat preferences. In Alabama streams, juve-

nile Flathead Catfish occurred almost exclusively in shallow habitats with fast velocities or coarse substrates, but with growth, they tended to leave shallow habitats for deeper, faster-water areas (Irwin et al. 1999b). Juvenile Flathead Catfish (16–277 mm SL, 0.6–10.9 inches) in a flow-regulated river in Missouri selected low velocity (0–0.4 m/s, 0–15.7 inches/s) habitats with a range of cobble (20–100%), boulder (40–100%), and pebble (60–100%) in summer during the day, but at night the species generally selected a broader range of boulder and cobble substrates (20–100%) (Brewer & Rabeni 2008). In autumn, selection of cobble substrates narrowed (40–100%), as did boulder substrate selection (10–69%). Laboratory trials with PVC tubes mimicking interstitial spaces of different sizes and at different depths revealed selection for interstitial diameter of the smallest (<40 mm TL, 1.6 inches) juveniles, selection for size and depth of interstitial space in 41–60 mm TL (1.6–2.4 inches) juveniles, and selection for interstitial depth in 60–152 mm TL (2.6–6.0 inches) juveniles (Daugherty et al. 2011). Adult Flathead Catfish in Michigan predominantly used large wood and riprap substrates in water <3 m (9.8 feet) deep throughout the year, except in winter when they used main-channel pools with coarse substrates and greater depth (>4 m, 13.1 feet). Current velocities were consistent throughout the year (0.1–0.7 m/s, 0.33–2.30 feet/s) (Daugherty & Sutton 2005). In Wisconsin rivers, depth averaged 2.1 m (6.9 feet) and large woody structures were the dominant habitat (Piette & Niebur 2011). In Alabama rivers, Flathead Catfish were found almost exclusively in shallow waters (<35 cm, 13.8 inches) with fast velocities (>55 cm/s, 21.7 inches/s) or coarse substrate (gravel or larger) (Irwin et al. 1999a). Similarly, in a reservoir in west Texas, Flathead Catfish used hard-bottom substrates (gravel, boulder) during all seasons and woody habitats during all seasons except winter when fish moved to deeper waters (>5 m, 16.4 feet) than in spring and summer (1.0–4.9 m, 3.3–16.1 feet) (Weller & Winter 2001). Fish of all size classes in a Nebraska reservoir sampled along the shoreline avoided woody habitats but selected rocky substrates (Vrtiska et al. 2003). In the unimpounded section of the Mississippi River (mouth upstream to the Missouri River), Flathead Catfish were less abundant in upstream reaches and were associated with bank stabilization structures (concrete mattresses and riprap) and steep sand banks (Miranda & Killgore 2011). Fish were also associated with riprap banks in the lower Missouri River; however, these habitats contained smaller individuals (mean 206 mm TL, 8.1 inches) and had lower proportional size density (13%)

(index of fishery-quality individuals) than creek mouths (320 mm, 12.6 inches, TL; 41%) (Travnichek 2011).

Habitat of *Noturus*

Madtoms occupy a variety of habitats from small headwater streams (e.g., Black Madtom) to North America's largest rivers (e.g., Stonecat) as well as some lakes (e.g., Tadpole Madtom), although most inhabit small-medium streams and rivers (Burr & Stoeckel 1999). Microhabitat preferences in higher-gradient, upland streams usually consist of gravel, cobble, or boulder riffles with moderate current. In lowland streams, madtoms occur in undercut banks and near detritus or woody debris and gravel bars in larger rivers. For syntopic species, microhabitat use appears to overlap considerably within streams, although some evidence indicates limited partitioning. One study of three species in Missouri found Slender Madtoms in all microhabitats; Black River Madtoms (then Ozark Madtom) used shallow depths (0.06–0.57 m, 0.20–1.87 feet) and swift currents (0.0–0.6 m/s, 0.00–1.97 feet/s) and were similar to Stonecats (0.03–0.46 m, 0.10–1.51 feet, depth; 0.00–0.68 m/s, 0.00–2.23 feet/s, velocity). Checkered Madtoms were associated with deeper water (0.14–2.45 m, 0.46–8.04 feet). Preference for substrate composition appeared to differ little among the focal madtom species (Banks & Distefano 2002). However, in a summer study of the rare Smoky and Yellowfin Madtoms in Abrams Creek, Tennessee, although the two species had similar macrohabitat (200 m reaches) associations (likely due to high habitat heterogeneity of reaches), they were never found in the same microhabitats (0.25 m² units), suggesting partitioning. Smoky Madtoms occurred in cobble- and bedrock-dominated substrates >18.5 cm deep (and a greater variety of microhabitats) and Yellowfin Madtoms in microhabitats >3 m from riffles in cobble and boulder substrates (Gibbs et al. 2014). Juvenile Stonecats (12–65 mm SL, 0.47–2.6 inches) in a flow-regulated river selected daytime summer habitats with moderate cobble (40–100%) and pebble (20–39%) substrates, but night-time habitats had a narrower (shifted higher) range of cobble (60–100%) and were 0.00–0.20 m (0.00–0.66 feet) deep. Autumn habitats had velocities of 0.20 to >1.0 m/s (0.66 to >3.3 feet/s) and 0.0–0.3 m (0.00–0.98 feet) deep (Brewer & Rabeni 2008). Although general habitat characteristics are documented for many species in life-history studies, habitat suitability or true selection is evaluated in only a few species. Relative streamflow (complex, run, or pool habitat) was the only significant predictor of presence in the Brown Madtom with fish preferring woody habitats and undercut banks in varying (complex) flow areas (Chan & Parsons 2000). In laboratory trials, Carolina Madtoms selected the artificial substrate (inverted clay flowerpots) more often (63% of trials) than the most-preferred natural substrates, rock (23%) and leaf pack (13%). One substrate, mussel shells, was not selected (Midway et al. 2010a). Stream reaches seeded with artificial habitats had significantly greater abundance of madtoms than those with no artificial cover, indicating preferential use of these habitats in the field as well (Midway et al. 2010b). Carolina Madtoms use of natural habitats was nonrandom with fish selecting shallow to moderate depths (< 0.5 m, 1.6 feet) with swift current (0.10–0.24 m/s, 0.33–0.79 feet/s) and sand and gravel substrates with cobble cover. Availability of this habitat throughout the range of the species suggests that other factors besides simply habitat availability are responsible for the species' decline (Midway et al. 2010b). Sand and silt were significantly lower and small cobble, gradient, and water depth were significantly higher at sites with Orangefin Madtoms. These variables, along with the presence-absence of several species, in a discriminant function analysis correctly predicted 88% of sites without the species and 85% of sites with the species (Simonson & Neves 1992). Slender Madtoms in two Oklahoma streams selected significantly higher current velocities (37.8 cm/s, 14.9 inches/s) than the available currents (30.8 cm/s, 12.1 inches/s), but depths were similar to availability (Vives 1987).

Habitat of Blindcats

The three genera and four species of troglobitic blindcats are denizens of cave streams and karst aquifers and were first discovered through drilling for drinking water wells (Eigenmann 1919). Specific microhabitat preferences of the blindcat genera are obscure; however, some information is known for the genus *Prietella* (Figs. 15.7 and 15.8). The Phantom Blindcat, *Prietella lundbergi*, was first found in a "subsurface thermal spring . . . at the base of a limestone escarpment . . . in the Sierra Madre Oriental mountain range" in northeastern Mexico (Walsh & Gilbert 1995:851). It was hand-captured about 30–40 m (98–131 feet) from the cave entrance at a depth of about 4.5 m (14.8 feet) near the surface of a deeper cave system. Water temperature was 26.7°C (80.1°F) and substrate consisted of "fine clay silt interspersed with solid rock." Flow was negligible, but stronger outflow during rain events could force fish toward the cave outlet (Walsh & Gilbert 1995).

Extensive sampling in cave systems of Texas and Mexico for *Prietella* has provided additional details on habitat. The fish are mostly found in the dark zone of low-elevation caves, usually in still pools with silt substrates or in deep, high-flow systems (but not in shallow, flowing water) where environmental conditions are relatively stable (Hendrickson et al. 2001). Water chemistry at Phantom Blindcat sites ranged as follows: temperature, 21–31.5°C; pH, 7.45–7.9; dissolved oxygen, 0.75–5.4 mg/L; specific conductivity 0.425–0.75 mS/cm; redox potential 335–362 mV (Hendrickson et al. 2001). Toothless Blindcats (*Trogloglanis pattersoni*) and Widemouth Blindcats (*Satan eurystomus*) occur only in the San Antonio Pool of the Edwards Aquifer near San Antonio, Texas, at depths of 297–567 m (975–1860 ft) (Langecker & Longley 1993).

Diet

The large and medium-sized Catfishes (genera *Ictalurus*, *Ameiurus*, and *Pylodictis*) are considered omnivores (e.g., Forney 1955; Edds et al. 2002). For example, vegetation, filamentous algae, and plant seeds are common diet items for Brown Bullheads, Blue Catfish, and Channel Catfish (e.g., Hubert 1999; Chick et al. 2003; Eggleton & Schramm 2004; Flotemersch & Jackson 2003; Adams et al. 2007; Braun & Phelps 2016). Although plant material may be taken incidentally while ingesting animal matter, plant material also might form a seasonally important energy subsidy during times of low animal food availability (e.g., Bailey & Harrison 1948). Notably, many Channel Catfish in lowland rivers of the Mississippi River commonly ingest riparian plant seeds (e.g., Red Mulberry, *Morus rubra*; Swamp Privet, *Forestiera acuminata*), sometimes in large numbers (100 to >1,000 seeds/fish) (Chick et al. 2003; Adams et al. 2007). Ingested seeds of these species defecated by Channel Catfish are viable (Chick et al. 2003; Adams et al. 2007), and in one experiment, germination of ingested seeds was improved after passing through the gut of the Channel Catfish (Chick et al. 2003). This is the only documented incidence of ichthyochory (plant dispersal by fish) in North America. The extent of omnivory and its importance to Northern American Catfish bioenergetics warrants further investigation.

Diet of *Ictalurus*

The primary foods of adult *Ictalurus* spp. are invertebrate and vertebrate organisms, but diets can vary from mostly invertebrates to nearly all fishes depending on food resources (e.g., Crumpton 1999; Eggleton & Schramm 2003,

2004). Almost all of the large Catfishes show seasonal shifts in food consumption based on food availability. Rapid changes in diet often are associated with increased water levels. For example, during flooding, Channel Catfish in the Yockanookany River, Mississippi, aggregated where the river channel and floodplain were coupled and foraged heavily on a terrestrially burrowing crayfish that was using the open water of the floodplain (Flotemersch & Jackson 2003). Fatty acid profiles of tissues may also reveal patterns of resource and habitat use. In the lower Kaskaskia River, Illinois, Channel Catfish from the main channel had higher levels of terrestrially derived fatty acids compared to floodplain lake individuals suggesting greater use of allochthonous energy sources, while patterns in floodplain lake individuals suggested greater autochthonous sources (Young et al. 2016). Blue Catfish in the lower Mississippi River use floodplain habitats extensively during warmer (>15°C, 59°F) periods (Schramm et al. 2000; Schramm & Eggleton 2006). Low water temperatures (1–9°C) generally curtail feeding in Channel Catfish in wild settings and spawning usually stops feeding altogether (Hubert 1999). Most foraging occurs on the bottom rather than in the water column; however, dominance of pelagic prey (e.g., shad) in the diet indicates variation in foraging mode (e.g., Crumpton 1999). *Ictalurus* also takes insects from the water surface at least opportunistically. For example, during the 2015 emergence of 13-year periodical cicadas (Hemiptera: *Magicicada*), Channel Catfish caught at night by hook-and-line from Crab Orchard Lake, southern Illinois, contained large quantities of these insects (Eric Schauber pers. comm.).

Like many fish, young Catfishes depend largely on plankton and aquatic insect larvae, but adults are opportunistic and will eat nearly any invertebrate, fish, other vertebrate, and some plants that are available (e.g., Michaletz 2006). Juvenile Channel Catfish in the Illinois River, Arkansas, fed mainly on midge larvae (Chironomidae) in pools and not on drift (Armstrong & Brown 1983). The onset of piscivory in Channel Catfish ranges from 15 to 40 cm TL (5.9–15.7 inches; Hubert 1999). Fishes (Perch, Percidae; New World Silversides, Atherinopsidae) and algae (pondweed, order Charales) made up >50% of the diet (by weight and frequency of occurrence) in all sizes (29 to >50 cm TL, 11.4 to >19.7 inches) of Channel Catfish in Durango, Mexico (Martinez et al. 2011a). Blue Catfish begin consuming fishes at about 10 cm TL (3.9 inches). Of 11–18 cm TL (4.3–7.1 inches) Blue Catfish from the Ohio River, most of the stomach contents by volume consisted of unidentified organic matter, odonate larvae, unidentified fishes, and mayfly larvae (Minckley

1962). At 20–30 cm TL (7.9–11.8 inches), fishes are the main source of food, although large invertebrates also are taken (Brown & Dendy 1961).

Diets of *Ictalurus* can include an incredible diversity of food items. For example, Blue Catfish from main channel, secondary channel, and floodplain lake habitats in the lower Mississippi River were highly omnivorous consuming >30 types of prey. Collectively, across all habitats the Blue Catfish diet comprised (percentage wet mass) 47% fishes (>15 species, principally juvenile Catfishes; Freshwater Drum, *Aplodinotus grunniens*; and Sunfishes, *Lepomis* spp.), 15% mollusks, 12% chironomids and oligochaetes, 7% detritus and plant material, 6% decapods, 6% scavenging (unidentified fishes, fish scales, birds, and turtles), 1% terrestrial arthropods, and 1% sediment (Eggleton & Schramm 2004). They are sometimes major consumers of freshwater mussels (Graham 1999). Blue Catfish appear to be predominantly benthic feeders but may feed more by sight and in midwater in clear-water reservoirs and tailwaters. There are reports of Blue Catfish suspending in deep water and picking off wounded and dead Gizzard Shad (*Dorosoma cepedianum*) that were being fed on by Striped Bass (*Morone saxatilis*) or that pass through hydroelectric turbines (Graham 1999). Channel Catfish in the middle Mississippi River also had diverse diets, including a mammal (a vole), a bird, and a turtle, although vegetation, crayfishes, and fishes predominated (Braun & Phelps 2016). In two creeks in Texas, Headwater Catfish consumed mainly algae and detritus (mean 85% of diet by weight); juveniles (86–162 mm SL, 3.4–6.4 inches) consumed less of these items and more aquatic insect larvae (Littrell et al. 2003).

Diet of *Ameiurus*

Bullheads, the medium-sized Catfishes, consume aquatic insects and crustaceans, and nearly always eat some fishes, especially once they have reached adult size, although this is variable (Moore 1972). Feeding is reportedly at night along the bottom by means of taste buds on the barbels and body skin (Simon & Wallus 2004). Young feed primarily on zooplankton and amphipods with much feeding associated with midday-schooling activity (Simon & Wallus 2004). Crepuscular feeding is common in bullheads with one peak in activity just before dawn and another just after dark (Darnell & Meierotto 1965). With rising water levels, a great variety of food items may be found in bullhead stomachs, including terrestrial earthworms, insects, slugs, spiders, centipedes, millipedes, isopods, and snakes (Applegate & Mullan 1967), indicating opportunistic foraging. Evidence for selective

feeding comes from studies of Brown Bullheads in a lake in New York in which adults selectively fed on amphipods (*Hyalella* sp.) and chironomid larvae (and avoided snails and mayfly larvae), and juveniles selected chironomids (Kline & Wood 1996); however, non-native Black Bullheads may be more opportunistic or generalist (Leunda et al. 2008). The diet of the White Catfish is little studied, but a study in Florida found about 37% empty stomachs in 104 individuals examined. Phantom midges (*Chaoborus*; 41.7%), amphipods (Tallitridae), and mayflies made up the majority of invertebrate prey and were associated with large amounts of detritus in the stomach (66.8% of contents) (Crumpton 1999).

Diet of *Pylodictis*

With growth, Flathead Catfish show decided shifts in diet. Individuals <100 mm TL (3.9 inches) consume insects, mostly ephemeropteran and trichopteran larvae. Between 100 and 250 mm TL (3.9–9.8 inches) this species tends to be dispersed and solitary, and consumes insect larvae, fishes, and crayfishes (Pflieger 1997; Vrtiska et al. 2003). As large adults, Flathead Catfish are considered lie-in-wait predators and are one of the least gape-limited piscivores in North America (Slaughter & Jacobson 2008). They wait, often hidden, for suitable prey to come near enough so that they can practically inhale the prey when opening their enormous mouths. In one study, summer diel feeding pattern was variable in *Pylodictis* with multiple peaks in July (daily ration 3.1% of body weight) and a single, mid-day feeding peak in August (daily ration 7.4%) (Baumann & Kwak 2011).

As in *Ictalurus*, Flathead Catfish may use floodplains as favorable foraging habitats during floods as evidenced by increased growth (Jones & Noltie 2007). Some studies suggest the benefits of floodplain foraging may not be as great as for *Ictalurus* (Eggleton & Schramm 2004); however, in the middle Missouri River, Flathead Catfish had fuller stomachs, were in better condition, and transitioned to piscivory at smaller sizes during the record flooding of 2011 compared to the drought of 2012 (Hogberg & Pegg 2016).

Flathead Catfish introduced to Atlantic Coast rivers appear to be predominantly piscivorous. Over 50% of stomach contents (percentage occurrence, number, and weight) comprised fishes and crayfishes, and feeding was essentially random (non-selective) with respect to prey availability (Pine et al. 2005; Baumann & Kwak 2011) except they selected prey occurring in similar benthic microhabitats (Baumann & Kwak 2011). This, along with evidence of predation on imperiled Atlantic Sturgeon

(*Acipenser oxyrinchus*) (Flowers et al. 2011), suggests that Flathead Catfish could restructure native fish communities of the Atlantic Slope as well as threaten rare species (see diversity and distribution section).

Diet of *Noturus*

Species of *Noturus* are benthic invertivores feeding largely at night with peaks in feeding activity near dawn and dusk (e.g., Clark 1978; Mayden & Burr 1981; Gutowski & Stauffer 1993). Limited feeding in some populations takes place during the day (e.g., Curd 1960; Dinkins & Shute 1996), and terrestrial prey is consumed occasionally (Creed & Reice 1990). Predominant food items across the genus are chironomid, ephemeropteran, trichopteran, and plecopteran larvae and small crustaceans. Only the largest madtoms consume fishes and crayfishes (e.g., *Noturus flavus*, Walsh & Burr 1985; *N. funebris*, Bennett & Kuhajda 2008; *N. phaeus*, Chan & Parsons 2000).

Similar to other ictalurids, the use of olfactory and especially gustatory structures and their concomitant thigmotactic responses in locating food are probably far more important than vision (Bowen 1980), a primary sense used to locate food in many other diverse groups of North American fishes. Competition for food resources may be somewhat reduced since madtoms are often the dominant food consumers at night in streams where potential competitors (e.g., darters, minnows) are largely diurnal in their feeding activity. The daily average ingestion rate is known for only one madtom species, *N. phaeus*, as 1.2% of body weight (Chan 1995). Limited information suggests some selectivity based on prey size and identity; for instance, the Margined Madtom consumed significantly smaller prey than that found in the benthos on two of the four sampling days (Gutowski & Stauffer 1993).

Diet of Blindcats

Few specifics are known for the diets of blindcats. Specimens have mostly empty stomachs, occasionally contain the skeleton of a crustacean, and sometimes have fairly substantial lipid deposits in the body cavity (Langecker & Longley 1993). In the natural habitat, potential prey, however, is abundant, and shrimps, amphipods, and isopods occurred in stomachs of *Satan*, and the Widemouth Blindcat may prey on the Toothless Blindcat. The Toothless Blindcat might feed on fungal growths and dead or dying organisms in soft substrate (Longley & Karnei 1979).

Age, Size, and Growth

Documented lifespans of North American Catfishes, based largely on annuli detected on cross-sections of pectoral spines, but also on vertebral annuli and growth rings on otoliths (sometimes preopercle bones and dorsal spines), range from one year of age in tiny madtoms to >20 years in the largest species, Blue, Flathead, and Channel Catfishes. Work on otolith aging strongly suggests spine-based ages underestimate age of some large and many older Catfishes. For example, spine-based ages underestimated otolith-based age of Flathead Catfish by as much as 7–17 years (Nash & Irwin 1999). An 18-year-old otolith-aged Brown Bullhead was estimated as only 9-years-old by spine-based aging (Maceina & Sammons 2006). In contrast, otoliths and spines showed high agreement in Channel Catfish (Buckmeier et al. 2002; Colombo et al. 2009), and an 80% probability of ≤1 year difference was estimated in the two methods for ages ≤16 (Channel Catfish), ≤13 (Blue Catfish), and ≤9 (Flathead Catfish) (Olive et al. 2011). For older Catfish, the correspondence of otolith and pectoral spine ages may decrease, usually beyond age four or five (Flathead Catfish, Nash & Irwin 1999; Blue, Channel, and Flathead Catfish, Olive et al. 2011) but sometimes ≤11 years (Channel Catfish, Barada et al. 2011). Ages of older fish may thus be underestimated by pectoral spine techniques, and otolith estimates usually have greater accuracy and precision than other methods but require sacrificing fish (Nash & Irwin 1999; Buckmeier et al. 2002; Maceina & Sammons 2006; Barada et al. 2011). We suspect that the large Catfishes may be quite long-lived, even longer than aging studies have documented.

On the opposite end of the age spectrum, otoliths have the advantage of daily ring deposition in age-0 fish. Daily rings are deposited through 119 days post-hatching (Channel Catfish) and are accurate (compared with known age) through 60 days (Blue and Channel Catfishes) and 72 days (Flathead Catfish) (Sakaris & Irwin 2008; Sakaris et al. 2011a).

Age, Size, and Growth in *Ictalurus*

In *Ictalurus*, most Blue Catfish adults are 400–872 mm SL (15.7–34.3 inches). The species reaches a maximum size of about 1.65 m SL (5.42 feet) and (incredibly) a historical weight of 142.8 kg (315 pounds) (Cross 1967); recent fishing records are near 58.97 kg (130 pounds). Historically, Blue Catfish weighing 68–91 kg (150–200 pounds) were not uncommon in the Mississippi and Missouri Rivers (Pflieger 1997). Blue Catfish reach ≥20 years of age and at that age are about 40 kg (88.2 pounds) in weight. In samples from

Lake of the Ozarks, Missouri, many fish achieved 9–10 years of age, fewer 13 years of age, and one 18 years (reviewed by Graham 1999).

Most Channel Catfish adults are 240–650 mm SL (9.4–25.6 inches). The species reaches a maximum size of about 71 cm SL (28 inches; and 19.96 kg, 44 pounds) in the Ohio River basin and about 100 cm (39.4 inches; and 26.31 kg, 58 pounds) on the Atlantic Slope (Santee-Cooper Reservoir, South Carolina). Introduced populations in the Colorado River and in northern waters reach an age of 21–23 years. Other populations in Montana, South Dakota, Alabama, and Oklahoma reach 15–17 years. Most studies indicated a maximum age of eight years, and no relationship between maximum age and growth rate was identified (reviewed by Hubert 1999). In contrast, individuals from a heavily managed fishery in the Red River of the North averaged almost 12-years-old with a maximum age of 27 years and many >20 years old, placing them among the longest-lived individuals reported in North America (based on otoliths; 93–995 mm TL, 3.7–39.2 inches) (Siddons et al. 2016).

Two of the Mexican species of *Ictalurus* are considerably smaller (about 24–27 cm, 9.4–10.6 inches, maximum SL; Miller et al. 2005) than the Channel Catfish and appear to be more bullhead-like in size attained (e.g., Kelsh & Hendricks 1990). The Yaqui Catfish (*Ictalurus pricei*), however, grows to >60 cm (23.6 inches) and weighs >10 kg (22 pounds) in captivity (Miller et al. 2005). Three of the Mexican *Ictalurus* reach at least 1 m (3.3 feet) in TL and are valued food fishes (Miller et al. 2005).

In dynamic floodplain rivers, *Ictalurus* growth appears to be largely density-independent, influenced primarily by abiotic factors (Shephard & Jackson 2009; see Mosher 1999). In several studies of environmental correlates of growth in Channel and Blue Catfishes, growth was positively related to water velocity and instream cover (Putman et al. 1995), length of growing season (Rutherford et al. 1995; Hogberg et al. 2016), duration of floodplain inundation which were above active feeding temperatures (Schramm et al. 2000), and soil fertility (which likely correlates with food availability) (Mosher 1999; Shephard & Jackson 2006). Growth was negatively related to pool abundance and amount of gravel substrate (Putman et al. 1995), and altitude (which likely correlates with water temperature) and amount of the watershed composed of bottomland hardwood forest (Shephard & Jackson 2006). In the lower Platte River, Nebraska, which is subjected to extreme natural and anthropogenic flow variability, juvenile Channel Catfish growth increased during sustained high-flows in the spring and was reduced during prolonged low-flows, perhaps related to higher predator susceptibility and reduced food resources during these conditions (Spurgeon & Pegg 2017).

Along with Flathead Catfish, Blue Catfish were the focus of the most substantial tests of the validity of the flood pulse concept in temperate rivers. Blue Catfish in the lower Mississippi River obtained prey with greater energy content (chironomids and oligochaetes) in floodplain lakes compared with the main channel (Zebra Mussels); however, substantial annual variation occurred in use of off-channel habitats (Eggleton & Schramm 2004). When temperature was taken into account, growth increased with greater area and duration of floodplain inundation (Schramm & Eggleton 2006). Channel Catfish may also use floodplains extensively for foraging and other activities (e.g., Schramm et al. 2000; Flotemersch & Jackson 2003; Burgess et al. 2013); however, in the channelized Missouri River, Nebraska, young-of-the-year growth was related more to duration of low discharge (<25th percentile of 30-year daily discharges) and unrelated to high discharge duration, in contrast to some predictions from the lower Mississippi River (Hogberg et al. 2016).

Blue Catfish abundance in Texas reservoirs was also related to primary productivity and reservoir surface area (Bartram et al. 2011). In a meta-analysis of growth studies for North American Catfishes, Channel Catfish had higher growth in lentic habitats, but growth was not related to climate. In contrast, Blue Catfish had higher growth in lotic habitats, and growth was significantly related to several climatic variables (Rypel 2011). Similarly, Blue Catfish were larger in tailwater areas than impounded habitats in the Coosa River, Alabama (Jolley & Irwin 2011). In stocked small lakes and impoundments, Channel Catfish growth is often density dependent; however, growth in these populations may not respond quickly to changes in stocking rate (Michaletz et al. 2011).

Age, Size, and Growth in *Ameiurus*

In *Ameiurus*, most adults are 90–390 mm SL (3.5–15.4 inches). They range in TL from about 28 cm (10.25 inches) in the Spotted Bullhead to 62 cm (24.25 inches) in the White Catfish and Black bullhead and a maximum weight of 3.5 kg (7.8 pounds) in White Catfish. Bullheads have an average life span of about 5–6 years with some individuals and populations living >10 years (e.g., Maceina & Sammons 2006). The White Catfish lived 11 years in a California study (McCammon & Seeley 1961). The other bullhead species achieve ages of 5–6 years, sometimes 7–8,

but most studies find predominance by younger ages, usually 2–4-years-old. The rarely studied Snail Bullhead achieved ages ≤8 years in Nickajack Creek, Georgia. The population grew slowly compared with conspecific populations and other bullheads as a possible result of resource limitation due to high density; an estimated 246 Snail Bullheads (>130 mm TL, 5.1 inches) occurred within the 0.7 km (0.43 miles) sampling reach (Sakaris et al. 2011b). A population of Yellow Bullheads in the Everglades, Florida, achieved a maximum age of 12 years but grew more slowly and were smaller at a given age than other populations in the United States (Murie et al. 2009). This population exhibited much slower growth than the Black Bullhead, Brown Bullhead, or Yellow Bullhead, which rarely achieve weights approaching 2.3–2.7 kg (5–6 pounds). Catching a Black Bullhead or Yellow Bullhead in the range of 0.91–1.36 kg (2–3 pounds) is unusual. Bullheads are subject to overcrowding and slow growth, especially in ponds.

In a meta-analysis of Catfish growth, Black Bullheads grew faster in lentic systems, but Brown Bullheads grew faster in lotic systems. Growth of both species was related to several climatic factors, although some of the significant factors differed between the species (Rypel 2011). Annual mortality rates of Black Bullheads in three natural Iowa lakes were variable (24–79%) but were lowest in the lake with highest nutrient inputs and lowest water clarity (Mork et al. 2009). In South Dakota, lake populations (n = 35) of Black Bullheads showed a negative relationship between growth and abundance and a positive relationship between growth and size structure, indicating density dependence. Growth was also positively related to lake depth and negatively related to productivity, but relationships with abundance and size structure were stronger (Hanchin et al. 2002). In 23 lakes in Nebraska, however, Black Bullhead growth and weight were not related to abundance. Instead, growth was positively related to Largemouth Bass abundance, a result likely stemming from increased predation and thinning of smaller size classes, which leads to more resources and faster growth for remaining individuals. Length at age three was positively related to total phosphorus concentration. Differences in these findings may be related to relative productivity of lakes and population sizes or densities supported by different lake types (Phelps et al. 2005).

Age, Size, and Growth in *Pylodictis*

Most Flathead Catfish adults are 295–1005 mm SL (11.6–39.6 inches); the species reaches a maximum size of ≥1.55 m TL (5 feet, 8 inches). Most state angling records are between 30 and 45 kg (66–99 pounds) (reviewed by Jackson 1999). The largest fish was from Kansas at 55.79 kg (123 pounds; caught in 1998). Subsequently, the fish was estimated to be ≥22-years-old from pectoral ray cross-sections from the frozen specimen, which the original angler kept for nearly 18 years (Neely & Lynott 2016). Compared with other Flathead Catfish populations, the individual had grown at about the 90th percentile through age five and still rapidly through age 10, but growth was more comparable to other populations through age 22 (Neely & Lynott 2016). Mississippi River mainstem fish live ≤15 years based on vertebral annuli. Flathead Catfish grow rapidly, growing on average about 10 cm/year (3.9 inches/year; reviewed by Jackson 1999). In the upper Mississippi River, fish grew 0.25 mm/day (0.01 inches/day) during summer and 32 mm/year (1.3 inches/year) based on recaptured individuals, which compared well with otolith and spine estimates (Steuck & Schnitzler 2011). One otolith-aged individual from Alabama was 28 years old, but others indicate ages of 34 years old (Nash & Irwin 1999; Marshall et al. 2009).

In a meta-analysis of growth in Catfish, Flathead Catfish grew more quickly in lentic systems than lotic systems (Rypel 2011). This pattern is consistent with findings on non-native populations in Atlantic Coast rivers where growth rates are higher than native river populations of the species but similar to native reservoir populations and slower than other introduced river populations (Kwak et al. 2006). In the Kansas River, growth rates to age one and age three were positively related, and growth rate was lower in urbanized reaches (Paukert & Makinster 2009). Growth increments, abundance, and sizes in the middle Missouri River were greater in channelized reaches than in unchannelized sections, but body condition was poorer (Porter et al. 2011). Unlike Blue Catfish, growth rates of *Pylodictis* in the lower Mississippi River were not related (or only weakly so) to extent and duration of floodplain inundation (Mayo & Schramm 1999; Schramm & Eggleton 2006; see also Hogberg et al. 2016).

Age, Size, and Growth in *Noturus*

Madtoms as a group are the smallest ictalurids, with nearly 70% of the species reaching <100 mm SL (3.9 inches; range 36–265 mm SL, 1.4–10.4 inches). *Noturus* are relatively short-lived with 14 of 18 species studied reaching only 1–4 years of age, although extremes include three annual species and another six species that live 5+ years (Burr & Stoeckel 1999). As with other North American fishes, no direct relationship

appears to exist between maximum size attained and greater age reached. The largest madtom, *Noturus flavus*, at 265 mm SL (10.4 inches), reaches ≥9 years of age in Lake Erie (Gilbert 1953), but only 5–6 years and about 180 mm maximum SL (7.1 inches) in stream populations (Walsh & Burr 1985). Interestingly, the ages for *N. flavus* at seven and nine years are based on only one individual in each case (Gilbert 1953). In a study of the Northern Madtom, which is rare in the study area of the Detroit River, Michigan, and Ontario, seven individuals from about 70–140 mm SL were between 2- and 6-years-old based on otolith and pectoral and dorsal spine annuli (Manny et al. 2014). The smallest species studied, *N. hildebrandi*, is almost certainly an annual species and apparently does not live >18 months (Mayden & Walsh 1984; Wilkins 1992). The tiniest madtom, *N. stanauli*, is assumed to be an annual species as well. Species approaching or reaching 130–150 mm SL (5.1–5.9 inches) live 4–6 years (e.g., *Noturus flavater*, *N. nocturnus*, *N. phaeus*). An aquarium-held, 2- or 3-year-old Brindled Madtom lived to 5–6 years of age, making it 2- or 3-years-older than indicated for wild populations (Mayden 1983). At the northeastern limits of their distribution, Stonecats in the LaPlatte River, Vermont, had lowest survival rates in the fall, perhaps the result of post-spawning mortality. Seniority (i.e., probability that an individual remained in the population between successive sampling periods) was highest in summer and may have been affected by nest-guarding behavior, which could cause males to be less mobile. Overall, the 3-year-study revealed a slightly declining population; however, this could have been affected by an inability to track young individuals (<90 mm TL), the sampling intensity, and the relatively short timeframe compared to potential lifespan of Stonecats (Puchala et al. 2016).

Age, Size, and Growth in Blindcats

The blindcats are all small species, reaching a maximum size of about 60 mm SL (2.4 inches) in *Prietella* (Fig. 15.7), to <90 mm SL (3.5 inches) in *Trogloglanis*, and to 117 mm SL (4.6 inches) in *Satan* (Page & Burr 2011). Ages of blindcats are unavailable, but they may live many years despite their small size. For example, tagged amblyopsid cavefishes, which are small, live ≥10 years in the wild (Niemiller & Poulson 2010).

Effects as Predators

Although Catfishes are generally omnivorous and feed at multiple trophic levels, the large size and predatory habits of some species can have large impacts on prey (see also North American Catfishes as non-natives subsection, diversity and distribution section and diet subsection, ecology section). Blue Catfish may severely impact non-native Zebra Mussels (*Dreissena polymorpha*) or other native mollusks. In the lower Mississippi River, for instance, Blue Catfish feed heavily on Zebra Mussels in the main channel during certain times of the year; however, the proportion of total food composed of mussels varied widely from 38% in one year to 17% in the next (Eggleton & Schramm 2004). It is unknown how these consumption rates compare to Zebra Mussel population turnover. Bullheads apparently do not have large effects on populations of other species through predation. In Nebraska lakes, for instance, population characteristics of four fish species, Bluegill (*Lepomis macrochirus*), Green Sunfish (*Lepomis cyanellus*), Pumpkinseed (*Lepomis gibbosus*), and Yellow Perch (*Perca flavescens*) were not correlated with Black Bullhead size, structure, or abundance (Phelps et al. 2005). However, introduction of Brown Bullheads into Hadley Lake, British Columbia, Canada, is implicated in the extinction of an endemic Stickleback (*Gasterosteus* spp.) species pair (Hatfield 2001). Despite their opportunistic and generalist foraging habits, *Ameiurus* has the potential to affect native fish communities where introduced (Leunda et al. 2008), although declines in native fauna have rarely been documented. The largely piscivorous *Pylodictis olivaris* may have major effects on fish populations, especially where it is introduced (see North American Catfishes an non-natives subsection, diversity and distribution section).

As benthivorous fishes, Catfishes, like the Black Bullhead and Yellow Bullhead, are often tolerant of the degraded conditions that follow non-native species introductions (e.g., Common Carp, *Cyprinus carpio*, bioturbation increases suspended sediments and nutrients in water). These Catfishes are sometimes thought to contribute to altered ecosystem states in these habitats (e.g., Egertson & Downing, 2004; Schrage & Downing, 2004). However, in mesocosm experiments, Black Bullheads in comparison with Common Carp were responsible for few changes to water quality (increased total phosphorous and chlorophyll a), macrophytes, and macroinvertebrate abundance (increased copepod abundance) and were simply indicators of certain eutrophic conditions. Unlike Common Carp, they were not a source of physical damage to the environment known to cause self-reinforcing degradation of water quality, but rather they simply could persist under negative changes brought on by Common Carp (Fischer et al. 2013). Hence, bullheads should not be the target of lake management measures in this context where they are native.

Predators

Ictalurids, especially young stages, are eaten by turtles, herons, cormorants, water snakes (*Nerodia* spp.), alligators, raccoons, and otters; filial cannibalism of larvae occurs in *Ameiurus*, *Ictalurus*, and *Noturus* (Burr & Stoeckel 1999). Cottonmouths (*Agkistrodon piscivorus*) eat Channel Catfish, Black Bullheads, and Yellow Bullheads (Yerger 1953; Ernst & Ernst 2003). On several occasions we observed species of the water snake genus *Nerodia* in the process of consuming bullheads (Fig. 15.52) and madtoms in stream and bayou habitats. In one instance, a *Nerodia rhombifer*, Diamondback Water Snake, had just finished eating a large bullhead and was so heavy that it could barely move (e.g., see also Ernst
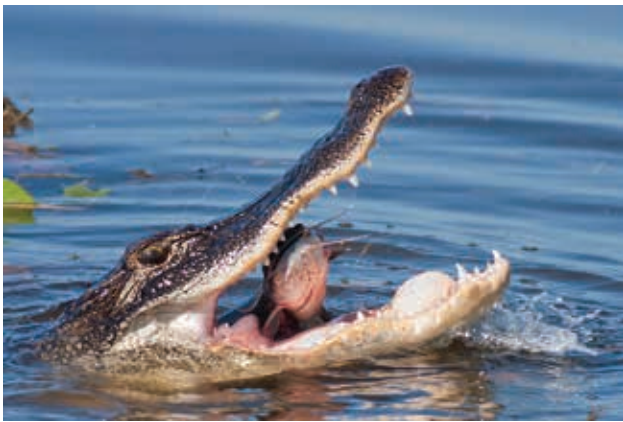
Figure 15.52. Reptile predators often use North American Catfishes (Ictaluridae) as prey. (*upper*) A Diamondback Watersnake, *Nerodia rhombifer*, eating a Yellow Bullhead, *Ameiurus natalis*, along the Arkansas River near Barling, Sebastian County, Arkansas (courtesy of © Steve Creek). (*lower*) An American Alligator, *Alligator mississippiensis*, catching a bullhead Catfish (probably a White Catfish, *Ameiurus catus*) in Orlando Wetlands Park, Orange County, Florida (courtesy of Scott Simmons).

& Ernst 2003 and references therein). In other instances, we observed the spines of ictalurids piercing through the skin of water snakes, which otherwise appeared unharmed. Ictalurids pose a dangerous challenge for gape-limited predators as the locking of the pectoral spine can more than double the fish's width (e.g., in Channel Catfish; Sismour et al. 2013). Handling time for Black Bullhead prey was significantly different from other prey (Yellow Perch, Pumpkinseed) for water-bird predators such as herons and grebes, but did not differ among prey types for Osprey, which tear apart their prey. For this reason, Osprey chose Black Bullhead prey ≤2 times more often than did herons or grebes (Forbes 1989). Similar results were found in experiments with Largemouth Bass offered a choice of Goldfish, Bluegill, and Channel Catfish prey. Goldfish and Bluegills were consumed equally and about 3–4 times more than Channel Catfish (Sismour et al. 2013).

Parasites and Diseases

North American Catfishes serve as hosts to an array of parasites, including other fishes, mollusks, and a host of other invertebrate species. The large Catfishes are attacked by some Lamprey species (see Cochran 1994), and the Ohio Lamprey (*Ichthyomyzon bdellium*) attacks the Stonecat (Cochran & Jenkins 1994).

North American Catfishes are parasitized by the glochidia (larvae) of several species of freshwater mussels, but evaluation of actual mussel host-fish relationships for ictalurids (and other fish groups) can be clouded by acceptance of non-standard host-trial results and oft cited non-peer reviewed reports of uncertain validity (e.g., compilation for ictalurids by Tiemann et al. 2011). Here we restrict our review of these relationships to peer-reviewed papers that followed standard, replicated host-trial protocols and comprehensively reported rates of rejection or transformation of glochidia on trial fishes. These criteria are necessary to objectively evaluate whether reported host relationships represent primary host use (i.e., glochidia transform consistently and robustly, suggesting that the host is important in the wild), marginal host use (i.e., glochidia transform inconsistently or weakly, suggesting that the host is of little importance in the wild), or simply spurious associations due to poor laboratory practice or other factors (see discussions by Haag & Warren 1997; O'Brien & Brim Box 1999).

Specialization by freshwater mussels on North American Catfishes is apparently limited to two widespread freshwater genera in the tribe Quadrulini. Host specialization occurs in the monotypic *Cyclonaias tuberculata* (Purple Wartyback)
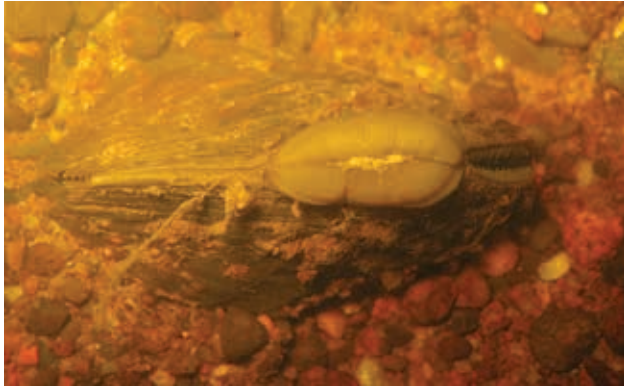
Figure 15.53. North American Catfishes (Ictaluridae), such as the Channel Catfish, *Ictalurus punctatus*, serve as specialized hosts for the Purple Wartyback, *Cyclonaiais tuberculata*, a widespread North American freshwater mussel, which uses two strategies to transfer its larvae to the appropriate Catfish host. The female displays a large, pale lure or mantle magazine (*upper* dorsal view; *middle* lateral view), which is bulging with larvae and mimics food of the host Catfish. When the lure is attacked by the host fish, the larvae are released and attach to the gills of the fish. The female Purple Wartyback also releases glochidia in streaming mucoid conglutinates (*lower*) that also may serve as generalized mimics of Catfish food items (see text for references) (photographs taken in the St. Croix River, Chisago County, Minnesota, by and used with permission of Bernard Sietman, Minnesota Department of Natural Resources).

and the genus *Quadrula* (except the "*Quadrula*" *metanevra* group, which represents a separate clade that specializes in minnows, Serb et al. 2003; Fritts et al. 2012). Interestingly, madtoms, a highly diverse group, are not reported as primary host for any mussel species despite having feeding ecology and habitat use similar to darters, which serve as hosts for many mussel species (Haag 2012).

Use of North American Catfishes as hosts by the Purple Wartyback and *Quadrula* spp. is mainly restricted to *Ictalurus* spp. and Flathead Catfish; bullheads and madtoms are
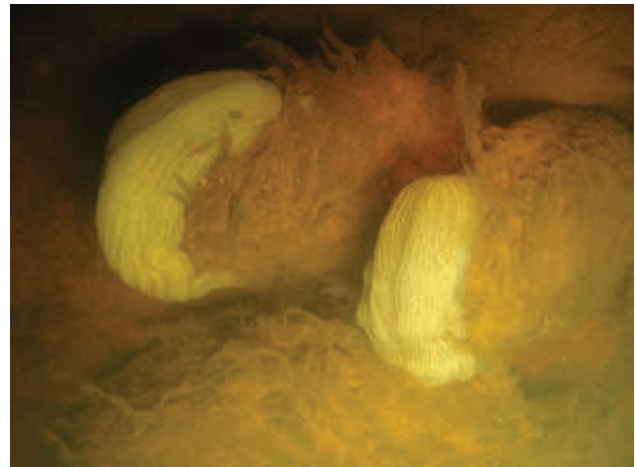

Figure 15.54. Species of the freshwater mussel genus *Quadrula* specialize on North American Catfishes (Ictaluridae) as hosts. Similar to the Purple Wartyback (Fig. 15.53), females of the Winged Mapleleaf (*Quadrula fragosa*; *upper*) and Pistolgrip (*Quadrula verrucosa*; *lower*) display large, conspicuous lures that elicit attacks from host Catfish resulting in transfer of mussel larvae (glochidia) to the fish. The Winged Mapleleaf uses *Ictalurus* spp. as hosts, and the Pistolgrip uses the Flathead Catfish, *Pylodictis olivaris*, as a primary host (see text for references) (photographs taken in the St. Croix River, Chisago County, Minnesota, by and used with permission of Bernard Sietman, Minnesota Department of Natural Resources).

at best marginal hosts on which glochidial transformations typically are weak. In trials using 11 co-occurring fish species, glochidia of the Purple Wartyback transformed only on Channel Catfish and Yellow Bullheads but not on Black Bullheads or Tadpole Madtoms; no other ictalurids were tested (Hove et al. 1997). Of 65 fish species tested, *Quadrula verrucosa* (Pistolgrip) glochidia transformed robustly only on Flathead Catfish and marginally on Yellow Bullheads and Brown Bullheads (Hove et al. 2011). *Quadrula fragosa* (Winged Mapleleaf), a federally endangered species, transformed only on Blue Catfish and Channel Catfish but not on 67 other fish species tested, which included Black Bullheads, Brown Bullheads, Yellow Bullheads, Flathead Catfish, Stonecats, Tadpole Madtoms, and Slender Madtoms (Steingraeber et al. 2007; Hove et al. 2012). In host trials of *Quadrula asperata* (Alabama Orb) using 28 fish species, only the Channel Catfish served as a robust host. The Speckled Madtom was a marginal host, and the Yellow Bullhead was not a host (Haag & Warren 2003).

These species and other *Quadrula* have ≥2 related strategies that appear to facilitate host infection by exploiting ictalurid feeding behavior (Barnhart et al. 2008; Haag 2012; Sietman et al. 2012). The most widespread strategy involves display of mantle magazines, a modified, pigmented portion of the mantle that may mimic dead or moribund fish; bloated, dead caterpillars; or even perhaps moribund or dead freshwater mussels, all of which may attract Catfishes (Figs. 15.53 and 15.54). The mantle magazines are generally pale in color, displayed mainly at night, and apparently are not actively moved by the female (Sietman et al. 2012). Glochidia are stored in mantle magazines and released abruptly when the magazine is touched. The Winged Mapleleaf and Pistolgrip release free glochidia, but the Purple Wartyback (and Pimpleback, *Quadrula pustulosa*) releases glochidia in mucoid conglutinates, large structures (≤200 mm long), which also may serve as generalized mimics of Catfish food items (Fig. 15.53). An intriguing, but untested, hypothesis is that a chemical signal associated with these lures attracts and elicits attacks from Catfishes, further facilitating glochidial transmission (Barnhart et al. 2008; Hove et al. 2011; Sietman et al. 2012).

North American Catfishes probably are used as hosts by a large number of host-generalist mussel species (i.e., their glochidia can transform on a phylogenetically diverse array of fishes), particularly members of the tribe Anodontini, but few comprehensive studies of host use are available for generalists. In the Anodontini, North American Catfishes are confirmed hosts for *Strophitus* (on *Ameiurus*, Hove et al. 1997; van Snik Gray et al. 2002), *Ut-*

terbackia (on *Ictalurus*, Keller & Ruessler 1997), and *Lasmigona* (on *Ameiurus*, Eads et al. 2010). Other species such as *Pyganodon grandis* (Giant Floater) can apparently use virtually any fish species as host (e.g., Trdan & Hoeh 1982), but suitability of ictalurids has not been evaluated. Anodontine glochidia can be prevalent on many fish species in natural settings (O'Brien et al. 2013), including ictalurids (Weiss & Layzer 1995), further suggesting that ictalurids are widely used as hosts by generalist mussel species. Apart from the Anodontini, transformation of glochidia on ictalurids occurs in a few putative generalists in other mussel tribes, including *Megalonaias nervosa* (Washboard, tribe Quadrulini, on *Ameiurus* and *Ictalurus*, Woody & Holland-Bartels 1991) and *Elliptio* spp. (tribe Pleurobemini) on the Atlantic Coast (e.g., *Elliptio shepardiana*, Altamaha Lance, on *Ameiurus*, Johnson et al. 2012).

In *Ictalurus*, Channel Catfish and Blue Catfish parasite communities have been studied most extensively. Blue Catfish are hosts to protozoan (4 species), monogenean (4), trematode (6), cestode (3), nematode (4), and crustacean (3) parasites. Channel Catfish, which are studied in more depth for aquaculture, is a host to fungal (2 species), protozoan (29), monogenean (6), trematode (30), cestode (10), nematode (12), acanthocephalan (5), hirudinean (6), and crustacean (10) parasites. The helminth parasites of two Mexican species were studied as well with a documented three cestode, two trematode, and six nematode parasites in *I. balsanus* and one trematode, one nematode, and two cestode parasites in *I. dugesii* (Hoffman 1999; Caspeta-Mandujano et al. 1999; Scholz & Salgado-Maldonado 2000; Perez-Ponce de Leon & Choudhury 2002; Rosas-Valdez et al. 2007; Moravec et al. 2009).

In *Ameiurus*, parasites are studied less extensively; however, studies are available for six species. White Catfish contain fungal (1 species), monogenean (1), trematode (3), cestode (4), nematode (3), hirudinean (3), and crustacean (2) parasites. Black Bullheads host protozoan (7 species), monogenean (7), trematode (33), cestode (16), nematode (12), acanthocephalan (8), hirudinean (5), and crustacean (14) parasites. Yellow Bullheads harbor monogenean (3 species), trematode (19), cestode (6), nematode (9), acanthocephalan (7), hirudinean (2), and crustacean (9) parasites. The most speciose parasite community of bullheads studied to date are for the Brown Bullhead, which hosts protozoan (14 species), monogenean (7), trematode (41), cestode (13), nematode (22), acanthocephalan (12), hirudinean (7), and crustacean (14) parasites. A small number of parasites are documented for the Flat Bullhead, including a monogenean

(1 species), a trematode (1), and nematode (2). Only a trematode parasite is known for the Spotted Bullhead (Hoffman 1999).

Likewise, Flathead Catfish harbor a diverse array of parasites. These include protozoan (2 species), monogenean (2), trematode (7), cestode (7), nematode (4), acanthocephalan (1), hirudinean (1), and crustacean (4) parasites (Hoffman 1999).

Parasites for six species of madtoms are documented, and the total diversity of parasite species inhabiting the genus appears lower than most other Catfishes. The Stonecat harbors monogenean (1 species), trematode (7), cestode (3), nematode (4), acanthocephalan (4), and crustacean (1) parasites. The Tadpole Madtom is host to the same major groups, including protozoan (3 species), monogenean (4), trematode (13), cestode (3), nematode (3), acanthocephalan (3), and crustacean (2) taxa. The Margined Madtom hosts trematode (3 species), cestode (2), and acanthocephalan (1) parasites. The Brindled Madtom hosts trematode (6 species) and cestode (2) parasites. Speckled and Freckled Madtoms have only one documented parasite each, a protozoan and a crustacean, respectively (Klassen et al. 1985; Hoffman 1999, Muzzall & Pracheil 2007). Parasites of blindcats were studied for their interesting adaptation to underground karst habitats. One nematode, *Rhabdochona longleyi*, parasitizes both *Satan* and *Trogloglanis* (Moravec & Huffman 1988; Hoffman 1999).

Because of the significance of Channel Catfish in aquaculture, the species has received extensive study of its diseases as well as its parasites (reviewed by Hawke & Khoo 2004). Of perhaps greatest interest in terms of Catfish diseases, was the discovery of the first fish herpesvirus (referred to now as Channel Catfish Virus or CCV) isolated from outbreaks in farm-raised Channel Catfish in the late 1960s (reviewed by Kucuktas & Brady 1999). Herpesviruses are now known from salmonids (Trouts and Salmons), cyprinids, and percids (Perch). CCV causes major mortality in areas where the species is cultured. Potential vaccines have been under investigation for years.

CONSERVATION

The North American Catfishes contain both widespread, common species (e.g., Channel Catfish) and rare, endemic (e.g., Pygmy Madtom, Chucky Madtom, and Yaqui Catfish), and recently extinct species (Scioto Madtom). About 57% of the species in the family are imperiled to some extent based on American Fisheries Society rankings (Jelks

et al. 2008) with >20% of species considered Endangered (Table 15.2). The most speciose genera, *Ictalurus* (>66% imperilment), *Ameiurus* (>42%), and *Noturus* (>53%), all have a high percentage of imperilment (all imperiled rankings considered) as do the blindcats, which all have Endangered status (Table 15.2). If the estimated future extinction rate of 2.4% per decade for freshwater fish species in the United States (Ricciardi & Rasmussen 1999) is reasonable about 10% of the ictalurid fauna could be extinct by 2050. Other estimates indicate a higher 3.2% per decade extinction rate for North American fishes through 2050, representing even higher potential losses of ictalurid diversity (Burkhead 2012).

Strangely enough in 1970, the Mexican Blindcat, known only from wells and aquifers associated with subterranean environments in Mexico, was among the first of fishes to be considered as Endangered by the U.S. Fish and Wildlife Service. This is especially curious because at the time the species was not known to occur in the United States or any of its territories or protectorates (since discovered in a cave near Del Rio, Texas; Yuhas 2016), and it was listed before the enactment of the 1973 U.S. Endangered Species Act. Shortly thereafter in 1975, the Scioto Madtom was protected under the Act as Endangered. The first medium-sized Catfish species to be protected under the Act as Endangered in the United States was the Yaqui Catfish in 1984, originally known from Arizona. After apparent extirpation, the species was reintroduced in San Bernadino Creek, Arizona (San Bernadino National Wildlife Refuge), in 1997 and 1999 (Stewart et al. 2017). Samples from Mexican waters indicated that hybridization with introduced Channel Catfish has eroded genetic integrity (McClure-Baker et al. 2010; see genetics section), and broodstock and progeny from the only successful hatchery rearing operations in the United States are long-deceased (Stewart et al. 2017). Population parameters estimated from mark-recapture and Bayesian hierarchical models suggest that the Yaqui Catfish in Arizona is on the verge of extirpation (perhaps as early as 2018); annual population declines of 15% have occurred since 2001 (from estimated abundance of 258 to 9) and no recruitment. Given high survival, existing individuals represent stocked fish from the late 1990s that may not have spawned due to suboptimal habitat in spring ponds and competition from Channel Catfish outside of ponds. Despite habitat enhancement and non-native species removals that stabilized other endangered fish populations (e.g., Yaqui Chub, *Gila purpurea*; Yaqui Topminnow, *Poeciliopsis sonoriensis*), the Yaqui Catfish continued

to decline (Stewart et al. 2017). Given its perilous status throughout Mexico (Varela-Romero et al. 2011), the species is in danger of global extinction without substantial, coordinated international efforts (Stewart et al. 2017).

At least two madtom species are extinct or nearly so and over half the species carry an imperiled ranking from the American Fisheries Society or the U.S. Fish and Wildlife Service (Table 15.2). The Scioto Madtom is probably extinct, last seen alive in the autumn of 1957 in Big Darby Creek, Ohio (Trautman 1981), and is the only recorded modern ictalurid extinction in North America to date (Burkhead 2012). The Chucky Madtom (protected as Endangered in 2011) has not been seen since 2004 despite repeated sampling efforts in historic localities (Federal Register 2011a). Four other species of madtoms, including the Yellowfin Madtom, Smoky Madtom, Neosho Madtom, and Pygmy Madtom, are protected as Threatened or Endangered species by the U.S. Fish and Wildlife Service. Only two federally protected madtoms have both a recovery plan and critical habitat designated—the Smoky Madtom and Yellowfin Madtom (USFWS 2015). Others have only critical habitat (Chucky Madtom) or only a recovery plan (Pygmy Madtom, Neosho Madtom), or neither (Scioto Madtom). At least 10 other madtom species (or populations within a species) are considered imperiled by the American Fisheries Society (Table 15.2); all are of conservation concern because of present or threatened habitat loss and narrowly restricted ranges (Jelks et al. 2008).

Several species of madtoms will reproduce in captivity, including some imperiled species, allowing for reintroduction of extirpated populations (Shute et al. 2005). In 1986 a reintroduction program began for Yellowfin Madtoms and Smoky Madtoms into a tributary of the Little Tennessee River (Abrams Creek) in the Great Smoky Mountains National Park. Since that time, >1,800 Yellowfin Madtoms and >3,400 Smoky Madtoms were released in the stream, and since reintroductions ceased in 2002, both species appear to have active reproduction and recruitment. With this success, other experimental populations (designated by the U.S. Fish and Wildlife Service) were established in various tributaries of the upper Tennessee River (Petty et al. 2011ab). All of these rare madtom species have highly restricted ranges and apparently never were abundant. Because they are now protected under the U.S. Endangered Species Act, their status will be monitored into the foreseeable future.

The Northern Madtom (Endangered) is the only species of ictalurid protected (as of 2016) by the Government of Canada (Species at Risk Public Registry 2016). It occurs at a few localities in Lake St. Clair and two riverine tributaries, Ontario (MacInnis 1998). The Stonecat is also of conservation concern in Canada, especially in the Milk River, a tributary of the Missouri River; however, its conservation status was considered Undetermined (Pollard 2004), and to date, it is not recognized for protection by the Government of Canada (COSEWIC 2017).

Some other madtom species are experiencing localized declines or extinctions (e.g., Tadpole Madtom, Lyons 1989; Slender Madtom, Lyons 1996), especially on the edges of their ranges (Parker & McKee 1987; Goodchild 1990, 1993), although most appear to have maintained stable populations. In one case, the Stonecat was brought to near extinction in tributaries along the southwest corner of Lake Superior because of chemical toxicants used to control the Sea Lamprey, *Petromyzon marinus* (Dahl & McDonald 1980). The Frecklebelly Madtom, a riffle-inhabiting Catfish, is one of the few species for which quantitative historical data are available on its distribution and relative abundance. Piller et al. (2004) compared these historical data sets (1950–1964, 1965–1988) with a 1999 survey and concluded that the species had experienced a significant decline since the 1960s in the Pearl River. Similar declines were evident in the Brighteye Darter, *Etheostoma lynceum*, another riffle-inhabiting species. These authors suggested that channel changes and loss of gravel substrates are related to and contribute to the decline of the Frecklebelly Madtom in the Pearl River system. The species has similarly declined in other large river systems in its range (Jelks et al. 2008) and is being considered for federal protection (Federal Register 2011b) but remains abundant in a few areas (Bennett et al. 2008).

After considerable field efforts in searching for blindcats in Mexico, Hendrickson et al. (2001) recommended that *Prietella phreatophila* (Fig. 15.7) be protected by the Mexican government as Threatened and that *P. lundbergi* was clearly Endangered. Rapidly expanding human populations and exploitation of groundwater for municipal, agricultural, and industrial uses threaten blindcats into the foreseeable future. Proposals to use desert areas as waste disposal sites could potentially contaminate aquifers inhabited by these unique species. Of interest, Hendrickson et al. (2001) did find about six individuals of *P. phreatophila* per visit to a site; numbers ranged from 9–66 fish / well pump. Reasonably large populations may be sustained near energy sources in the deep aquifers.

The two blindcats (genera *Satan* and *Trogloglanis*) restricted to artesian wells near San Antonio, Texas, are threatened by overpumping of the aquifer in a rapidly expanding urbanized environment. Numerous individuals of both

species are lost to the surface by discharge from wells, and drawdown of the aquifer threatens to allow the intrusion of poor-quality water into the presumed habitat of these two species. Although under review, neither species is protected as Endangered or Threatened by the U.S. Fish and Wildlife Service (O'Donnell 1998; USFWS 2015), but NatureServe (2013), the American Fisheries Society (Jelks et al. 2008), and the Southeastern Fishes Council (Warren et al. 2000) assigned both species their most Endangered ranking.

All of the other medium-size and large ictalurids in the United States, except the Snail Bullhead, have been widely stocked and are now well established far beyond their native ranges (see diversity and distribution section; Fuller et al. 1999). Because so many of the large ictalurids are of commercial, sport, and aquaculture significance, it seems unlikely that any of them will need State or Federal protection as endangered species into the foreseeable future. In fact, species of *Ictalurus* and *Pylodictis* are regulated by the states through licensing and appropriate use of gear types, season limits, size limits, bag limits, and other regulations placed on the sport and commercial take of Catfishes. Committees assisting the Government of Canada are considering other Catfishes (e.g., Stonecat) for protection in that country.

In conclusion, many ictalurid species are worthy of conservation concern, protection, and further study in North America. Considering that there are now about 50 valid species of Ictaluridae, about 66% of species are imperiled to some degree and nearly 40% are considered Endangered or Threatened by the American Fisheries Society and other professional groups. Most species of concern are threatened by habitat modification or reduction, and many are naturally range-restricted. Overexploitation and hybridization are an additional concern for the Mexican and central American *Ictalurus* spp. (Jelks et al. 2008).

COMMERCIAL IMPORTANCE

Recreational Fishery

The large and medium-size Catfishes (genera *Ameiurus*, *Ictalurus*, *Pylodictis*) provide the resource foundation for diverse fisheries in sport, commercial, and aquaculture industries. An estimated 7.0 million anglers expended 96 million days seeking Catfishes in the United States in 2011. This is equivalent to about 26% of the anglers and 22% of the days fishing for all freshwater fishes in the United States (excluding the Great Lakes) and these metrics have stayed relatively stable for about a decade. The recreational fishery for Catfishes closely approaches the number of fishers for trout and pan-

fish (*Lepomis* spp.) and exceeds that for crappie (*Pomoxis* spp.) and the various Temperate Basses (Moronidae) (excluding the Great Lakes) (USFWS 2002, 2014). A survey of natural resource agencies in the 50 U.S. states, the District of Columbia, and two Canadian provinces (Manitoba and Ontario) showed the importance of Catfishes to fishers with 32 of 53 agencies (>60%) indicating that Catfishes were of high or moderate importance to anglers. Commercial fishing was allowed by 28 agencies, and Catfish populations were managed most often by creel limits or gear restrictions rather than size limits. Most agencies, however, indicated that they do not intensively manage Catfish populations with the exception of put-and-grow fisheries and small impoundments (Michaletz & Dillard 1999). As of 2016, 37 U.S. states and three Canadian provinces had statewide creel limits ranging from catch-and-release regulations (Nebraska) to 100-daily limits (Louisiana) (Eder et al. 2016). In agreement with the earlier survey (Michaletz & Dillard 1999), only 20 states use some minimum length limit regulation, which are generally implemented to prevent harvesting of fish before they reach full growth and contribute to the population. Most states do not impose length limits despite strong interest in Catfish as recreational targets and the potential for these regulations to increase the number of large fish in the fishery (Eder et al. 2016). Long-term data from the Red River of the North suggested that conservative harvest regulations that protect large and small individuals through length and creel limits have maintained the Channel Catfish trophy fishery there, preserving desirable age and size structure for the >20 years even with low individual growth rates (Siddons et al. 2016).

An analysis of recreational harvest in 349 reservoirs in the United States found five clusters differing in harvest rates, dominant Catfish species harvested, and amount of fishing effort targeted at Catfishes. A northern cluster across the northern third of the United States had low annual harvest (0.07 kg/ha, 0.062 pounds/acre) and low effort for Catfishes (12% of anglers targeted Catfishes); Catfishes were harvested in one-fifth of reservoirs. In the southwestern cluster, where Catfishes are introduced, Catfishes were harvested in half of the reservoirs, but annual harvest was low (0.35 kg/ha, 0.31 pounds/acre), *Ictalurus* spp. were dominant, and only 22% of anglers fished for Catfishes. A third cluster in the eastern and central United States had *Ictalurus* spp. as the dominant Catfishes harvested, but annual harvest was moderate (0.65 kg/ha, 0.58 pounds/acre), Catfish harvest was more frequent (9/10 reservoirs), and 40% of anglers targeted Catfishes. A fourth cluster, located in central and southern portions of the United States, had *Ictalurus* spp. as the dominant Catfishes harvested. Catfish were harvested in

all reservoirs in this region, annual harvest was high (3.6 kg/ha, 3.2 pounds/acre), and 46% of anglers targeted Catfishes. A final cluster was interspersed throughout the eastern and central United States and had *Ameiurus* spp. as the dominant Catfishes harvested. Catfishes were harvested in all reservoirs, annual harvest was high (6.3 kg/ha, 5.6 pounds/acre), and 38% of anglers targeted Catfishes (Miranda 1999). These clusters were also associated to some degree with environmental variables such as depth, watershed area, water-level fluctuation, and shoreline development, but only tests for differences among clusters, not statistical associations between cluster characteristics and the environmental variables, were conducted. This classification of reservoir types can aid managers in selecting techniques for Catfish fishery improvement. For instance, the low-harvest reservoir fisheries would benefit from efforts to enhance abundance (stocking, habitat manipulation), but high-yield reservoirs need more focus on harvest management (Miranda 1999).

Aquaculture Production

All of the species in these genera can be and have been propagated (little work has occurred with Mexican *Ictalurus* and several bullheads), and the Channel Catfish is undoubtedly the most important culture fish in the family. A major industry is involved in mass production of this species (see Geibel & Murray 1961; Simco & Cross 1966; Walsh & Lindberg 1986). The Channel Catfish is served in many restaurants throughout the United States, especially in the South. In fact, when ponds are built, the owners invariably request that Channel Catfish or bullheads be included in the initial stocking by state agency personnel (Marzolf 1957). Fishers have accepted low catch rates for Flathead Catfish and Blue Catfish because of the opportunity to catch a few, exceptionally large fish (i.e., trophy angling). In fact, breaking traditional fishing records will be best accomplished by fishing for Catfishes, not Largemouth Bass or trouts. In Waterville, Minnesota, bullheads are elevated to celebrity status during the annual 4-day Bullhead Days (angling and cooking) Festival (Buffler & Dickson 1990).

Channel Catfish farming is a major industry in the United States, beginning in the 1960s with the first processing plant. In 1981, >40,469 ha (>100,000 acres) of water were used to produce >102 million kg (about 225 million pounds) of Catfish yearly in the United States (Walsh & Lindberg 1986). From 1982 to 2002 total pond area almost doubled and production increased sixfold, peaking in 2003 at 300,000 metric tons (295,262 tons) worth $384 million, which was equivalent to 64% of U.S. aquaculture production. In 2002 Americans age 18 and older consumed an average 0.4 g (0.01 ounces) of Catfish per person per day, putting Catfish (mostly Channel Catfish) behind only tuna, shrimp, and flounder, and making it the most-consumed freshwater fish (EPA 2002). Production has declined since then due to higher feed prices from corn ethanol production and increasing imports of Asian Catfishes (*Pangasius* spp.). Since 2002, pond area has declined by 25%, and the number of farms has declined 31% (Olin et al. 2011).

Commercial Harvest

Bullheads, forktail Catfishes, and Flathead Catfishes are commercially harvested year-round with trot lines, hoop nets, gill nets, and trammel nets. Slat traps are used primarily during the spawning season. Channel Catfish are often the second or third most frequently captured species after buffaloes and carps in the Mississippi River basin. In 1994 the FAO reported that excluding production from aquaculture, a total of 5,892 metric tons (5,799 tons) of all species of Catfishes (clearly excluding all madtoms) were caught in the United States (Heidinger 2000). In the early 1990s, the price of wild-caught Channel Catfish ranged from $0.16 to $0.34/kg ($0.35 to $0.75/pound). To place this in perspective, during 1994 sales of cultured Channel Catfish in the United States were expected to be between 1,973 and 2,018 metric tons (435 and 445 million pounds), a 3–5% decrease from 1993. Fish farm level prices averaged $0.36/kg ($0.785/pound) for a gross fish farm revenue of $340 million (USDA 1994). In large quantities, Blue Catfish and Flathead Catfish sell for prices similar to Channel Catfish (Heidinger 2000). In 1992 the Missouri River was closed to all commercial Catfishing to allow full access to recreational anglers. This has apparently increased the harvest and release rates for Catfishes, especially Flathead Catfish, for which harvest rates tripled and release rates doubled after the commercial ban (Stanovick 1999). Average length of Channel Catfish, Blue Catfish, and Flathead Catfish has also increased since the ban (Mestl 1999; Stanovick 1999) and Channel Catfish populations have shifted from dominance of age-1 and age-2 individuals to those ≥4-years-old (Mestl 1999).

Hand Fishing

The sport of hand fishing (also grappling, grabbling, hogging, noodling, grabbing, yanking, snatching, tickling, or logging) for Flathead Catfish is a traditional fishing method that is still popular in rural areas of southern and midwestern states (Figs. 15.55–15.59), and targets individuals >15 kg

Figure 15.55. (*upper*) Hand fishers (grabblers or grapplers) prepare to catch a Catfish from a wooden grappling box (Fig. 15.56) previously sunk in the water near a large log in the Tallahatchie River, near Coldwater, Mississippi. (*lower*) A fisher holds a large Blue Catfish, *Ictalurus furcatus* (16.5 kg, 36.4 pounds), that was extracted from the box (courtesy of Mickey Bland and Bryan Simmons).

Figure 15.56. (*upper*) A wooden grappling (or grabbling) box designed to attract spawning Blue Catfish, *Ictalurus furcatus*, and Channel Catfish, *I. punctatus*, of about 13.6–18.1kg (30–40 pounds) in size. The box measures 139.7 cm long, 38.1 cm wide, and 33.0 cm in height (55×15×13 inches) with one end left open as an entrance (*lower*) and the other end closed. The rather narrow, long shape mimics that of a large, hollow log. The boxes are secured to cypress trees with wire or staked to the bottom at depths ranging from about 1.2–7.6+ m (but usually <3.1 m) (4–25+ feet, <10 feet). Larger boxes are used to target larger Blue Catfish but produce fewer fish in areas with heavy pressure. Grapplers indicate breeding male Blue Catfish also tend to readily occupy submerged cylindrical metal tanks (e.g., core tanks from discarded water heaters with an entrance cut in one end), but for unknown reasons seem less prone to nest in barrels made of plastic (M. Bland pers. comm.; courtesy of Mickey Bland).
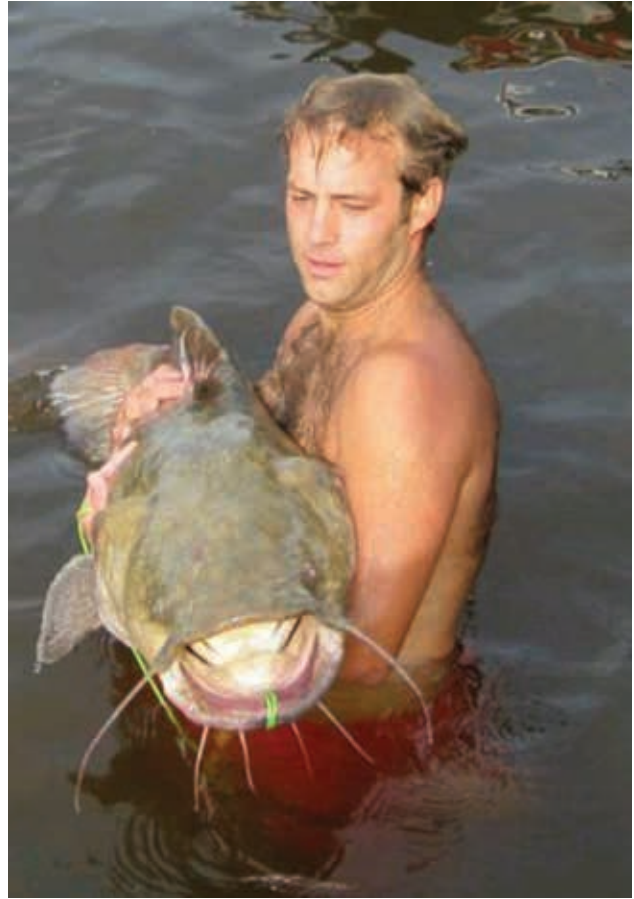
(33 pounds) (Salazar 2002; Morgan 2008). Channel Catfish and Blue Catfish (Figs. 15.55 and 15.56) are also taken by grappling fishers (Jackson 1999). The technique was practiced by Native Americans, described by early American settlers in the late 1700s, and has been passed down for many generations (Salazar 2002; Morgan 2008). One can either place their hand inside the mouth of the targeted fish (usually while it is resting, mating, or guarding an egg clutch inside a hollow log or other cavity) and pull it out or reach in and set a grappling hook in the fish to pull it out. Others use a rope placed through the mouth of the fish, then out through the gill cover, then pulled around and tied together near the mouth. Once this is accomplished, the fish can be

Figure 15.57. (*upper*) A hand fisher (grabbler or grappler) displays a large gravid (or partially spent) female Flathead Catfish, *Pylodictis olivaris* (11.5 kg, 25.4 pounds), taken from a cavity beneath a concrete boat ramp in Moon Lake, Mississippi. A second fisher (background) prepares to hand extract the breeding male from the cavity. (*middle*) The male Flathead Catfish (9.1 kg, 20 pounds) is successfully extracted from the cavity and brought to the surface. Note the specialized equipment, such as diving masks and wet suits as well as the air regulators and hoses, which lead to a gasoline-powered, surface-supplied air (hookah) rig in a nearby boat. This equipment allows hand fishers to set and fish their grappling boxes (Figs. 15.56 and 15.58) in deep water (1.5 to >3.7 m, 5 to >12 feet, M. Bland pers. comm.). (*lower*) A hand fisher holds a large, male Flathead Catfish (about 20.4 kg, 45 pounds) caught from Kentucky Lake (Tennessee River drainage) near Paris, Tennessee (photographs courtesy and used with permission of Mickey Bland and Bryan Simmons).

pulled out. If just using a hand, the fish often bite down on the hand and fingers and can cause severe damage, or if the fish is really huge (e.g., 34 kg, 75 pounds), it can pull a person underwater and hold them there. Grapplers often use relatively sophisticated gear, like masks, snorkels, and surface-supplied air (hookah) rigs, to seek fish in deep water (Figs. 15.55 and 15.57). Many sink weighted homemade wooden boxes in rivers and reservoirs to attract spawning fish (Figs. 15.56 and 15.58), particularly large guardian males. The sport is largely harvest-oriented with only about 10% of Catfishes released as reported in fisher surveys in Mississippi (Brown 2011), although this may be no different than most anglers (Steffen & Hunt 2011). In one Mississippi reservoir in 2007 and 2008, an estimated 3,313 and 2,589 Catfishes, respectively, were harvested (Brown 2011;

Fig. 15.59). Hand-grappling is a highly social sport compared with other forms of fishing (Brown 2011; Steffen & Hunt 2011). A reality television program entitled "Hillbilly Hand-fishin'" included several episodes in 2012 of amateurs being schooled by experienced grapplers in capturing large Cat-fishes, and other programs feature the sport as well.

Figure 15.58. Grappling (or grabbling) boxes for Flathead Catfishes, *Pylodictus olivaris*, are designed in several styles, configurations, and sizes. (*upper*) A nearly square, floorless (inset) Flathead Catfish box is designed for use in non-flowing waters (e.g., reservoirs or bayous). The box measures about 117 cm (46 inches) on each side and 37 cm (14.5 inches) in height. The entrance to the box is about 41 × 22 cm (16 × 8.5 inches). Flathead Catfish in the 9.1–18.1 kg (20–40 pound) range are frequently extracted from boxes of this size during the breeding season. The box is sunk and secured on the bottom by placing sandbags on the top. (*lower*) The trapezoidal (inset), floored Piebox, shaped to facilitate hand-extracting fish, is used to catch Flathead Catfish in flowing waters (e.g., rivers). The floor helps prevent the box from being buried in the substrate over time as flowing water deposits and erodes substrate around the box. The Piebox measures about 152 cm (60 inches) long, tapers from 122 cm (48 inches) wide in the back to 53 cm (21 inches) wide in the front, and is about 46 cm (18 inches) in height. The entrance is about 41 × 25 cm (16 × 10 inches). It is sunk and secured to the bottom by partially filling the interior with natural substrate and if needed, placing sandbags on top (M. Bland pers. comm.; courtesy of Mickey Bland).

Currently ≥18 southeastern and midwestern states allow hand fishing, and some controversy exists over the practice among recreationists and state conservation agencies (Morgan 2008; Campoy 2011). For example, the high harvest numbers of large Catfishes have prompted some state fishery agencies to promulgate possession and size limits on grapplers (e.g., Alabama, some waters in Mississippi). In Missouri, a five-year trial study of hand fishing in portions of three rivers was ended abruptly after managers found unacceptably high harvest rates from all types of angling across the state. The main concern of the management community is that hand fishing targets the largest individuals most often during the nesting season, removing some of

Figure 15.59. Hand fishers (grabblers or grapplers) display their catches of Flathead Catfish, *Pylodictis olivaris*, at a tournament in north Mississippi, June 2013. The fish were caught primarily in preset grappling boxes placed in rivers and reservoirs in the region (Fig. 15.58). The 2013 tournament winner for largest fish (not shown) was 32.8 kg (72.4 pounds); the 2012 winning Flathead Catfish weighed 36.8 kg (81.2 pounds), which at that time set a new state record for the species (from Crownover 2013; courtesy of Joe Worthem courtesy of Oxford Invitation).

Figure 15.60. Artificial bait mimicking madtoms (genus *Noturus*) produced by Case Plastics (courtesy of © T. Taylor and J. Jackson).

Other Uses

Madtoms and other Catfishes are used as bait for sport fishing (Cochran 2011), they are popular as aquarium fishes, and when endangered, some species are propagated in hatcheries. One artificial bait company (Case Plastics, Fishing Complete, Inc.) even has a line of 8.9 cm (3.5 inch) madtom lures in a variety of natural colors (Fig. 15.60). The albino form of the Channel Catfish, common in hatcheries and fish farm ponds, is sold in the aquarium trade and also used as bait. Propagation of endangered Catfish species, usually small madtoms or the Yaqui Catfish, has been accomplished at Conservation Fisheries, Inc. of Knoxville, Tennessee, at the Southwestern Native Aquatic Resources and Recovery Center (formerly, Dexter National Fish Hatchery and Technology Center) near Roswell, New Mexico, and the Uvalde National Fish Hatchery in Uvalde, Texas (BMB pers. obs.).

Negative Effects

Introduced Catfishes, especially the forktail Catfishes and Flathead Catfish, have caused negative impacts on other species (and other Catfishes) deemed important in the fishery (Moser & Roberts 1999). For example, Flathead Catfish introduced into the Carolinas and Georgia have become major predators of traditional fisheries (see diversity and distribution section). Potential commercial significance on the negative side also includes the fact that nearly all ictalurids have some venom near their spines that can cause serious injury and anaphylactic shock for those allergic to Catfish venoms (BMB pers. obs.). A Catfish fisher on the Ohio River who had a large

the fittest males and leaving eggs to die (Figs. 15.55, 15.57, and 15.59). Hand fishing is also effective with an estimated 60% of capture attempts being successful (Morgan 2008). The few studies conducted to date, however, suggest that normal harvest practices have a far greater impact than hand fishing (Jackson 1999; Winkelman 2011). For instance, a 2013 study based on 255 tagged Flathead Catfish in Texas found that, although hand fishing could reduce abundance of trophy fish (>762 mm), exploitation of trophy fish alone would need to increase to >55% (from <5%) to have a substantial impact on Flathead Catfish populations through recruitment overfishing (Bodine et al. 2016). More studies are needed on the consequences of hand fishing for genetics, sustainability, population structure, and size structure of Catfish populations.

Figure 15.61. An expert on the anatomy and systematics of the North American Catfishes (Ictaluridae), William Ralph Taylor (1919–2004) published his revision of *Noturus* in 1969 and included a phylogeny of North American Catfishes. In his masterful review, Taylor described as new nearly half the species of *Noturus* that are recognized today (from the ichthyologists photograph collection of BMB).

Channel Catfish thrown to him (to be placed on ice in a cooler) was impaled in the chest by one of the spines resulting in a collapsed lung and an infection; he survived the incident (The Southern Illinoisan 1992). As noted earlier, fishers that mishandle Catfish and have a spine embedded in their finger may suffer from amputation of phalanges. The important message is to learn how to properly handle Catfish in the wild or the aquarium setting and to take it seriously when spined by any North American species.

LITERATURE GUIDE

Two volumes published by the American Fisheries Society from International Catfish Symposia in 1999 and 2011 (Irwin et al. 1999a; Michaletz & Travnichek 2011) represent substantial collections of knowledge on North American Catfishes. Particularly valuable are the reviews on biology and management of major groups and species, including the Channel Catfish (Hubert 1999), Flathead Catfish (Jackson 1999), and Blue Catfish (Graham 1999). The review of Burr & Stoeckel (1999) on madtoms in the first symposium remains the best synthesis of information up to that time on the genus. Earlier, Taylor's (1969) revision of *Noturus* laid a solid, systematic foundation for the most diverse group of North American Catfishes (Fig. 15.61). The reviews of electroreception in Catfishes (New 1999) and the functional morphology of the pectoral spine in Channel Catfish (Fine et al. 1999) were particularly helpful in summarizing sometimes difficult literature. The proliferation of studies on non-native introductions of ictalurid Catfishes and Catfish movement in the second volume prompted syntheses in this chapter. The book *Biology and Culture of Channel Catfish* (Tucker & Hargreaves 2004) summarized much information on environmental tolerances and physiology of that species. Simon & Wallus (2004) provided summaries and illustrations of embryo and larval development.

Acknowledgments