

Chapter 22 Aphredoderidae: Pirate Perches

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The Pirate Perch, *Aphredoderus sayanus* (Gilliams), of eastern and central North America is the only extant species of the family Aphredoderidae, which is endemic to North America. Pirate Perches have long been associated phylogenetically with Cavefishes (Amblyopsidae), because the two families share prominently exposed cephalic neuromasts occurring in ridge configurations and the well-known jugular position of the vent (anus and urogenital pore). The vent is in the normal position in small Pirate Perch but migrates forward to attain the jugular position by the late juvenile or early adult stage (Mansueti 1963; Fig. 22.1). The generic name refers to excrement from or in the throat because of the position of the vent. The specific epithet, *sayanus*, is a patronym

for Thomas Say, the late 18th century entomologist and conchologist who did much of his work in the utopian society established in New Harmony, Indiana, along the banks of the Wabash River. The common name apparently originated with one of our early naturalists, Charles C. Abbott, who found that Pirate Perch ate only fish in his aquarium, and from the superficial perch-like resemblance (Abbott 1862).

Because of the jugular-placed vent in adults and the documented habit of branchial (mouth) brooding in the Northern Cavefish, *Amblyopsis spelaea* (a member of the sister family, Cavefishes), the reproductive behavior and actual spawning mode of the Pirate Perch were of great curiosity to ichthyologists and aquatic ecologists.



Plate 22.1. Pirate Perch, *Aphredoderus sayanus*.

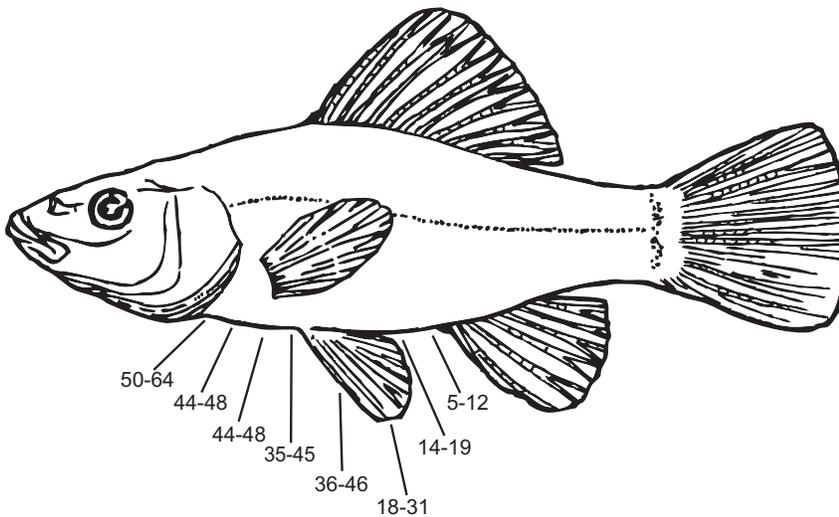


Figure 22.1. The vent of the Pirate Perch, *Aphredoderus sayanus*, migrates from just anterior of the anal fin in juveniles to the jugular (under the throat) position in adults. Lines indicate the approximate position of the vent at corresponding ranges of SL (redrawn from Mansueti 1963).

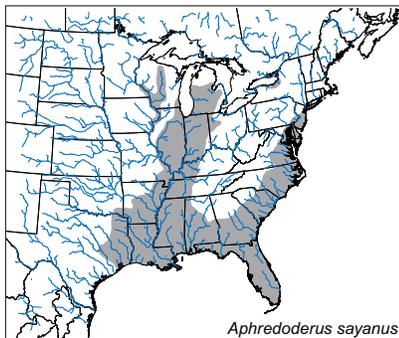


Figure 22.2. Geographic range of the Pirate Perch, *Aphredoderus sayanus*, the only extant species in the family Aphredoderidae, which is endemic to North America.

Many authors speculated that Pirate Perch were branchial brooders based on some physical traits but not until recently has this question been solved (Poly & Wetzel 2003; Fletcher et al. 2004; see reproduction section).

Pirate Perch are primarily nocturnal and hide during much of the day. Their chemical camouflage, likely especially effective at night, acts through mimicry, crypsis, or cloaking and apparently renders them as virtual ghosts to potential prey species (see physiology section). They do not often occur in habitats where the water is clear for observation, and we encourage other aquatic biologists to continue to observe and film the reproductive behavior of this indigenous species in a natural setting. Much is still to be learned about this shy and retiring species.

DIVERSITY AND DISTRIBUTION

The Pirate Perch occurs on the Atlantic and Gulf Slopes from Long Island, New York, to the Colorado River drainage, Texas, and in the Great Lakes and Mississippi river basins from Michigan, Wisconsin, and southern Minnesota to the Gulf (Fig. 22.2). Isolated populations occur in Lakes

Ontario and Erie drainages, New York (Page & Burr 1991). This species is generally common throughout the central portions of its range but seems to be most abundant on the Coastal Plain and other lowland regions. Widely separated, apparently introduced populations occur in the Wisconsin and Embarrass Rivers, Wisconsin (Becker 1983), but the source of the introduction is unknown (Fuller et al. 1999).

The Pirate Perch clearly consists of two distinct lineages if not two full species. The species was originally described (as *Scolopsis sayanus*) from fishponds near Philadelphia (Pennsylvania) (Gilliams 1824). Bailey et al. (1954:135) noted that “Pirate-Perch from the Middle Atlantic States differ consistently in a number of characters from those of the Mississippi Valley and Great Lakes.” Subsequent morphological analysis revealed two recognizable subspecies of Pirate Perch (Boltz & Stauffer 1993; Fig. 22.3). Genetic evidence indicates, however, at least two highly diverged, undescribed cryptic species are now subsumed under the name *A. sayanus*. In an extensive DNA barcoding survey of North American fishes (using 652 bp of the COI mitochondrial gene), the Pirate Perch showed a maximal intraspecific genetic divergence of >15%. This is closer to the level of divergence observed among genera (13.5%) and families (15.9%) of North American fishes than between sister-species (5.7%) (April et al. 2011). In a limited geographic sample not including the putative intergrade zone, fossil-calibrated divergence times between the two taxa from eight nuclear and one mitochondrial gene were estimated as Late Miocene (about 6 mya, 4–8 mya, 95% highest posterior density intervals of age estimates); the taxa were treated as full species (Niemiller et al. 2012).

Based on morphology, the nominotypical subspecies, *Aphredoderus sayanus sayanus*, occurs on the Atlantic Slope



Figure 22.3. (upper) Adult *Aphredoderus sayanus gibbosus* (123 mm TL), from Brush Creek (Obion River drainage), Hickman County, Kentucky (May 2009) and (lower) *Aphredoderus sayanus sayanus* (47 mm SL) from Coppahaunk Swamp, Sussex County, Virginia (July 1984) (upper courtesy of Matt Thomas; lower courtesy of Noel Burkhead and Robert Jenkins, courtesy of Virginia Division of Game and Inland Fish).

south to the Satilla River, Georgia, and *A. s. gibbosus* (originally described by Lesueur 1833 from Lake Pontchartrain, Louisiana; Fig. 22.4) occurs on the Gulf Slope west of the Mississippi River and in the Mississippi River and Great Lakes basins (Fig. 22.2). Populations from the Saint Marys River of the Atlantic Slope west to the Pearl River of the Gulf Slope were considered intergrades based on morphological intermediacy. The two subspecies are distinguished as follows: *A. s. sayanus* has usually 3 anal spines, 4 dorsal spines, 11 pectoral rays, and 36–47 (usually <42) lateral-line scales; *A. s. gibbosus* has usually 2 anal spines, 3 dorsal spines, 12 pectoral rays, and 42–56 (usually >45) lateral-line scales. In addition, *A. s. sayanus* usually has a lateral pigment stripe, lacking in *A. s. gibbosus*. Putative intergrade samples have usually 2–3 anal spines, 3 dorsal spines, and 37–56 (usually 43–48) lateral-line scales.

PHYLOGENETIC RELATIONSHIPS

Phylogenetic analyses place *Aphredoderus sayanus* as the sister-group of the Amblyopsidae (Cavefishes), which together are sister to the Percopsidae (Trout-perches) (Dill-



Figure 22.4. An explorer, naturalist, and artist, Charles Alexander Lesueur (1778–1846) described the genus *Aphredoderus* in 1833. Several emendations to this name are present in the early literature but Lesueur's spelling and description of the genus remains valid (courtesy of the ichthyologist photograph collection of Brooks M. Burr).

man et al. 2011; Near et al. 2012b; Niemiller et al. 2012; Betancur-R. 2013ab; Grande et al. 2013) forming the Percopsiformes (Trout-perches). This relationship also was recovered using 10 nuclear genes, and the deep-sea Polymixidae (Beardfishes) were resolved as sister to the percopsiforms with an Early Cretaceous divergence estimated between the polymixids and percopsiforms (mean 127.8 mya; 111.6–141.0 mya, 95% highest posterior density interval) (Near et al. 2012b, 2013). In an expanded analysis using 21 molecular markers and incorporating the Near et al. (2012b) data, the same sister-group relationship was indicated among the three percopsiform families, but the group was basal to a clade consisting of Zeiformes (Dories), Stylephoriformes (Tube-eyes or Threadtails), and Gadiformes (Cods) with divergence estimated as the Early Cretaceous (Betancur-R. et al. 2013a). Within percopsiforms, fossil-calibrated estimates from the mitochondrial ND2 gene placed divergence between the Percopsidae and Aphredoderidae + Amblyopsidae in the late Cretaceous (estimated divergence 69.6 mya, confidence interval 83.2–64.9 mya). The diversification between Aphredoderidae and Amblyopsidae was placed in the Early Eocene (54 mya, confidence interval 56.8–51.9 mya) (Dillman et al. 2011). Divergence estimates from multiple genes (nuclear and mitochondrial) with

fossil-calibrated nodes were also Early Eocene but somewhat more recent (48.1 mya, 37.8–56.1 mya) (Near et al. 2012b; Niemiller et al. 2012). Hypothesized relationships of these three families are discussed and presented in the phylogenetic relationships section in the chapter on amblyopsids (Adams et al., this volume).

FOSSIL RECORD

A fossil Pirate Perch, †*Trichophanes hians*, was first described from North America by E. D. Cope (Cavender 1986). This aphredoderid occurred west of the Western Continental Divide in a Paleogene lignite locality (about 65.5–22.0 mya) in Nevada and was associated with an extinct Sucker (Catosomidae), †*Amyzon mentale* (Cavender 1986). Two other aphredoderids of the same genus were described from Oligocene-age (about 33.7–22.8 mya) lake beds in Colorado (Cavender 1986), located just east of the Western Continental Divide. The number of actual fossil species is controversial because †*T. copei* was placed in synonymy with †*T. foliarium* (Rosen & Patterson 1969). The fossil record shows the family clearly had a wider distribution in the past.

MORPHOLOGY

Obvious phenotypic and distinctive features of the Pirate Perch (Fig. 22.3) include a deep, robust body, large head and mouth, tubular anterior nostrils, a large round protuberance at the isthmus of the adult, the anus and urogenital openings between the gill membranes (in adults), the head with conspicuous ridges of exposed neuromasts (Figs. 22.5 and 22.6), ctenoid scales on the head and body, and thoracic pelvic fins. Two or three stout spines occur in front of the dorsal and anal fins, the lateral line is complete or incomplete, the opercle has a sharp spine, the opercle and preopercle are serrate, and the caudal fin is emarginate with rounded tips. The species has six branchiostegal rays, about 10–12 blunt gill rakers, 12 pyloric caeca, and a simple air bladder (summarized by Wallus & Lowery 2006). Meristic features are geographically variable (see diversity and distribution section; Boltz & Stauffer 1993). Several authors provide illustrations of aspects of the skeletal and muscular anatomy (Gregory 1933; Rosen 1962a; Mansueti 1963; Borden et al. 2013). Most adults are 64–106 mm SL (2.5–4.2 inches) (maximum about 126 mm SL, 5 inches). The largest adults reach 144 mm TL (5.7 inches).

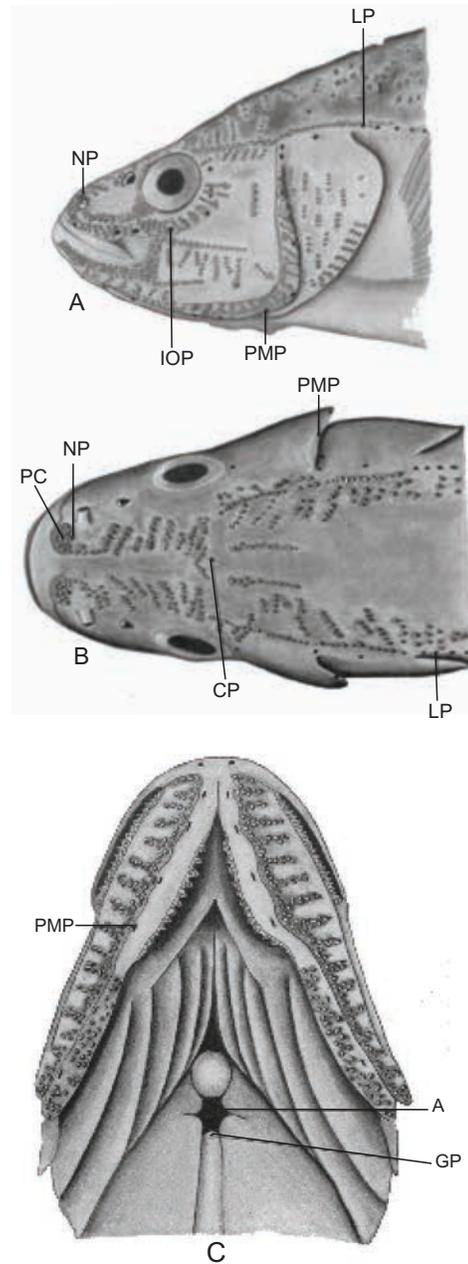


Figure 22.5. Cephalic sensory areas of the Pirate Perch, *Aphredoderus sayanus*. (A) lateral view of the head; (B) dorsal view of the head; and (C) ventral view of the head. Because of representational difficulties with the medium used (originally drawn from a photograph using a pantograph), the number of superficial neuromasts shown in a given area are much fewer than an equal area of the specimen. Scales are not shown (redrawn in part and used with permission of the American Society of Ichthyologists and Herpetologists from Moore & Burris 1956). Key: A = anus; CP = coronal pore; GP = genital pore; IOP = infraorbital pore; LP = lateral-line pore; NP = nasal pore; PC = pre-nasal cluster; PMP = preoperculumandibular pore.

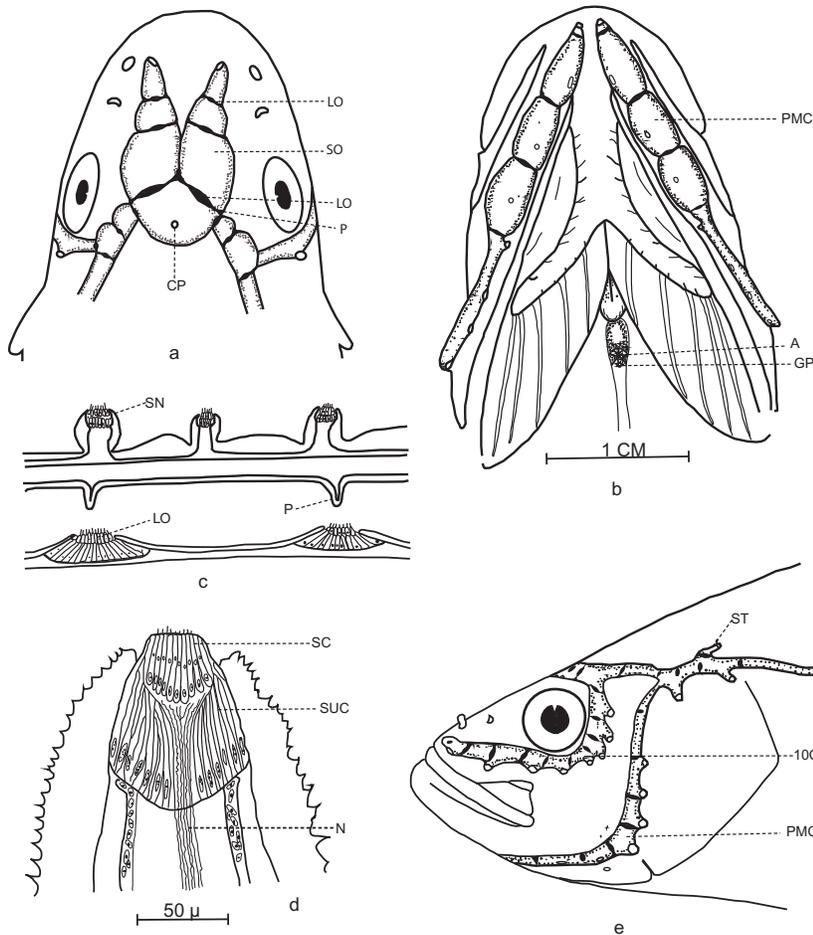


Figure 22.6. Aspects of the cephalic lateral line of the Pirate Perch, *Aphredoderus sayanus*. (a) dorsal aspect of head; (b) ventral aspect; (c) longitudinal section of mandibular ramus of the preoperculo-mandibular canal showing two canal organs and three of the numerous superficial neuromasts; (d) enlargement of a superficial neuromast; and (e) lateral aspect of head (redrawn in part and used with permission of the American Society of Ichthyologists and Herpetologists from Moore & Burris 1956). Key: A = anus; CP = coronal pore; GP = genital pore; IOC = infraorbital canal; LO = lateral-line organ; N = branch of lateral line nerve; P = partial partition in lateral-line canal; PMC = preoperculo-mandibular canal; SC = sensory cell; SN = superficial neuromast; SO = supraorbital canal; ST = supra-temporal canal; SUC = supporting cell.

Vent Migration

Beginning at about 5–12 mm SL (0.2–0.5 inches), the vent is in the preanal region and at 50–64 mm SL (2.0–2.5 inches) reaches the jugular position (Mansueti 1963; see also Martin & Hubbs 1973; Hogue et al. 1976; Minton et al. 1985; Wallace & Lowery 2006; Fig. 22.1). During the migration the urogenital duct and intestine migrate forward, but the gonads remain essentially in their original position (Figs. 22.7 and 22.8). The intestine curves forward during the migration accompanied by an elongation of the distal end of the intestine. Upon migrating forward to just above the origin of the pelvic fin, the duct and intestine pass through a foramen formed by the crossed posterior forks of the pelvic girdle and through a ventral abdominal muscular area anterior to the pelvic fins (Fig. 22.8). At the time of passage through the foramen the bones are not fully ossified but upon ossification the pelvic bones form a rigid lip for the opening (Mansueti 1963).

Life Color

The color is olive-gray or brown to deep purple on the head and body; the venter and throat are whitish or yellowish but usually heavily speckled with melanophores; a dark, vertical bar (sometimes appearing as two blotches) often is at the base of the caudal fin; a black suborbital bar is usually prominent; all fins are dusky; and the median fins have black subdistal margins and usually narrow white edges. Young often appear almost black on the head and body but ventrally are lighter and usually speckled.

Sexual Dichromism and Dimorphism

Males in breeding condition become dark overall, almost black; the sides have a purplish or violet cast; the iris is copper; the black ocular bars are vague; the side of face is silver-blue; and the belly is often densely peppered with melanophores. The female is less darkened overall and has a lighter colored abdominal area. The Pirate Perch is

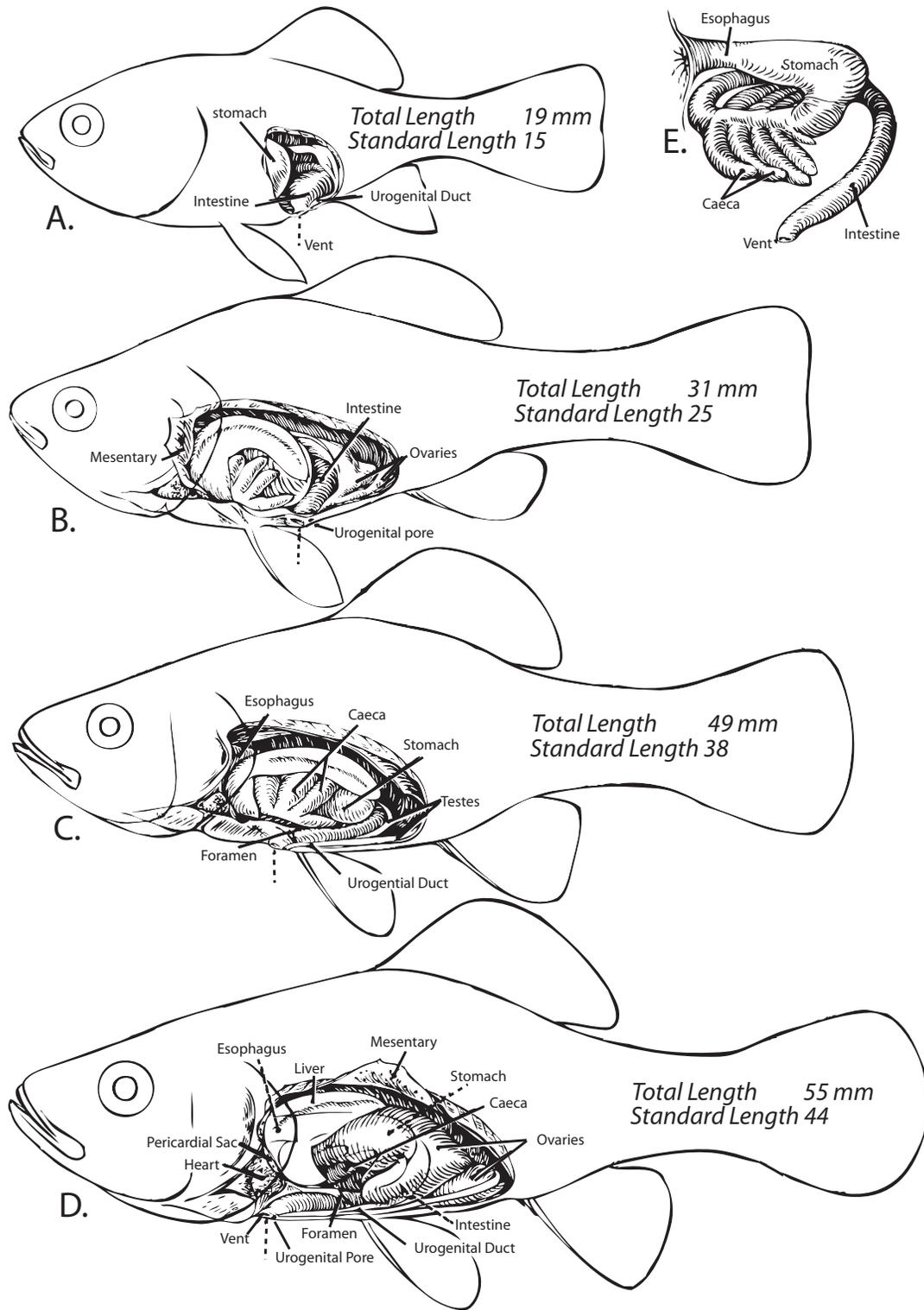


Figure 22.7. Changes in the gross internal anatomy of the Pirate Perch, *Aphredoderus sayanus*, with respect to fish length and the anterior migration of the vent (A–D). The alimentary tract, unobscured by other organs, is expanded and depicted in E (redrawn from Mansueti 1963).

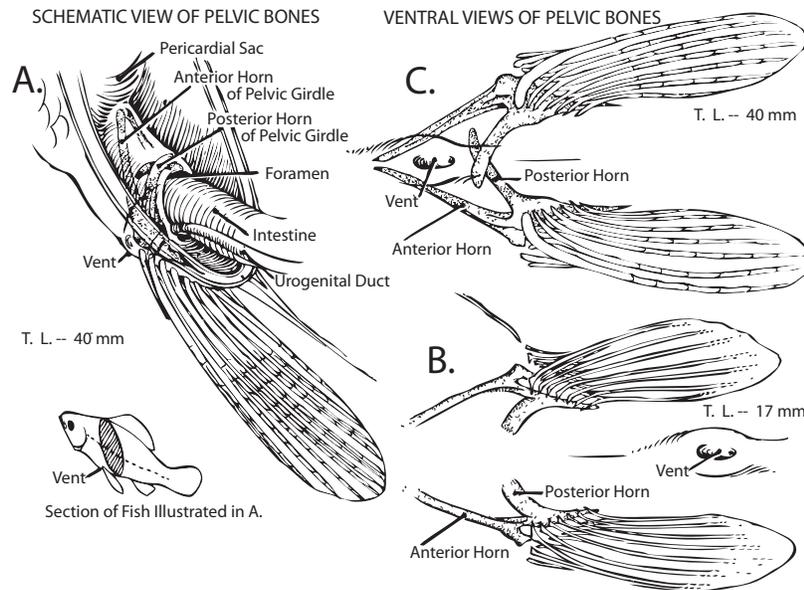


Figure 22.8. Pelvic region of the Pirate Perch, *Aphredoderus sayanus*, illustrating (A) schematic view of the pelvic bones in relation to the intestine and vent in a 40-mm TL individual; (B) incomplete ossification of the pelvic bones in a 17-mm TL individual (ventral view); and (C) complete development of the pelvic girdle in a 40-mm TL individual (ventral view) (redrawn from Mansueti 1963).

apparently sexually dimorphic (contra Murdy & Wortham 1980) in that mature females are longer and deeper-bodied than males (Tiemann 2004).

Sense Organs

The lateral-line canal and cutaneous sense organs on the head of the Pirate Perch are rather conspicuous and relatively well described (Figs. 22.5 and 22.6). The lateral canal extends from the gill cleft to just below the dorsal-fin origin, and pores (13–18) are present at the posterior border of each scale. Most scales behind those with tubes have exposed neuromasts, which lack pigment cells. Adults have a conspicuous pattern of cutaneous organs in transverse rows on each side of the middorsal line of the head and in vertical rows on the sides of the head, opercles, and mandibles (Figs. 22.5 and 22.6). Most scale pockets also bear a vertical row of organs situated on the exposed posterior fields. Anterior to the nostrils is a cluster of organs, the prenasal cluster; each cluster is composed of about 80 separate papillose neuromasts closely matted together (Fig. 22.5). Clearly, the Pirate Perch has an extensive and extremely well-developed lateralis system not unlike that of the amblyopsid Cavefishes. Pirate Perch are largely nocturnal and secretive and have developed a specialized sensory system (see physiology section), which undoubtedly enables them to be aware of their environment both at night and during the day. Even so, little to nothing is actually documented on the sensitivity or functionality of this rather elaborate sensory system.

GENETICS

Other than DNA sequences used primarily in the construction of phylogenetic trees (see Chapter 21 on Amblyopsidae, phylogenetic relationships section) or DNA barcoding (see diversity and distribution section), the Pirate Perch has not been the subject of genetic study. The species is in need of a thorough phylogeographic study throughout its range to clarify genetic distinctiveness among populations and ascertain if morphological differences are indicative of distinct evolutionary lineages in Atlantic Coastal populations compared with those of the Mississippi basin and the Great Lakes. Aligned sequences of DNA of Trout-perch (*Percopsis omiscomaycus*) and Pirate Perch, along with morphology, showed that these two species, when analyzed phylogenetically along with acanthomorph fishes (Spiny-rayed Fishes), consistently (except in one instance) formed a monophyletic group (but the putative sister of the aphredoderids, the amblyopsids, were not included; Wiley et al. 2000).

Karyotype and Genome Size

Based on limited specimens from near College Station, Texas (Gold et al. 1988), the standard karyotype contains $2n = 48$ chromosomes. Fundamental arm number estimates ranged from 68 to 72, and sex chromosomes may be present. The genome sizes of two individuals were 1.14 and 1.24 pg DNA / diploid erythrocyte nucleus. The $2n$ karyotype number of 48 is common in many teleost fishes, but the genome size is somewhat lower than for

other teleosts and paracanthopterygians. Gold et al. (1988) provided other specific data about base composition.

PHYSIOLOGY

pH

Pirate Perch range from slightly alkaline and neutral habitats in Piedmont and upland streams to more acidic swamps and sloughs. The species was abundant in a North Carolina Coastal Plain stream where pH varied over a year from 5.4–7.2 (mostly 5.5–6.5) (Shepherd & Huish 1978). In the New Jersey Pine Barrens, the Pirate Perch is associated with waters and a fish community that functions well at pH \geq 4.0 (Hastings 1984). Across naturally acidic lakes in the region the species occurred at a median pH of about 4.9 (range, about 4.0–7.4) (Graham 1993). The probability of occurrence dropped from 80% at pH 4.0 to about 20% at pH 6.0. The species was associated with similar pH values in Pine Barren streams (about pH 4.5–6.1) (Zampella & Bunnell 1998; Hernandez et al. 2007). In a geographically broad assessment of tolerance indicator values (>60 sites, >100 individuals), Pirate Perch occurred at an abundance weighted average pH of 6.6 (Meador & Carlisle 2007).

Salinity

The species is rarely captured in estuaries but occurs at salinities <10.15 ppt (Keup & Bayless 1964). A single specimen from Chickasaw Creek, Mobile County, Alabama, occurred at a salinity of 19.7 ppt (Swingle & Bland 1974), certainly an unusual occurrence. In the Escambia River, Florida, Pirate Perch only occurred in tidal fresh water. In the spring, the species occurred well downstream from the upper limit of salt water of the preceding autumn, “indicating a rapid spread into a newly available habitat” (Bailey et al. 1954:135).

Dissolved Oxygen

The Pirate Perch also can withstand long periods of low dissolved oxygen (0.2–3.0 mg/l), a condition prevalent in summer months in isolated floodplain ponds or thick vegetation beds in southern waters (Shepherd & Huish 1978; Leitman et al. 1991; Killgore & Hoover 2001). In a geographically broad assessment of tolerance indicator values (>60 sites, >100 individuals), Pirate Perch occurred at an abundance weighted average of 5.7 mg/l dissolved oxygen,

a value among the lowest of 105 freshwater fishes included in the analysis (Meador & Carlisle 2007). Their solitary nature and relatively low levels of activity are likely adaptive for reducing metabolic rates in hypoxic waters (Killgore & Hoover 2001). These traits undoubtedly have contributed to their success in wetlands.

Evidence for Chemical Camouflage

Colonizing aquatic beetles and ovipositing frogs generally avoided water containing chemical cues from various fish species but did not show an avoidance response to water containing chemical cues from Pirate Perch (summarized by Resetarits & Binckley 2013). One study of colonizing beetles involved pools without fishes (controls) and pools that contained insectivorous fishes (Pirate Perch or Banded Sunfish, *Enneacanthus obsesus*). The fishes were housed in the pools so that they could only emit chemical cues into the pool water. In stark contrast to the Banded Sunfish treatment, the Pirate Perch treatment was not avoided by aquatic beetles and showed no statistical differences in beetle abundance or species richness compared with the fishless control pool (Fig. 22.9). In similar experiments across three major North American freshwater fish families, Pirate Perch did not elicit significant avoidance from multi-species assemblages of dytiscid and hydrophilid beetles; all six other fish species had significantly lower numbers of beetles relative to the fishless controls in their respective experiments (Fig. 22.10). In studies of ovipositing tree frogs (*Hyla* spp.), the Pirate Perch was the only species of 11 fish species tested that showed no difference from the fishless controls in number of eggs laid (Fig. 22.11). The actual mechanism of chemical deception used by Pirate Perch may be a form of camouflage, through crypsis or mimicry, that confounds signal reception by the target prey, or even cloaking, in which the predator does not produce or somehow masks the signals that might register with potential prey species. Regardless of the mechanism, the experiments clearly establish that Pirate Perch present a different chemical signature than a broad range of fishes tested and that signature renders the species more difficult to detect or identify to prey organisms as diverse as beetles and frogs. This is apparently the first example of a predator possessing a generalized chemical camouflage effective against a broad array of prey organisms, and it may be a novel weapon in the predator-prey arms race (Resetarits & Binckley 2013). Intriguingly, the author’s asked whether chemical camouflage is another shared character among percopsiforms, all of which, because of their lightless habitat or nocturnal

habits (e.g., Cavefishes, Amblyopsidae), would likely benefit greatly by being chemically camouflaged from their prey.

Radioactive Contamination

The Pirate Perch was included in a study of the concentrations of radiocesium over a 24-year period in Steel Creek (a tributary of the Savannah River), a flowing stream contaminated by nuclear reactor effluents (Peles et al. 2000). The ecological half-life of radiocesium was 4.43 years for *Aphredoderus*. The authors concluded that consumption of fish from this ecosystem posed little risk to humans and sensitive wildlife species.

BEHAVIOR

Non-reproductive Territoriality and Aggression

Despite their solitary nature, Pirate Perch demonstrate aggression not only in feeding but toward conspecifics

and show territorial behaviors as well. Pirate Perch observed in aquaria fed aggressively, striking at just about anything that moved. Large Pirate Perch generally fed before smaller ones, but smaller individuals guarded their part of the aquarium aggressively (Parker & Simco 1975). When a large individual entered the area guarded by a smaller fish the two fish briefly assumed a side-to-side position before the large fish was driven out. The smaller fish occasionally nipped at larger individuals entering its area and even used its head as a battering ram to remove larger adults. In other aquarium observations, Pirate Perch killed other species and conspecifics (Becker 1983).

Diurnal Activity

Experiments revealed the Pirate Perch as mostly benthic, nocturnal, and negatively phototactic (avoiding light). Most of their active or inactive time was spent on or near the bottom of the aquarium. In a typical 24-h day, individuals interrupted photoelectric beams 4, 8, 15, and 125

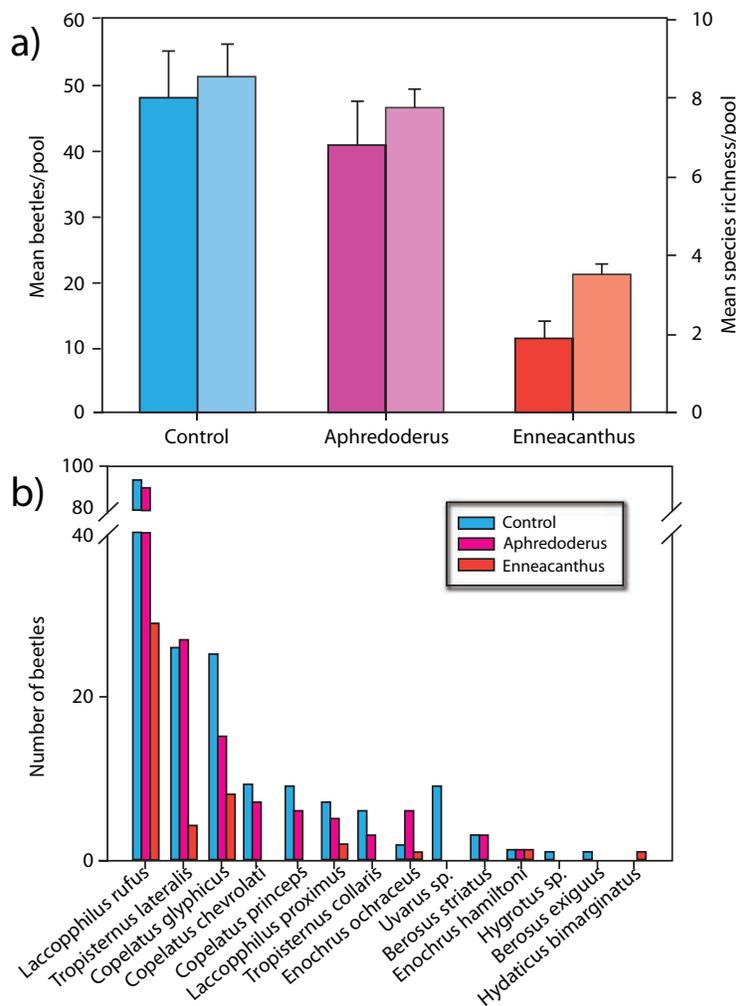


Figure 22.9. (a) Beetle colonization in fishless controls and pools with Pirate Perch, *Aphredoderus sayanus*, or Banded Sunfish, *Enneacanthus obsesus*: mean number of beetles/pool (± 1 SE, standard error; solid bars) and mean beetle species richness/pool (± 1 SE; hatched bars). Control and Pirate Perch treatments were not significantly different for either response variable, but both were significantly different from Banded Sunfish for both variables. (b) Responses of 14 species of colonizing beetles to treatments, as in (a) (redrawn from Resetarits & Binckley 2013).

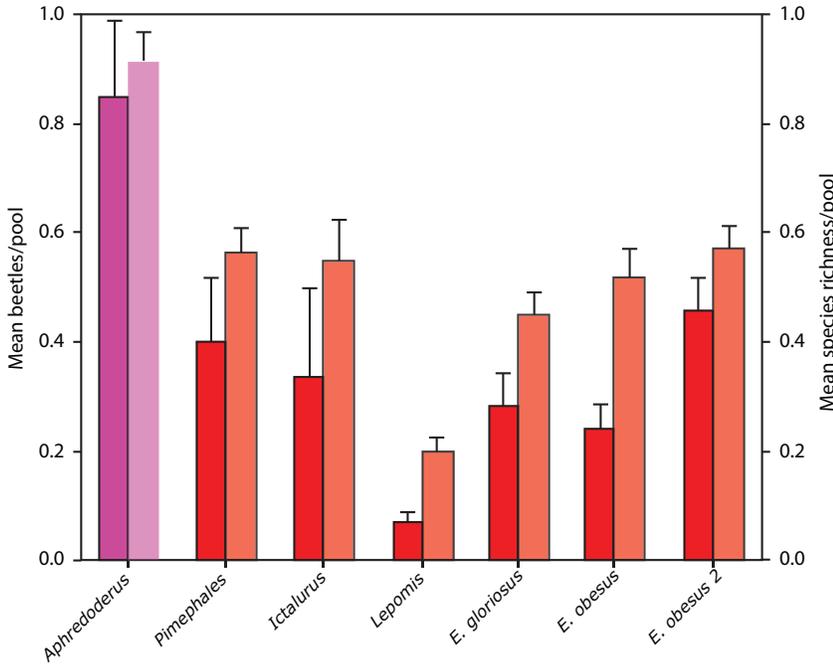


Figure 22.10. Colonization responses of multispecies assemblages of aquatic beetles to fishes, including the Pirate Perch, *Aphredoderus sayanus*: mean number of beetles / pool (± 1 SE, standard error; solid bars) and mean beetle species richness / pool (± 1 SE; hatched bars). The Pirate Perch did not elicit significant avoidance by ovipositing beetles, but all other fish treatments, representing three major North American freshwater fish families, were significantly different (reduced oviposition) from fishless controls in their respective experiments (redrawn from Resetarits & Binckley 2013).

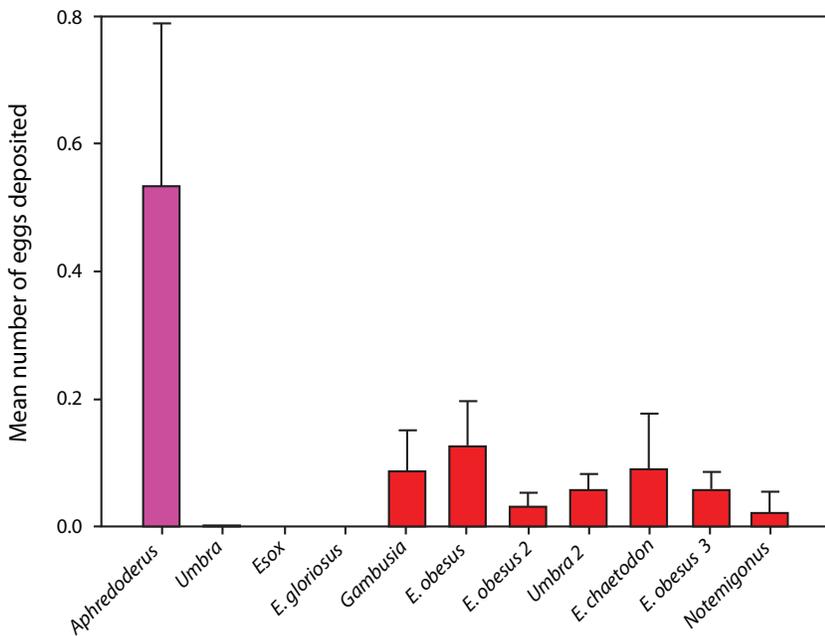


Figure 22.11. Responses of ovipositing tree frogs (*Hyla* spp.) to fishes, including the Pirate Perch, *Aphredoderus sayanus*. Oviposition in treatments containing fish is expressed as a proportion of the fishless control values for that experiment (± 1 SE, standard error). The Pirate Perch did not elicit significant avoidance, but all other fish treatments, representing five other North American freshwater fish families, were significantly different (reduced oviposition) from fishless controls in their respective experiments (redrawn from Resetarits & Binckley 2013).

times from top to bottom of the aquaria, respectively. Daytime activity was minimal; peak activity occurred at dawn, dusk, and (inexplicably) just before midnight, regardless of when food was offered. Only when live food was offered was there any daytime activity. Activity was repressed under visible light conditions but was not repressed under red or infrared light (Parker & Simco 1975).

In laboratory tests, when available, Pirate Perch always sought cover, such as rocks, limbs, or plants. Using their pectoral fins the fish often assumed rather odd positions

on plants either head up or down at 30–90 degrees from the horizontal. Fish sometimes held the same position for hours during the day. These behaviors likely are attempts to avoid light or to camouflage themselves (Parker & Simco 1975). In a natural setting, Pirate Perch also passed considerable time at rest with their heads facing upstream, their dorsal fins expanded, their caudal fins partly closed, and their pectoral fins moving slowly (Becker 1923). In winter, Pirate Perch partially bury themselves in sand (Abbott 1862).

In other aquaria observations, Pirate Perch spent daytime resting with their heads slightly elevated in their refuges. The head-up position may aid in ambush predation (Tiemann 2004), but observations were too limited to be conclusive. Defecation was observed on three different daytime occasions, when a male would venture outside its refuge about to the point that only its head and anus were exposed; the fish defecated and then backed into its refuge. As inactive fish of sluggish water habitats, the jugular position of the anus in the Pirate Perch (Figs. 22.1 and 22.5), in addition to being reproductively adaptive (see reproduction section), also may be adaptive in allowing the fish to partially leave its refuge to defecate while avoiding degrading water quality in the refuge and full exposure to potential predators (Tiemann 2004).

Movement

Although often characterized as largely sedentary, movement studies reveal a capacity for exploratory, colonization, and relatively long-distance movement given the small size of the Pirate Perch. One-way weir traps maintained for a year in a North Carolina swamp stream indicated high movement of Pirate Perch. The species made up 28.3% of the catch (of 17,937 individuals of all species) (Pardue & Huish 1981). The Pirate Perch is often trapped or netted on floodplains inundated by short-term or seasonal floods (e.g., Guillory 1979; Pardue & Huish 1981; Ross & Baker 1983; Leitman et al. 1991). The species was captured commonly in the channel of a small, blackwater stream in Mississippi, but during short-term flood events was captured on the inundated floodplain only at night (Ross & Baker 1983). Pirate Perch also moved from a floodplain ditch to the Kankakee River in response to decreasing post-flooding water levels (Kwak 1988). The species apparently moves onto inundated floodplain habitats to seek food or perhaps refuge from high water velocity.

The Pirate Perch is also an adept colonizer of new stream habitats and capable of fairly rapid long-distance dispersal. In a defaunation study, Pirate Perch were among the first species to move back into defaunated pools of small blackwater streams in South Carolina (Sheldon & Meffe 1993). Similarly, the species showed high recolonization of formerly dry, drought-affected stream reaches once flows resumed in the Upper Coastal Plain, Mississippi (Adams & Warren 2005). Long distance movements of 4.7–5.2 km (2.9–3.2 miles) in 28–45 days occurred in a North Carolina swamp stream. Most movement occurred from March to June and most movement was downstream; no

marked individuals were captured after June (Whitehurst 1981). Similar movement patterns occurred in a Piedmont stream in North Carolina (Hall 1972). The movements may be related to spawning or post-spawning dispersal.

REPRODUCTION

Spawning Season

The Pirate Perch is a spring spawner over much of its range, the exact timing depending on latitude and seasonal conditions (Table 22.1). In Illinois, females are gravid in March, April, and May (Poly & Wetzel 2003), and in North Carolina reproductive activity occurs from January to March (Shepherd & Huish 1978). In the middle Savannah River drainage, South Carolina, spawning occurs from January through April, peaking in the middle of this range (Marcy et al. 2005). Farther south, spawning occurs as early as February in east Texas (Martin & Hubbs 1973), February to March (water temperature 12.6–21.2°C, 54.7–72.0°F) in Louisiana (Fontenot & Rutherford 1999), and in northern Florida and southern Georgia spawning occurs in January (Swift et al. 1977).

Fecundity

Two categories of ova occur in mature females during the spawning season. Gravid females ($n = 36$) from Illinois averaged 78 mature eggs and 124 immature eggs (Tiemann 2004). The number of eggs laid by three females in aquaria were 129, 232, and 290 (normal and abortive spawns) (Poly & Wetzel 2003). Depending on female size, Fletcher et al. (2004) noted clutch sizes of 100–400 mature eggs in a Savannah River drainage population (Table 22.1). A 57-mm TL (2.2 inches) fish from southern Illinois had a total (all size classes) of 769 ova (Gunning & Lewis 1955), and individuals in St. Johns River, Florida, had 129–160 ova (McLane 1955).

Nest Site and Spawning

For almost two centuries, naturalists were puzzled by the jugular position of the urogenital opening of the Pirate Perch and the knoblike structure anterior to it (Lesueur 1833; Fig. 22.5). The mystery surrounding these structures and their relevance to reproduction remained unsolved until the 21st century (Poly & Wetzel 2003; Fletcher et al. 2004). Prior to this, two spawning modes were postulated from circumstantial evidence: branchial brooding and

Table 22.1. Life-history characteristics of the Pirate Perch, *Aphredoderus sayanus* (Aphredoderidae). Sources are given in the text.

	<i>Aphredoderus sayanus</i>
Number of species	1
Strictly fresh water	Yes, primary
Maximum size recorded	144 mm TL, 5.7 inches
Maximum age	3–4 years
Age and size at first reproduction	Presumably age 1, but not confirmed
Iteroparous versus semelparous	Iteroparous
Fecundity estimates from ovarian counts	78–300 mature eggs/female, but needs confirmation
Egg deposition sites	1–2 cm diameter canals in root masses (small ellipses of 20 × 15 cm, 7.9 × 5.9 inches, to large mats 100 × 20 cm, 39.4 × 7.9 inches)
Clutch size and egg size (diameter)	100–400 eggs; 1.0–1.7 mm, 0.04–0.07 inches (mature eggs)
Range of nesting dates and temperatures	January–May (varies with latitude); 12.6–22.2°C, 54.7–72.0°F
Habitat of spawning sites; average water depth	Root masses anchored to the bank
Incubation period; larval type at hatching	5–6 or 7 days at 19–20°C (66.2–68°F); protolarvae
Mean size at hatching	3.0 mm TL (0.1inches)
Sex building nest; sex incubating eggs; other care-giving behaviors	No nest, egg incubation, or parental care-giving behaviors
Major dietary items	Primarily invertebrates (i.e., dipteran larvae and pupae, mayflies, caddisflies, beetle larvae, aerial and terrestrial arthropods); occasionally crayfish and fish
Migratory or diadromous	None known
Imperilment status	Declining at northern periphery of range

broadcast spawning. When holding a ripe female one can strip the eggs, which follow a groove from the vent to the branchial chamber. The knoblike structure with lateral grooves presumably directs the eggs into the right or left chamber (Martin & Hubbs 1973; Jenkins & Burkhead 1994; BMB pers. obs.), suggesting branchial involvement with eggs. In addition, Boltz & Stauffer (1986) found one museum-preserved female with three eggs inside the branchial cavity. Eggs or young do occur in the branchial chambers of the Northern Cavefish, which is a confirmed branchial brooder (Eigenmann 1909; G. Adams & BMB pers. obs.). A reasonable argument discounting the idea of branchial brooding in the Pirate Perch was that the branchial cavity was too small to hold a full complement or even a single clutch of eggs (Katula 1992). Aquarists and early naturalists also suggested that a nest was made and that eggs were broadcast in the nest (Abbott 1862, 1868, 1870b; Brill 1977; Katula 1987, 1992; Fontenot & Rutherford 1999). In the 1980s, ripe females brought back to our (BMB) laboratory in styrofoam coolers had broadcast thousands of apparently aborted eggs over the bottom and sides of the coolers, perhaps explaining how the broadcasting idea came about. Despite these anecdotal observations and speculations, direct evidence and documentation of the spawning of the Pirate Perch in nature remained elusive.

The spawning mode question was resolved when 23 nests (actually tunnels in root masses) were found in a Savannah River tributary (Figs. 22.12 and 22.13) in spring of 2001 (Fletcher et al. 2004). Water velocities at the nest sites averaged 15 cm/sec (0.49 feet/sec). Most nests were 20-m apart (65.6 feet). Small canals or tunnels in underwater root masses of woody riparian plants or aquatic macrophytes were the sites of fertilized eggs. Root masses were anchored to the banks, stumps, or logs; some were suspended and others were flowing root masses, anchored at the upstream end and oriented parallel to water flow (Fig. 22.13). Egg clusters were accessed by one or more narrow canals (1–2 cm in diameter, 0.4–0.8 inches) tracing to the surface of the root mat (Fig. 22.13). These canals were made by the fish themselves, or they used burrows made by salamanders and dobsonfly larvae. Most eggs were deep enough inside the canals so that they were not visible from the exterior of the root mat (Fig. 22.13). In the largest nests >2,000 total offspring were present (range 82–2,736), many more than contained in a single clutch.

Underwater videography at night revealed females thrusting their heads and releasing their eggs into the sheltered canals of the root masses (time was about 4 s) (Fletcher et al. 2004). Males congregated at these sites and also entered the canals headfirst to release sperm



Figure 22.12. Composite drawing showing a root-mass nesting site with multiple canal entrances and illustrating various behaviors displayed by the Pirate Perch, *Aphredoderus sayanus*, in the immediate vicinity (from Fletcher et al. 2004; drawing by Trudy Nicholson and used with permission of Dean Fletcher).

observed as clouds of milt (time about 5 s). Thus the jugular-positioned urogenital pore facilitates spawning under this special nesting circumstance. No evidence of extended parental care was observed. Ovipositing in root masses may benefit the embryos and fry by protecting them from fast-flowing water, by exposing them to less damaging siltation, and by decreasing the probability of predation.

So, why the jugular vent? Release of gametes from an anterior position allows a Pirate Perch to back out of a canal with less dislodgment of eggs and sperm. Further, the headfirst spawning position brings into play the extensive array of sensory pores on the head (Moore & Burris 1956) to help adults locate eggs previously deposited in a dark canal. Females also possibly may be spitting eggs into the root masses (see next paragraph) because it would take considerable force to spray eggs as deeply into the roots interstitial spaces as they were found. Some of the canals were so narrow that it would be difficult for a female to raise her head and spray the eggs from her urogenital pore forcefully into the root mass.

Videography of spawning behaviors of adults from the Cache River in southern Illinois, revealed additional details of courtship behavior, egg deposition, and fertilization (Poly & Wetzel 2003). Prespawning courtship by males consisted of lateral displays, body undulations (possibly an agonistic behavior), and a rapid trembling of the male's body with the head oriented toward the spawning substrate (i.e., gravel, detritus). When the female was pre-



Figure 22.13. Spawning sites of the Pirate Perch, *Aphredoderus sayanus*, in Fourmile Branch (Savannah River drainage), North Carolina: (upper) stream bank and underwater flowing root mass used for spawning; (middle) spawning canal exposed (arrow) in a dissected root mass with eggs (encircled) clustered in the canal; (lower) close-up of eggs in the canal, egg diameter about 1.5 mm (0.06 inches) (courtesy of Dean Fletcher).

pared to oviposit, she thrust her head into the substrate, and the male assumed a parallel position. The female then flared her opercula as eggs were extruded from the urogenital pore and directed to the branchial cavity, likely by the grooves on the sides of the knoblike structure (Fig. 22.5). Eggs are thus passed through the orobranchial cavity during repeated opercular movements. Eggs are ejected from the orobranchial cavity through the mouth and into the spawning substrate during opercular movements. During egg extrusion the female's pelvic fins are extended, rigid, and pointed downward. As the eggs are ejected the male expels a large plume of sperm into the substrate. As with the eggs, the milt is passed through the orobranchial cavity of the male. Poly & Wetzel (2003) also found a previously undiscovered feature of the female, an inwardly curled branchiostegal-opercular fold, presumably helping retain eggs in the orobranchial cavity during passage of eggs from the urogenital pore. They named this unique spawning mode transbranchial spawning. The term refers to the passage of gametes from the urogenital pore through the branchial and buccal (oral) cavities and finally, out of the mouth and into the substrate. To our knowledge, this is the only fish in the world that engages in this particular type of spawning mode. Eggs found in the wild were in habitats (i.e., root masses) similar to those described by Fletcher et al. (2004). Neither study ever found any eggs retained in the oral or branchial chambers putting to rest the notion that Pirate Perch are true branchial brooders. Additionally, both studies ruled out any sort of parental care behavior. Eggs were clearly demersal but apparently nonadhesive.

Another attempt to make spawning and other observations on adults from Horseshoe Lake, southern Illinois, met with minimal success (Tiemann 2004). Although a nest was fanned out by caudal fin sweeps and putatively adhesive eggs laid in proximity to the nest, sample sizes were small, observations limited, and behaviors probably altered by confined aquarium conditions.

Paternity Competition

Male competition for paternity at the nest site is apparently high. In the Savannah River tributary population, a given root mass was used repeatedly by multiple spawners, and offspring in most nests were in different stages of development (Fletcher et al. 2004). Genetic analyses of embryos confirmed that ≥ 5 –11 sires and dams were the parents in each assayed nest. Many males were taken near active nest sites (many likely missed) and ≤ 30 were observed at the base of

the root masses, but female numbers near nests were apparently much lower (0–4). Aggregated individuals were engaged in almost continuous movement. The most frequent behavior involved an individual swimming vertically from substrate to root mass, hanging briefly by its pectoral fins on the root mass, and then drifting back to the bottom. This behavior was often accompanied by substrate thrashing with the caudal fin. Males at least briefly defended egg deposition sites that they had fertilized by body-plugging canal entrances after spawning, and these males attempted to cut off interloper males from boring alternative tunnels into the egg masses. Aggressive behaviors of males at the nest, following spawning, probably reflect paternity defense under intense competition for fertilization success, which almost certainly attends the group spawning situations (Fletcher et al. 2004).

Eggs, Development, and Larvae

Pirate Perch eggs are 1.0–1.7 mm (0.04–0.07 inch) in diameter, spherical, apparently nonadhesive, white, yellow or clear, and possess a single, large oil droplet (Martin & Hubbs 1973; Boltz & Stauffer 1986; Jenkins & Burkhead 1994; Table 22.1). Eggs hatch in 5–6 or seven days in water 19–20°C (66.2–68.0°F); newly hatched protolarvae are about 3 mm TL (0.12 inch) (Martin & Hubbs 1973; Minton et al. 1985). During development, the anus (and connecting gut) and urogenital pore (and connecting ducts) shift anteriorly from near the origin of the anal fin to a jugular position (see morphology section; Figs. 22.1, 22.7, and 22.8).

ECOLOGY

Habitat and Abundance

The Pirate Perch inhabits bottomland lakes, overflow ponds, cypress swamps, sloughs, and quiet pools and backwaters of sluggish, sometimes spring-fed streams (Fig. 22.14). The species generally occurs in clear, slow-moving water with cover in the form of aquatic plants, sticks, or organic debris (Meffe & Sheldon 1988; Monzyk et al. 1997). The species showed ontogenetic shifts in microhabitat use and a propensity for structurally complex diurnal cover in small Louisiana streams. Large individuals (59–95 mm TL, 2.3–3.7 inches) inhabited more structurally complex microhabitats, measured as a function of the number and length of woody components, than small individuals (27–58 mm TL, 1.1–2.3 inches). Overall, the diurnal cover occupied by Pirate Perch differed from unoccupied cover. The occupied cover was more complex and in deeper water, inside cover flows were



Figure 22.14. The Pirate Perch, *Aphredoderus sayanus*, inhabits a variety of lowland habitats with abundant cover, ranging from nonflowing oxbow lakes and bayous in bottomland hardwood forests (*upper*), like Cypress Bayou, in the Delta National Forest, Sharkey County, Mississippi, to low velocity habitats in cypress-lined, flowing creeks and rivers (*lower*) with abundant undercut banks and instream wood, like the Sipsey River, Greene County, Alabama (photographs by MLW).

lower, and densities of benthic and suspended leaves were higher. For example, although only 24% of available microhabitats had leaves trapped by instream wood, 75% of Pirate Perch came from those sites (Monzyk et al. 1997). Similarly, in blackwater streams in South Carolina, the species was associated most strongly in multivariate habitat space with slow, shallow currents over leafy, silty substrates and in deep, muddy pools with undercut banks (Meffe & Sheldon 1988). In lowlands of the Red River, Oklahoma, the species was associated in multivariate space with darkly stained, low conductivity, non-flowing habitats with silty substrates.

They occurred in those habitats with typical wetland fishes, such as the Flier (*Centrarchus macropterus*) and Banded Pygmy Sunfish (*Elassoma zonatum*) (Pyron & Taylor 1993). Pirate Perch are rarely found in main channel-associated habitats of the lower Mississippi River (e.g., natural or revetted banks or sandbars). They occur in moderate numbers in sloughs, oxbow lakes, and borrow pits along the river but are most abundant in seasonal floodplain and floodplain pond habitats (Baker et al. 1991). In rocky streams, Pirate Perch usually spend their time near or in undercut banks and root masses (Poly & Wetzel 2003).

Relative abundances of Pirate Perch show high variation among habitats. In the Atchafalaya basin, Louisiana, Pirate Perch were among the top 12 most abundant fishes in beds of submersed hydrilla (*Hydrilla verticillata*), emergent bulltongue (*Sagittaria lancifolia*), and floating water hyacinth (*Eichornia crassipes*), but unlike many other fishes in the plant beds, Pirate Perch showed no consistent pattern of use among the plant types or seasonal shifts among plant types at different water levels (Troutman et al. 2007). From 0.5-m² (5.1-foot²) throw traps, Pirate Perch densities were 0.96 fish/m² (0.09 fish/foot²) in heavily vegetated plant beds in the Wacissa River, Florida (Richardson et al. 2006). In small eastern Texas streams, the Pirate Perch ranked 3rd-4th in abundance in a 41 fish species assemblage. They were most common in streams with a preponderance of low flows, low depth diversity, and highly variable base flows (Herbert & Gelwick 2003). Pirate Perch were the second-most abundant fish and composed 9% of the fish biomass in a 29-species assemblage in small, relatively undisturbed blackwater streams in the South Carolina Piedmont (Meffe & Sheldon 1988, 1990). In the same system, the Pirate Perch again ranked second in abundance in stream sections undammed by beavers but dropped to ≥ 7 in rank abundance in active and abandoned beaver ponds and recovering stream sections (Snodgrass & Meffe 1998). Over a 5-year study in Illinois with spring and autumn samples, the Pirate Perch was caught at much higher numbers (average 20.3 fish/h) in a Kaskaskia River tributary than in surrounding lakes, which are only periodically connected to the river (≤ 0.5 fish/h) (Shoup & Wahl 2009). The Pirate Perch can be the most abundant fish species in small species poor, acidic streams in the New Jersey Pine Barrens (Hernandez & Sukhdeo 2008a). In contrast, the Pirate Perch ranked 18th (of 30 species) in abundance, averaging only about 2.5 fish/100–200 m (328–656.1 feet) in 12 relatively undisturbed rocky, upland streams in the Ouachita Mountains, Arkansas (Taylor & Warren 2001). However, in the

same system during summer drought, the species was second in relative abundance (8–15.3%) out of 21 species found in isolated stream pools (Love et al. 2008). In upper Piedmont streams of North Carolina, the species occurred in 24 of 39 small wadable streams surveyed within a 32-km (19.9-mile) radius encompassing the fast-growing metropolitan Raleigh-Durham area. Interestingly, the relative abundance of the species was not significantly correlated with any of a multivariate array of land use and land cover characteristics (Kennen et al. 2005). In contrast, Pirate Perch abundance and presence-absence in the Coastal Plain of Maryland was strongly and negatively related to urbanization, showing steep abundance and presence-absence declines when urbanization affected ≥ 12 and $\geq 13.8\%$ of the watershed, respectively (Utz et al. 2009).

Bottomland hardwood forests and associated wetland habitats are important nursery areas for larval Pirate Perch. In Cache River, Arkansas, the Pirate Perch was the most abundant species accounting for 21% of 8,113 larvae caught (Killgore & Baker 1996). Nets collected greater numbers of Pirate Perch larvae in the main channel and tupelo habitats, but light traps collected greater numbers in oak habitat. Pirate Perch do well in floodplain habitats and this appeared to be the center of abundance of larvae in the Cache River study. In this region of its geographic range, annual spring flooding clearly plays a major role in the life history of the Pirate Perch and other wetland fishes.

Feeding and Diet

Adults are suction feeders, feeding by forming a negative pressure in the oral cavity and quickly opening the mouth to pull in prey. Prey is approached from the side and the head is turned abruptly as the vacuum pressure is released (Parker & Simco 1975). Pirate Perch are primarily nocturnal in habits and their diurnal locomotor activity coincides with the activity of their potential prey (see behavior section; Parker & Simco 1975).

Pirate Perch are opportunistic feeders that exploit food from the top to the bottom of the water column. Estimates of biomass by volume of the food sources for age-0+ fish are 85% benthos, 5% zooplankton, 5% fish, and 5% terrestrial. Young-of-the-year consume slightly more zooplankton and terrestrial insects than adults (Ploskey & Jenkins 1982). The species obtained much of its diet from snag-dwelling insects in the sand-bottomed Satilla River, Georgia, but exploited other habitats as well. Gut analysis indicated 60% of the diet biomass was derived from snags, 30% from mud bottoms, and 5% from terrestrial

origin (Benke et al. 1985). Whether Pirate Perch actually gleaned the invertebrates off the snags or took them in the nighttime drift, when snag invertebrates drifted in highest abundance, is unknown.

Even though nocturnal, several diet studies that used specimens collected in the daytime suggest Pirate Perch feed opportunistically on a diverse array of organisms during the day (or have slow digestive rates). Of 327 stomachs examined from a North Carolina stream, 76% contained food (Shepherd & Huish 1978). Likewise, in an autumn diet study (22–95 mm SL, 0.9–3.7 inches) from blackwater streams of South Carolina, 68% of individuals sampled ($n = 231$) contained food. The diet was diverse. Guts contained 22 different food items of mostly invertebrates, being dominated in volume by chironomid larvae and pupae and other dipterans, followed in descending order by mayflies, caddisflies, crayfish, and aerial and terrestrial arthropods. Stomachs also contained megalopterans, beetles, copepods, oligochaetes, amphipods, fishes, and amphibians. The broad diversity of the diet placed the species at the center of the multivariate trophic space of an assemblage of 30 fishes (Sheldon & Meffe 1993).

Diet studies in other regions had similar results, the principal food items being dipteran larvae, mayfly larvae, caddisflies, odonate larvae, aquatic beetle larvae, amphipods, isopods, freshwater shrimp, crayfish, and occasionally fish and plant matter (Forbes & Richardson 1920; Becker 1923; Rice 1942; Gunning & Lewis 1955; Flemer & Woolcott 1966; Shepherd & Huish 1978; Hernandez & Sukhdeo 2008a; McCallum 2012). In one study, small Pirate Perch (10–29 mm) fed predominantly on cladocerans (Shepherd & Huish 1978). Pirate Perch also consume frog tadpoles, particularly those of *Hyla chrysoscelis* (Gray Treefrog), at least they did in some experimental ponds in Virginia (Binckley & Resetarits 2003). One of the surprising discoveries in this study was that the tadpoles avoided ponds with other fish predators but did not do so in ponds with Pirate Perch, which led to studies testing the species for chemical camouflage (see physiology section).

Interpopulational Variation in Age and Growth

The species shows evidence of geographic variation in longevity and growth, but analyses are limited. In an Oklahoma population, Pirate Perch lived four years (aged from scale annuli; Hall & Jenkins 1954), but in a North Carolina population maximum longevity was only three years (aged

from scale annuli; Shepherd & Huish 1978). Growth was most rapid during the first two years of life. The species averaged 55.8 mm TL (2.3 inches) at age 1, 84.5 mm TL (3.3 inches) at age 2, 101.6 mm TL (4.0 inches) at age 3, and 116.4 mm TL (4.6 inches) at age 4; the largest specimen was 126 mm TL (5.0 inches) (Hall & Jenkins 1954). A small sample of individuals from Wisconsin showed comparable growth reaching 52 mm TL (2.0 inches) at age 1, 85 mm TL (3.3 inches) at age 2, and 103 mm TL (4.1 inches) at age 3 (Becker 1983). Back-calculated lengths in North Carolina were 63 mm TL (2.5 inches) at age 1, 71 mm TL (2.8 inches) at age 2, and 81 mm TL (3.2 inches) at age 3 (Shepherd & Huish 1978). In the North Carolina population, females grew faster than males and were more numerous. Whether the interpopulational differences are attributable to growing season, local resource limitation, or genetic adaptation is unknown.

Predation

Predators of the Pirate Perch are not well known but probably include some species of *Esox* and *Ameiurus*. Two Pirate Perch occurred in the stomachs of two Grass Pickerel, *Esox americanus* (Burr & Page 1978). Cottonmouths (*Agkistrodon piscivorus*), Southern Water Snakes (*Nerodia fasciata*), and likely other *Nerodia* spp. also prey on the species (Ernst & Ernst 2003 and references therein).

Parasitism

Hoffman (1999) listed a protozoan, a monogenean, six trematodes, three cestodes, two acanthocephalans, and two species of the crustacean genus *Ergasilus* as parasites of the Pirate Perch. Four other acanthocephalans (Hernandez et al. 2007; McAllister & Amin 2008), three additional nematodes (Hernandez et al. 2007), one other unique trematode (*Azygia aphyredoderi* Barger 2014), an opportunistic cestode (*Protocephalus pearsei*, McAllister et al. 2012a), and an opportunistic leech (*Myzobdella reducta*, McAllister et al. 2012b) are also documented from the species. Two parasites are apparently host specific for the Pirate Perch, including the monogenean *Gyrodactylus aphyredoderi* (Hoffman 1999) and the acanthocephalan *Leptorhynchoides aphyredoderi* (Buckner & Buckner 1976); the latter infects at least the pyloric caeca. Later, Buckner (1991) reported *L. aphyredoderi* from five of seven Pirate Perch taken from McConnico Creek, Greene County, Alabama; one to four worms occurred in each infected fish. In a study in a New Jersey Pine Barrens stream of the

acanthocephalan parasite *Acanthocephalus tahlequahensis*, whose invertebrate host is a stream-dwelling isopod, the Pirate Perch showed the highest incidence (84.6%) and intensity (13.7 worms/fish) of infection among an assemblage of 13 fishes (Hernandez & Sukhdeo 2008b). In a related study, prevalence of infection, mean abundance, and total number of individuals for the five most abundant helminth parasites (*Acanthocephalus* sp., *Fessisentis* sp., *Phyllodistomum* sp., *Crepidostomum* sp., and a nematode) as well as overall helminth parasite richness were highest in the Pirate Perch (Hernandez et al. 2007). In a laboratory trial, five Pirate Perch were infested with glochidia of the Carolina Heelsplitter (*Lasmigona decorata*), but only one glochidium transformed to a juvenile (Eads et al. 2010). The Pirate Perch appears to be at best only a marginal host for this species. Even so, the Pirate Perch likely serves as host for host-generalist mussels that are common in lowland habitats.

CONSERVATION

The Pirate Perch generally occurs at low population levels but is widespread in distribution. Local abundance is sometimes achieved especially following the reproductive season. The Pirate Perch is secure and stable throughout most of its range in the lower Mississippi River basin and on the Coastal Plain (Warren et al. 2000; Jelks et al. 2008), but somewhat disjunct and uncommon on the northern periphery of its range in Iowa and the Lake Erie drainage, New York (Smith 1985). The Pirate Perch was last taken in about 1950 from Ohio waters and is now extirpated from that state (Trautman 1981). This species is also extirpated from Pennsylvania, where it occurred in the lower Delaware River and was last collected between 1899 and 1917 (Gilbert 1985). The species apparently is stable in the lower peninsula of Michigan (Bailey et al. 2004) but is considered Imperiled in New York, and Vulnerable in Texas, Iowa, Minnesota, and Wisconsin (NatureServe 2012). It is apparently sensitive to stream degradation from urbanization. Dramatic declines in numbers occurred in the now urbanized Tuckahoe Creek watershed, Virginia, where Pirate Perch were once widespread and common (Weaver & Garman 1994; see also Utz et al. 2009, ecology section).

Propagation techniques for the species are developed, and the Toledo Zoo has had some success in producing young Pirate Perch (Hemdal 2003). Nonadhesive but fertilized eggs were found scattered over the bottom of an

aquarium, and hatched in five days. Young were fed tiny brine shrimp. At some future date, the Toledo Zoo plans to introduce Pirate Perch back into their native range in Ohio (the Auglaize River drainage).

COMMERCIAL IMPORTANCE

Reaching only 140–145 mm TL (5.5–5.7 inches), the Pirate Perch is of little interest to commercial or recreational fishers. Similar to many small fishes, the species undoubtedly is used occasionally as bait by local anglers, but it is rarely, if ever, sold as commercial bait. The Pirate Perch is of scientific significance and value because of its peculiar combination of anatomical features, unique method of breeding, chemical camouflage, and close relationship to Cavefishes and because it and extinct relatives are known only from the North American continent. Aquarists interested in native North American fishes have kept Pirate Perch in their home aquaria for years, and numerous articles in aquarium magazines have recorded some anecdotes that focus more on the aquarium fish community of which the Pirate Perch is a part rather than having broad applicability to natural settings. Aquarium-held individuals probably do best being fed live food, such as whiteworms, earthworms, small fish, mosquito larvae, and *Daphnia*, especially at night or under low light conditions (e.g., Goldstein et al. 2000).

LITERATURE GUIDE

The natural history and ecology of the Pirate Perch is detailed in several state and regional fish books, including Becker (1983; Wisconsin); Etnier & Starnes (1993; Tennessee); Jenkins and Burkhead (1994; Virginia); Pflieger (1997; Missouri); Ross (2001; Mississippi); Boschung & Mayden (2004; Alabama); and Marcy et al. (2005; middle Savannah River). Page & Burr (2011) provided diagnostic characters for identification, a summary of habitats occupied, and a total range map. The research of Resetarits and colleagues (e.g., Resetarits & Binckley 2013) is on track to determine the mechanism underlying the chemical camouflage used by the Pirate Perch (and perhaps other percopsiforms). Fletcher et al. (2004), describing spawning and nest sites, is key reading for anyone interested in the natural history of the Pirate Perch.

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