

Chapter 20 Percopsidae: Trout-perches

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Except for several monotypic (containing only one species) families (e.g., Bowfins, Amiidae) that occur in North America, the Trout-perches (genus *Percopsis*, family Percopsidae) with only two extant species, like Hiodontidae (Mooneyes), represent the smallest indigenous families on the continent. The Trout-perch, *Percopsis omiscomaycus* (Walbaum), is so named because of its trout-like appearance with a free adipose fin, but perch-like (*Percopsis* means perch-like) in having ctenoid scales and spines in the fins (Figs. 20.1 and 20.2). The specific epithet (*omiscomaycus*) is attributed to an Algonkian language name, which includes the root for the word trout (McPhail & Lindsey 1970). The specific epithet of the Sand Roller, *Per-*

copsis transmontana means beyond the mountains, in reference to it occurring only west of the Western Continental Divide (Eigenmann & Eigenmann 1888). The common name, Sand Roller, is in reference to a predilection for sandy habitats. Both species are translucent and show a general pattern of movement from deeper or darker habitats during the day to shallower habitats at night.

DIVERSITY AND DISTRIBUTION

The Trout-perch and Sand Roller (Figs. 20.1 and 20.2) are primarily northern in distribution with large differences in

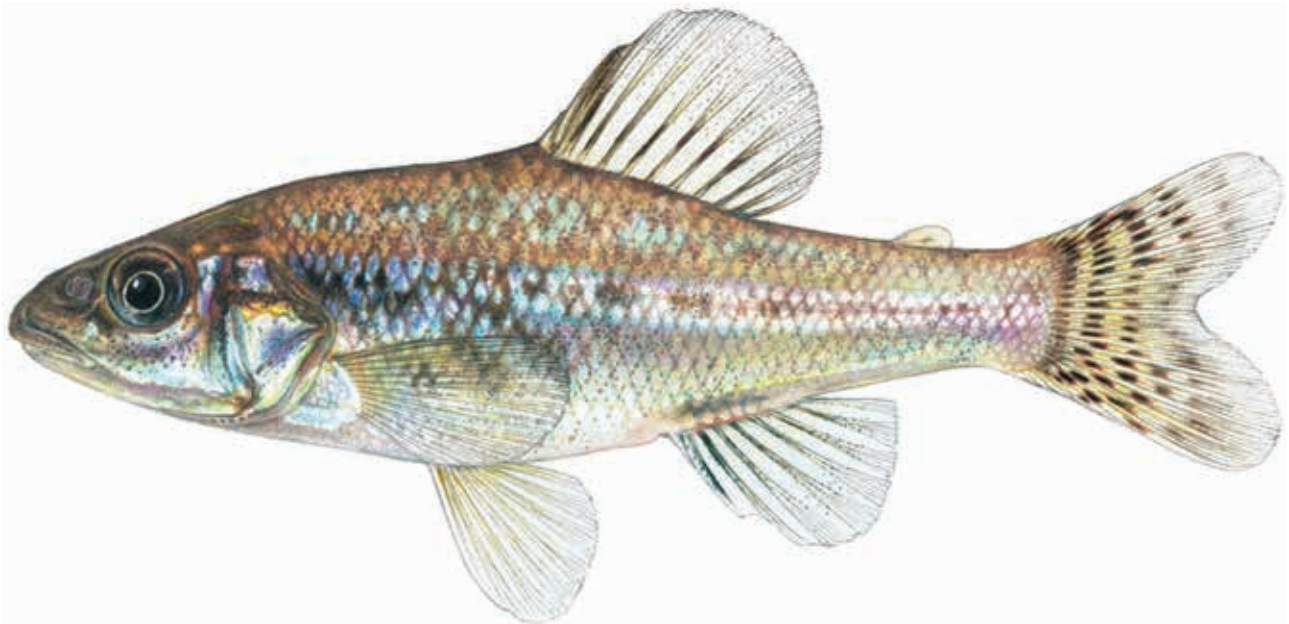


Plate 20.1. Sandroller, *Percopsis transmontana*.

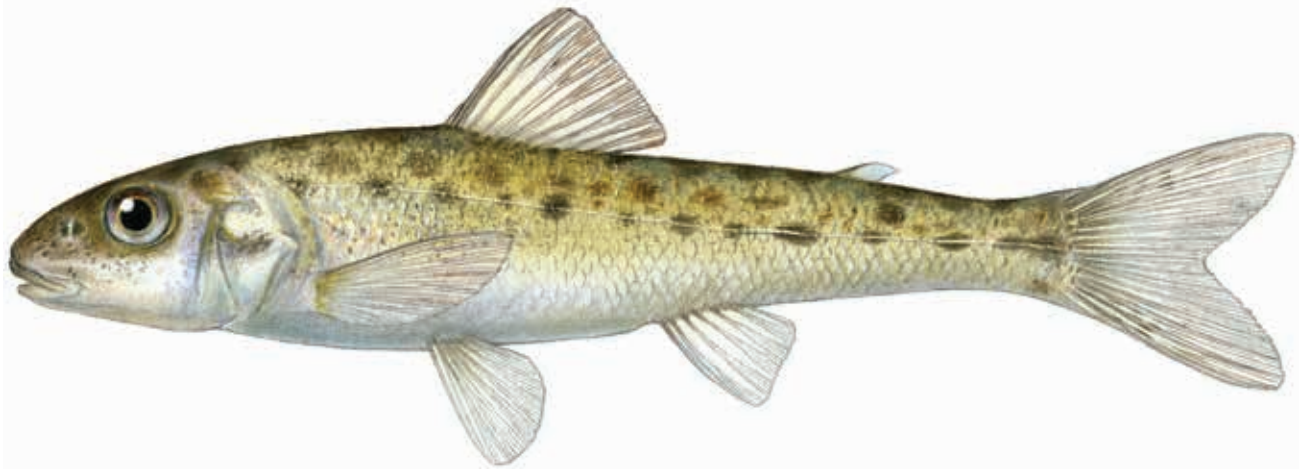


Plate 20.2. Trout-perch, *Percopsis omiscomaycus* (© Emily S. Damstra).



Figure 20.1. Trout-perch, *Percopsis omiscomaycus*, have a flattened ventral profile and straw yellow color, both of which are adaptive for foraging in and living cryptically on sandy substrates (photograph is in the public domain; from Ohio Department of Natural Resources, ODNR 2012).

range extent. The Trout-perch occurs north of the 37th parallel and the Sand Roller only occurs in the Columbia River drainage north of the 45th parallel (Fig. 20.3). The Trout-perch is found in the Atlantic and Arctic Ocean river basins throughout most of Canada from Quebec to the Yukon Territories and British Columbia, and south to the Potomac River drainage, Virginia. The species also inhabits the Yukon River drainage, Yukon Territories and Alaska, Great Lakes and Mississippi River basins south to West Virginia, eastern Kentucky, southern Illinois, central Missouri, North Dakota, and Montana (Page & Burr 1991, 2011; Fig. 20.3). The species likely repopulated northern North America post-glacially from refugia in the Mississippi River Valley (Crossman & McAllister 1986). The Sand Roller is a narrow-range endemic in the Columbia River drainage in western Idaho, southern Washington, and northern and western Oregon (Fig. 20.3).

No systematic review or phylogeographic study is available on this widely distributed, mostly northern and western genus. No subspecies of either species have been described. The number of pyloric caeca (tubular, finger-like pouches opening into gut) in Trout-perch (10–14) was consistent in specimens from widely separated localities in southern and central Canada (Ontario and Manitoba) (Scott & Crossman 1973). No consistent pattern of geographic variation occurred among populations in northwest Canada and Alaska; however, pyloric caeca ranged from 7–11 (McPhail & Lindsey 1970). Of several meristic features, Kentucky specimens (the most southerly population) have higher mean lateral-line scale counts (BMB unpubl.) compared with those from Canada (Scott & Crossman 1973) and Alaska (McPhail & Lindsey 1970). No other differences in meristic features or pigmentation were noted. The Sand Roller, endemic to one

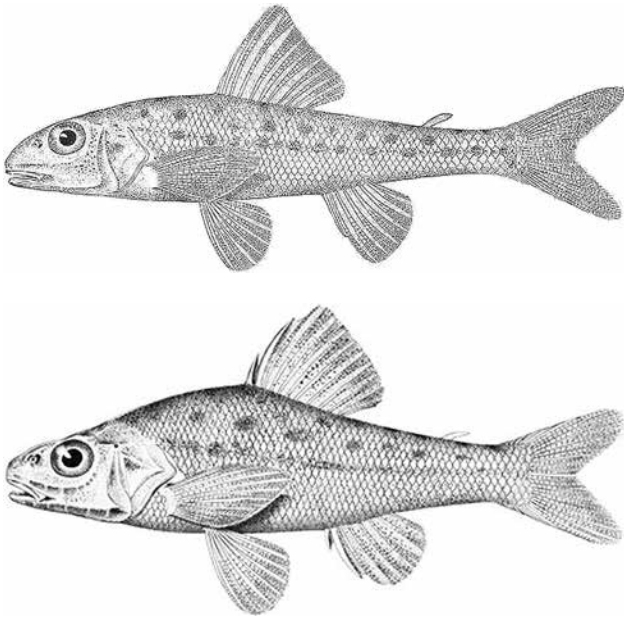


Figure 20.2. (upper) Trout-perch, *Percopsis omiscomaycus* (about 89 mm SL), illustration from a publication documenting 19th century ichthyological explorations of western Canada and the northwestern United States (modified from Eigenmann 1895: Plate 6C; in the public domain from Freshwater and Marine Image Bank, University of Washington Libraries Digital Collections). (lower) An illustration of one of the types (USNM 371921) of the Sandroller, *Percopsis transmontana* (about 106 mm SL), captured in September 1892 by Carl H. Eigenmann in the Colombia River, Umatilla, Umatilla County, Oregon (created by A. H. Baldwin; in the public domain and courtesy of Smithsonian Institution, National Museum of Natural History Image Collection).

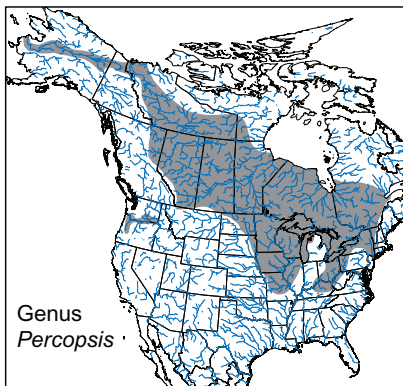


Figure 20.3. Geographic range of the two species of *Percopsis*. Note the extreme disjunction and isolation of *Percopsis transmontanus* in the state of Washington and Oregon just into western Idaho.

river drainage, is considered one large panmictic population.

Both species inhabit lakes (or reservoirs) and flowing pools of small to large rivers, and both have close association with sandy substrates and vegetation or undercut, vegetated banks. The two species are generally uncom-

mon but may be locally abundant in specific habitats. Many fish biologists have never seen either species alive. Their relatively small size, mostly nocturnal habits, occurrence at moderate population levels, and no known commercial value, has relegated the Trout-perches to mostly being of scientific interest due to their uniqueness as endemics on the North American continent.

Non-native Distribution

The Trout-perch apparently was introduced to Willard Bay reservoir and Lake Utah, Utah, in 1983 (Sigler & Sigler 1987), but the means of introduction and the current status is unknown (Fuller et al. 1999). Conflicting views exist concerning the native or introduced status of the species in the Potomac and Susquehanna Rivers and the Housatonic River (Connecticut and Massachusetts), but most workers now consider the species as native to those rivers (Fuller et al. 1999)—a view we take here. We are unaware of any introductions of the Sand Roller outside its native range.

PHYLOGENETIC RELATIONSHIPS

With only two species in the family and both placed in the same genus, the Trout-perch and Sand Roller (formerly placed in the monotypic genus *Columbia*) are clearly sister-species. Analyses of mitochondrial and nuclear genes indicated Percopsidae as the sister-group of the Amblyopsidae (Cavefishes) + Aphredoderidae (Pirate Perches) (Niemiller & Fitzpatrick 2008; Dillman et al. 2011), which form the Percopsiformes. Subsequent analyses using multiple mitochondrial and nuclear markers recovered an identical and strongly supported phylogeny (Niemiller et al. 2012; Grande et al. 2013). 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 additional molecular markers and incorporating the Near et al. (2012b, 2013) data, the same sister-group relationship was indicated among the three percopsiform families, but the group was sister to a clade comprising Zeiformes (Dories), Stylephoriformes (Tube-eyes or Threadtails), and Gadiformes (Cods) with divergence estimated as the Early Cretaceous (Betancur-R. et al. 2013ab). Within the percopsiforms, fossil-calibrated estimates from

the 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) (Dillman et al. 2011); estimates from fossil-calibrated nuclear genes placed the divergence later at 60.2 mya (58.9–62.1 mya) (Near et al. 2012b; Niemiller et al. 2012). The divergence times between *Percopsis omiscomaycus* and *P. transmontanus* was estimated as Eocene for the ND2 gene (estimated divergence 43.2 mya, confidence interval 53–37 mya) (Dillman et al. 2011), but a much later divergence of 8.6 mya (5.7–11.3 mya, late Miocene) was estimated using nuclear genes (Niemiller et al. 2012). Hypothesized relationships of these three families are discussed and depicted in the phylogenetic relationships section in the chapter on amblyopsids (Adams et al., this volume).

FOSSIL RECORD

The fossil record of Trout-perches extends to freshwater Paleogene deposits (about 65–23.0 mya) and the earliest records are from the Paleocene (65–54.8 mya) of Alberta, Canada (Rosen & Patterson 1969; Wilson 1979, 1980; Cavender 1986; Patterson & Rosen 1989; Murray & Wilson 1996). The fossil impressions of percopsids are similar to extant species (Fig. 20.4). Although percopsids clearly existed in the Paleocene, this is a minimal date for their origin. They could have had a Cretaceous origin (about 144–65 mya) (Cavender 1986) and may have formed part of the Old Fauna of North American fresh waters. Several extinct fossil genera have affinities with Percopsidae, but details of relationships changed as new fossils, characters, and analyses emerged. Within the family, phylogenetic analyses placed the fossil genera †*Lateopisciculus* as sister to †*Amphiplaga* + †*Erismatopterus*. This clade was sister to the genera †*Massamorichthys* + *Percopsis*. The genus †*Libo-*

tonius was relegated to a separate family, †Libotomidae, in an unresolved trichotomy with Aphredoderidae (Pirate Perches) and Percopsidae (Patterson & Rosen 1989; Murray & Wilson 1996, 1999). The sister to all other percopsiforms was the genus †*Mcconichthys* (family †*Mcconichthyidae*) (Murray & Wilson 1999). The Cretaceous marine genera †*Sphenocephalus* and †*Xenyllion* were considered closely related to the Percopsiformes and were suggestive of a marine origin for the fresh water percopsiforms (Rosen & Patterson 1969). Subsequent work placed these genera closer to the higher paracanthopterygians than to the more basal Percopsiformes and †Libotomidae (Patterson & Rosen 1989), dispelling a marine origin, or placed them as a basal group (†*Sphenocephaliformes*, †*Sphenocephalidae*) to the Percopsiformes and Anacanthini (Murray & Wilson 1999), which is supportive of a marine origin.

Fossil relatives inhabited lakes, but the preservation of material may be biased toward that environment. The sister to *Percopsis*, the monotypic †*Massamorichthys wilsoni* (Fig. 20.5) of Middle Paleocene age (about 61.6–59.2 mya), is known from nearly 1,800 specimens discovered in shallow-lake deposits in a mass-death layer, suggesting the burial occurred as individuals aggregated to spawn or feed (Murray 1996). Another closely related genus, †*Lateopisciculus* (one species), is known from a slightly older Late Paleocene site (about 62.5–61.5 mya) in Alberta, Canada, which possibly represented a small, shallow lake (Murray & Wilson 1996). The †*Amphiplaga* (Fig. 20.4) and †*Erismatopterus*, sister genera each with one species, are known from the Eocene (about 54.8–33.7 mya) of the Green River Formation. †*Amphiplaga* occurs only in Early Eocene (about 55.8–48.6 mya) Fossil Lake sediments of the Green River Formation, and †*Erismatopterus* is restricted to slightly younger Middle Eocene (about 48.6–37.2 mya) deposits of lakes Gosiute and Uinta (Grande 1984). †*Amphiplaga brachyptera*, the only species in the genus, reached about 140 mm TL and occurred in



Figure 20.4. The fossil percopsid, †*Amphiplaga brachyptera*, 72 mm TL from the Early Eocene (52 mya) Fossil Butte Member of the Green River Formation, Wyoming (FMNH PF15311; taken from Grande, L., 2013, *The Lost World of Fossil Lake*. University of Chicago Press, with permission of the author).

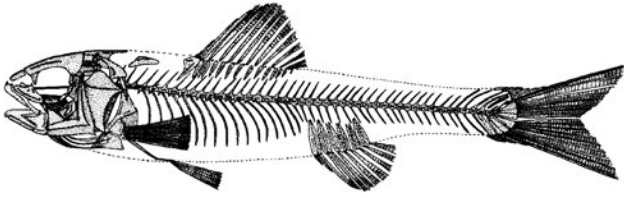


Figure 20.5. Reconstruction of the fossil percopsiform †*Massamorichthys wilsoni*, the sister to extant Trout-perches (Percopsidae). The abundant fossils were discovered in shallow-lake deposits in the Paskapoo Formation, Alberta, Canada (redrawn from Murray 1996).

Fossil Lake only near a northern tributary; the absence of any larvae in sediments of Fossil Lake suggests the species spawned upriver in the northern tributary (Grande 2013). Since extant Trout-perches spawn over gravel in shallow areas of lakes or streams and gravel was lacking in Fossil Lake, the hypothesis that †*Amphiplaga brachyptera* spawned in the tributary to the lake is plausible (Grande 2013). Fossil Trout-perches apparently fed mainly on insects or insect larvae and may have fed on ostracods that occur in abundance in the deposits with the fossils of †*Amphiplaga* and its close relative †*Erismatopterus* (Grande 1984, 2013). The genus †*Libotonius* (two species) is known from the Middle Eocene (about 48.6–37.2 mya) of north-central Washington and British Columbia (Wilson 1979). The basal-most percopsiform, the genus *Mcconichthys*, is from Early Paleocene deposits (about 65.5–55.8 mya) of the Tullock Formation, Montana (Grande 1988).

MORPHOLOGY

The Trout-perches have an elongate, slightly compressed almost translucent body with a small, well-developed free adipose fin, and narrow caudal peduncle (Figs. 20.1 and 20.2). A series of linear dark blotches occur along the mid-dorsum and lateral line. The head is large, unscaled, and flattened below; the mouth is small (upper jaw not reaching front of eye), subterminal, and nearly horizontal; and the eyes are moderate to large and located supralaterally (high on the head). Several rows of villiform (long, fine, crowded) teeth are on the upper and lower jaws. The lower jaw and edge of the cheek are lined with enlarged cephalic canals (silver-white chambers or pearl organs) (Fig. 20.2). The single dorsal fin is large with 1–3 weak spines (usually 1–2) and 9–12 soft rays; the caudal fin is deeply forked and the lobes are not pointed; the anal fin is small with 1–2 weak spines and 6–7 soft rays; the pelvic

fins are small and subthoracic (just posterior pectoral fin insertion) in position with one weak spine and eight rays; and the pectoral fins are long (extending past insertion of pelvic fins), narrow, and positioned on the lower side. The scales are finely ctenoid to cycloid; the lateral line is complete (Trout-perch) or incomplete (Sand Roller). The anus is in front of the anal fin. The pyloric caeca of Trout-perch are arranged laterally on either side of the gut (about 5/ side) and vary in number from 10 to 14 (Fig. 20.6). Most adults are 48–100 mm SL (maximum, 125 mm SL, or 20 cm TL). Aspects of skeletal and muscle anatomy are illustrated by various authors (Gregory 1933; Gosline 1963; Rosen 1962a; Rosen & Patterson 1969; Grande 1980, 1984; Hansel et al. 1988; Borden et al. 2013).

Coloration

Trout-perches are greenish-yellow or straw-colored on the dorsum; the venter is silvery or white, often appearing translucent; and a series of dark blotches occur in rows on the dorsum and upper sides of the body, 9–12 on the midline of the dorsum, 7–12 between the lateral midline and dorsum, and 10–11 along the midside of the body. The sides of the body are often silvery and the fins mostly transparent but occasionally spotted. No special breeding colors develop in either sex.

Sense Organs

The anterior cephalic lateralis canals, the pearl organs, of the Trout-perches are enlarged with quadrate chambers (Fig. 20.2), and the lower side of the head and jaw are covered with many small presumably sensory papillae. In this way, the Trout-perches are similar to the Cavefishes and Pirate Perches in having extensive sensory organs around the head, much more so than in other North American fishes. Unfortunately, the anatomy, physiology, or behavioral

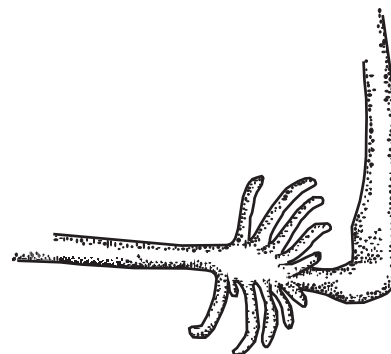


Figure 20.6. Pyloric caeca arrangement along the gut in the Trout-perch, *Percopsis omiscomaycus* (redrawn from Scott & Crossman 1973).

implications of the sensory organs of Trout-perches are little studied (e.g., Gosline 1963; Freihofer 1972; Yamana et al. 2010), but the wide canals certainly suggest the ability to detect and capture prey at low light levels (or high turbidities) (e.g., Janssen 1997).

GENETICS

Genetic studies of Trout-perches, including karyological data, are lacking except for DNA sequence data focusing on the phylogenetics of percopsid fishes and their relatives and one electrophoretic study. Wiley et al. (2000) presented aligned sequences of DNA of the Trout-perch and Pirate Perch (*Aphredoderus sayanus*). Phylogenetic analysis of these data along with morphology for acanthomorph fishes showed that these two species consistently (except in one instance) formed a monophyletic group; however, the amblyopsids, the putative sister-group of the aphredoderids, were not included. The electrophoretic mobility of the enzyme glucose-6-phosphate isomerase (GPI 5.3.1.9) distinguished the Trout-perch from 10 other potential prey fishes of the Walleye (*Sander vitreus*) (Hartman & Garton 1992).

PHYSIOLOGY

The physiology of the Trout-perches is decidedly understudied. Here we cover the little information available on environmental tolerances (e.g., temperature, pH) and hearing. Apparently, no information is available on any aspect of vision or any other sensory system.

Temperature

Little is published on temperature tolerances in either percopsid species. In the Columbia River, the Sand Roller occurs across temperatures of at least 2.5–24°C (36.5–75.2°F) (Gray & Dauble 1979; Parsley et al. 1989). Given winter conditions and depths at which individuals are captured at least the northern populations of the Trout-perch are adapted for cold waters. The range of the Trout-perch extends north to the Mackenzie and Yukon Rivers. When acclimated at 1.7°C, the critical thermal maximum was 22.9°C for the Trout-perch (Reutter & Herdendorf 1976). Sampling along isotherms in Lake Michigan with bottom trawls in the autumn found the Trout-perch in greatest abundance at 15–16°C in daytime, but at night the temperature range expanded to 7–16°C with two dis-

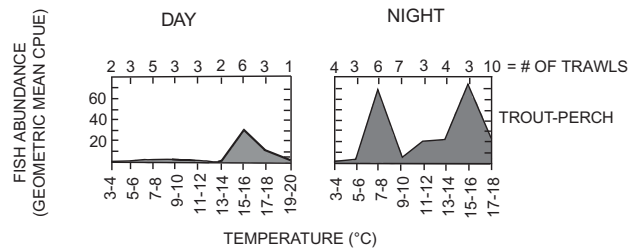


Figure 20.7. Abundance of Trout-perch, *Percopsis omiscomaycus* (geometric mean catch / unit effort, CPUE), in Lake Michigan during day and night for each 2°C temperature strata. Fish were captured using a bottom trawl during September 1977 (redrawn from Brandt et al. 1980).

tinct peaks in abundance at 7–8°C and 15–16°C (Brandt et al. 1980; see also Wells 1968; Fig. 20.7). The nighttime expansion of isotherms yielding high abundance may have resulted from thermal habitat shifts in other species (i.e., release from diffuse competition with the Spottail Shiner, *Hudsonius hudsonius* as *Notropis hudsonius*, and Yellow Perch, *Perca flavescens*) (Crowder et al. 1981) or availability of prey. Notably, the Trout-perch followed the isotherms even when they shifted dramatically inshore and offshore with the position of the thermocline (Crowder et al. 1981).

pH

Trout-perch are sensitive to human-induced acidification of northern lakes, but pH tolerance of Sand Rollers is apparently not documented. Trout-perch were present and apparently withstood pH 6 and an alkalinity of 8.78 (as HCO₃) mg/l in an acidified Ontario lake (Somers & Harvey 1984). In another acidified Ontario lake, the species disappeared with the Lake Trout (*Salvelinus namaycush*) and several other species between 1967–1969 as pH decreased from a background of about 5.9–5.4 (inferred from diatom and chrysophyte assemblages) to a mean annual pH of 4.6 (measured) in 1969. During the period of rapid acidification, dissolved aluminum levels were also high (>125 mg/l, diatom inferred) (Beamish & Harvey 1972; Dixit et al. 1992).

Other Environmental Tolerances

Little is known about salinity, dissolved oxygen, turbidity, or other tolerances for either species of Trout-perches. One Sand Roller occurred at Horseshoe Island Slough, about 40 km from the mouth of the Columbia River (Wydoski & Whitney 2003). We presume some tidal influence likely is present at this juncture in the river. Similarly, Trout-perch

occur in tidally influenced estuaries of the eastern James Bay coast, Canada, where they are associated with maximum salinities of 0.4 ppt and classified as freshwater fishes that occasionally enter brackish water (Morin et al. 1980). Trout-perch in the Wisconsin River were present, but rare, in reaches where average daytime dissolved oxygen was <5 mg/l; they occurred in greatest abundance where dissolved oxygen was >7 mg/l (Coble 1982).

Trout-perch exposed to thermomechanical pulp at the effluent plume of a Canadian pulp mill were compared to individuals upstream of the mill (reference samples) (Gibbons et al. 1998). Individuals at the effluent plume site were shorter, lighter, and younger than fish from the reference site. For both sexes, regression lines for size-at-age were higher at the reference than the effluent plume site. The length of both sexes of Trout-perch was less at the effluent plume site at any given age after fish were about 2–3 years old. No differences were detected in gonad size, testosterone production in male testicular tissue or female follicles, or liver weights. The results indicated a decrease in mean and growth without changes in gonad size or condition. The authors speculated that increased adult mortality was the most likely mechanism driving the change in age structure and growth response between the sites.

Hearing

Trout-perch from Canada were subjected to what we believe is the first hearing test for any member of the order Percopsiformes. The hearing (measured as auditory evoked potential thresholds, dB re 1 μ Pa) of the Trout-perch was typical of fishes with a swim bladder but without a specialized connection between the swim bladder and inner ear (e.g., connection present in Cyprinidae, Carps and Minnows, and other otophysan fishes). Sensitivity was highest at low frequencies (i.e., <400 Hz) (Mann et al. 2007).

BEHAVIOR

Dominance Hierarchies

Little information is available on the behavior of Trout-perches, but field and laboratory observations indicate Sand Rollers will establish dominance hierarchies and are territorial. When 10 Sand Rollers were placed in a small aquarium (18.9 l), they established a dominance hierarchy, but when transferred to a larger tank (bottom about 0.9×1.5 m), the fish went to the edges along the bottom

and were separated widely. They oriented their bellies toward the closest surface and remained still. One fish established a territory under a drainpipe, which was 38–46 cm off the bottom. Other fish stayed in contact with the bottom or sides of the aquarium, but the territorial fish exerted little obvious energy and maintained neutral buoyancy; it maintained a head-downward posture at a 45 degree angle for long periods of time. Once plastic plants were put in the tank, fish along the edges moved immediately under this artificial cover. Several fish used one plant but stayed on opposite sides and avoided one another. Fish fed on tubifex worms, apparently by sight, usually off the bottom rather than in the water column. They fed only on worms that drifted close to their territory (Wydoski & Whitney 2003).

Diel Periodicity, Habitat Shifts, and Schooling

Field observations show diel periodicity in habitat use and suggest territoriality in Sand Rollers. Sand Rollers occupied depths of 1.0–3.7 m in the mid-Columbia River during the night, but they were not observed at these depths during the day (SCUBA observations, Gray & Dauble 1976), suggesting movement to deep waters during the day and to shallow waters at night (Wydoski & Whitney 2003). During night observations, Sand Rollers occupied small depressions on sandy substrate where individuals were spaced about 90 cm apart. Similar diel habitat shifts occur in streams where the species seeks cover during the day, moving into riffles or the tail-end of pools at night (presumably to forage). Sand Rollers moved out of a flooded creek and took refuge from swift current in submerged clumps of grass on the inundated floodplain. Only one individual occurred in each clump of grass, again suggestive of territoriality or at least solitary habits (Wydoski & Whitney 2003).

The Trout-perch is also active nocturnally. Trout-perch in Georgian Bay, Ontario, tended to school near the bottom in deep water close to or below the thermocline during the daylight, moving into shallow water (2–15 m) at night (SCUBA observations; Emery 1973). Within the shallow observation area, they increased in abundance at night likely as a result of migration from deeper waters. Once in the shallows at night, they did not school, occurred patchily, and fed extensively over sandy, muddy substrates by swimming toward the bottom and snapping at organisms near or on it. Trawling and seining reveals a comparable diel pattern in northern lakes, where Trout-perch are only rarely caught by shallow-water seining during the daytime but can be abundant in seine hauls made

at night in such habitats (Scott & Crossman 1973; Becker 1983). Day and nighttime examination of Trout-perch stomachs from Lake Michigan did not detect any notable diel differences in foraging activity, but the species did broaden its thermal niche at night (see ecology section). Relatively few stomachs were empty (10–11%) during day or nighttime samples (Crowder et al. 1981). Even so, about 2–7 times more individuals were caught in night than daytime bottom trawls (depths usually <10–30 m) (Brandt et al. 1980; Crowder & Magnuson 1982). The species apparently undergoes massive onshore-offshore migrations (or avoids daytime trawls) (Scott & Crossman 1973; Brandt et al. 1980). Similarly, nighttime bottom-trawl catches (3–6 m depth) of young-of-the-year Trout-perch in Lake Erie were significantly higher than catches in morning or afternoon samples (Stapanian et al. 2007a). In Lake Erie before 1992 when the lake was quite turbid, catchability in Trout-perch was similar in daytime versus nighttime trawling. In 1992–2009, catchability shifted and became higher in nighttime hauls, the shift being attributable to the greatly increased clarity of the lake

caused by non-native filter feeding dreissenid mussels (Kocovsky & Stapanian 2011).

REPRODUCTION

Spawning Season

The Sand Roller spawns in the spring to early summer. Female Sand Rollers in the Columbia River, Washington, were gravid from late June through mid-July at water temperatures ranging between 13.9–16.1°C (Gray & Dauble 1979). Farther upriver in Idaho, spawning begins in early May and continues until early June (Pratt & Whitt 1952; Simpson & Wallace 1978; Table 20.1).

For the relatively wide-ranging Trout-perch the duration and timing of the spawning season are dependent on latitude (and likely to some extent temperature). Within the northern extent of its range, ripe individuals of the Trout-perch were taken in June in the Yukon River system, Alaska, and ripe males and females occurred from early June to late July in northern British Columbia (McPhail & Lindsey 1970). Spawn-

Table 20.1. Life-history characteristics of the Trout-perches, genus *Percopsis* (Percopsidae). Sources are given in the text.

	<i>Percopsis</i>
Number of species	2
Strictly fresh water	Yes, primary
Maximum size recorded	125 mm SL or 20 cm TL
Maximum age	4–8 years
Age and size at first reproduction	Age 1–2
Iteroparous versus semelparous	Iteroparous
Fecundity estimates from ovarian counts	126–1,329 mature eggs/female
Egg deposition sites	Sand, silt, rocks, or gravel substrates
Clutch size and egg size (diameter)	No clutches; 0.8–2.0 mm (mature eggs)
Range of nesting dates and temperatures	May–September (latitude dependent); 4.4–20°C or after water temperatures are >10°C for 44–46 days
Habitat of spawning sites; average water depth	Shallows of lakes, ≤1.3 m deep, and riffles of streams, <0.91 m and usually <0.45 m
Incubation period; larval type at hatching	6.5 days at 20–27°C; protolarvae
Mean size at hatching	5.3–6.0 mm TL
Sex building nest; sex incubating eggs; other care-giving behaviors	No nest, egg incubation, or parental care-giving behaviors
Major dietary items	Invertebrates and occasionally small fishes Sand Roller: dipteran larvae (58%), caddisfly larvae (24%), and microcrustaceans (15%) Trout-perch: benthic invertebrates (e.g., chironomid larvae, isopods) (61.5%), amphipods (16.7%), plankton (13.2%), and mysid shrimp (8.6%)
Migratory or diadromous	May migrate short distances to spawn
Imperilment status	Declining at periphery of range (Trout-perch, <i>Percopsis omiscomaycus</i>)

ing runs occurred in the latter half of May (water temperature 4.4–10.0°C) in Heming Lake, northern Manitoba; in late June or early July until late September in southeastern Lake Michigan; from May to mid-June (water temperatures 15.6–20°C) in Lake Winnebago, Wisconsin; and from early May to August in Lake Erie and Lower Red Lake (44–46 days after air temperatures are >10°C), Minnesota (Lawler 1954; Priegel 1962; Magnuson & Smith 1963; House & Wells 1973; Scott & Crossman 1973). Peaks of first spawning runs in Lower Red Lake occurred after air temperatures were >10°C for 44–46 days. Young-of-the-year abundances indicated ≥ 2 peaks about 1.0–1.5 months apart occurred in the spawning run (Magnu-

son & Smith 1963). Similarly, otoliths revealed multiple growth checks between the annuli during the spawning season, which is a good indication that Trout-perch females and males spawn multiple times during the summer (Nelson & Dick 2002). In a May to November trawling study in Saginaw Bay, Lake Huron, the change from an initially unimodal length frequency distribution to a bimodal distribution by August and September and the appearance of small (<50 mm TL) individuals in nearly all months also suggest multiple annual cohorts are produced (Blouzdis et al. 2013; see also Kovcovsky et al. 2014; Fig. 20.8). Near the southern boundary of its range in a West Virginia stream, Trout-perch were in

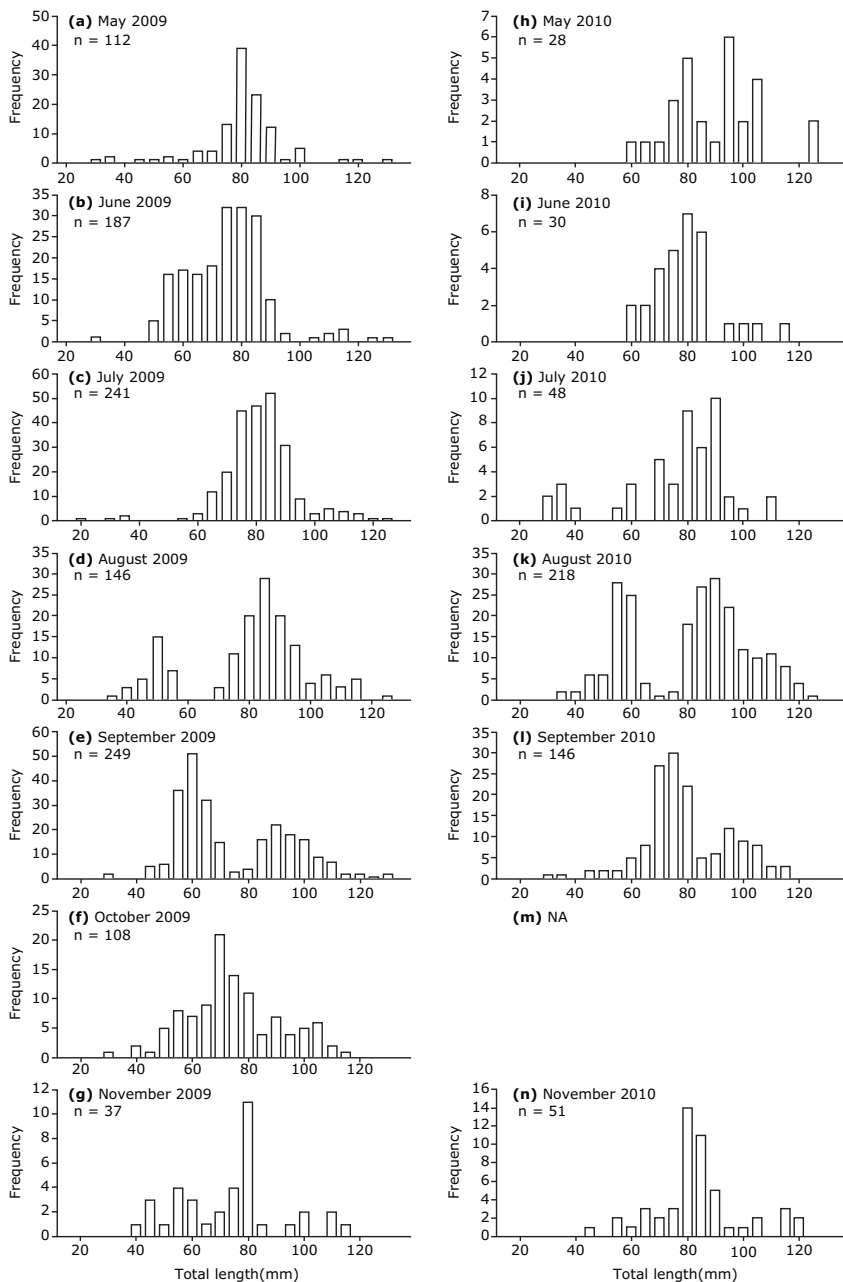


Figure 20.8. Frequency distribution (TL) of Trout-perch captured with a bottom trawl in 2009 and 2010 from May to November (October 2010 not sampled) for five sites in Saginaw Bay, Lake Huron (y-axes scales differ). Note the shift from unimodal to bimodal distributions by July and August and the occurrence of small (<50 mm TL) Trout-perch in most months (redrawn from Blouzdis et al. 2013).

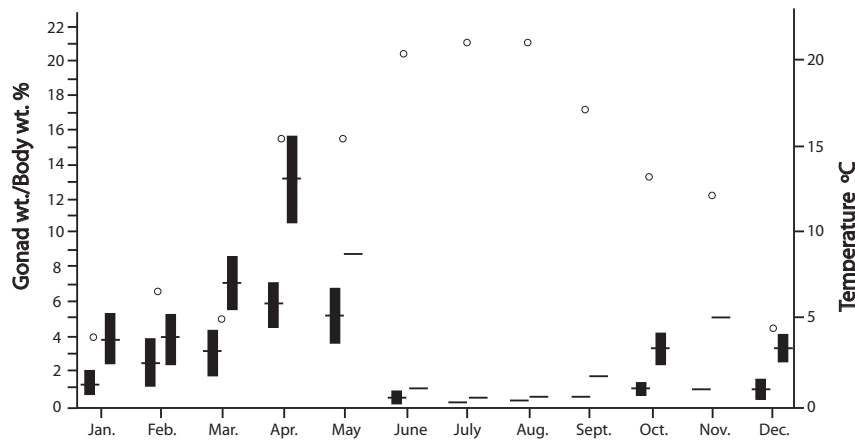


Figure 20.9. Seasonal variation of gonad weight to body weight for male and female Trout-perch, *Percopsis omiscomaycus* (sexes combined) and the monthly water temperatures in an upland West Virginia stream. Horizontal lines, means; rectangles, two standard errors of the mean; and open circles, water temperature (redrawn from Muth & Tartar 1975).

spawning condition in late April and May (water temperature about 15°C). Gonad to body weight ratio increased rapidly between March and April, peaking in April at 5.89% in males and 13.11% in females as water temperatures increased from 5 to 15.5°C (Fig. 20.9). All spawning was completed by June (Muth & Tarter 1975).

Spawning Migrations and Aggregations

Little is known about spawning migrations or aggregations in the Sand Roller, but the Trout-perch can make spawning migrations from lakes into tributary streams, aggregate and spawn in shallows of lakes, and in stream-dwelling populations, aggregate to spawn over riffles. The Sand Roller is believed to move from larger to smaller streams to spawn (Simpson & Wallace 1978). They also spawn in mainstems of large rivers and apparently in reservoirs (Wydoski & Whitney 2003).

In Lake Superior and other lakes, Trout-perch migrate in early spring into some tributary streams by the tens of thousands presumably to spawn (Lawler 1954; McLain 1957). In Lower Red Lake, Minnesota, spawning ready Trout-perch congregated at the mouth of a tributary before sunset and moved into the creek after dark to spawn; most left the creek by sunrise. The species also aggregates for spawning along sandy or gravelly beaches in water ≤ 1.3 m deep (Kinney 1950; Magnuson & Smith 1963). Peak abundance in spawning aggregations occurred between about 1900–2400 h (Magnuson & Smith 1963). Stream-dwelling populations also apparently spawn at night. Large numbers of ripe individuals easily stripped of milt and eggs were taken at night in a gravelly riffle in a West Virginia stream at depths < 0.91 m and usually < 0.45 m. Trout-perch were taken only at night on this riffle during the spawning season (Muth & Tarter 1975). The species also spawns during

the day, and no diurnal variation in spawning activity apparently occurs in some populations (Lawler 1954; Magnuson & Smith 1963). Males generally outnumber females in spawning aggregations, often by considerable numbers (2.2–5.7 males/female) (Lawler 1954; Magnuson & Smith 1963; Lawler 1954; Muth & Tarter 1975).

Spawning

No direct observations of spawning seem to be published for the Sand Roller, and only terse accounts of spawning behavior are available for the Trout-perch. The Trout-perch is a group spawner, spawning over sand, silt, rocks, or gravel substrates (Lawler 1954; Priegel 1962; Magnuson & Smith 1963; Muth & Tarter 1975) and providing no parental care to the eggs or young. In a Minnesota stream, spawning occurred within 10–12.5 cm of the surface and was concentrated near the edges of the stream. During spawning, ≥ 2 males cluster around a single female and just before the eggs are extruded, the males press close to the sides of the female, and both males and females occasionally break the surface of the water as the eggs and milt are simultaneously released (Priegel 1962; Magnuson & Smith 1963). The apparently nonadhesive eggs drift to the bottom. Some interesting and seemingly unusual spawning behavior occurred in Lake Winnebago, Wisconsin (Priegel 1962). Wave action sometimes forced the spawning Trout-perch onto rocks at the shoreline and as the water receded, the fish were stranded on the moist rocks where the eggs and milt were released. On the next wave, the fish were swept back into the water, and the eggs scattered about. The eggs did not adhere to the rocks but fell between them. Conspicuous post-spawning die-offs of Trout-perch are not uncommon (Priegel 1962).

Age and Size at Maturity

Age and size at maturity apparently vary among populations of Trout-perch and Sand Rollers, but factors producing the observed differences are unknown. Both sexes of the Sand Roller reached maturity in the Columbia River, Washington, at age 2, and all fish were mature at age 3. In Idaho waters, individuals matured at age 1 or 2 (Wydoski & Whitney 2003; see ecology section).

In southeastern Lake Michigan, a few Trout-perch are mature at the end of their first year of life but 84% of the males and 50% of the females are mature by the end of their second year; all fish were mature by the end of their third year. Males matured at about 60–64 mm TL, females at about 75–79 mm TL (House & Wells 1973). Trout-perch in Lower Red Lake, Minnesota, matured at smaller sizes. Some males and a few females matured at age 1 at about 51 mm TL. Fish maturing at age 1 were larger than age-1 fish that delayed maturation until age 2. Fish, particularly males, that mature at age 1 are subject to high spawning mortality in most seasons.

Sex Ratios

Population sex ratios in the Trout-perch vary depending on time of the year, age of the fish, and perhaps the population. In spawning aggregations, which are usually biased toward males, age 1+ males constituted 29% of all spawning fishes and age 1+ females only 2%. Most of the spawning aggregation (61%) consisted of age 2+ individuals that averaged 88.2 mm TL (male) and 92.2 mm TL (female); only 9% of the spawners were age 3–4+ (Magnuson & Smith 1963). Population sex ratios can be nearly equal in the first year of life (House & Wells 1973; Muth & Tarter 1975) or can be female biased (0.45 males/female), reflecting a high mortality rate in mature age-1 males (Magnuson & Smith 1963). Generally, females live longer than males and outnumber them in later year classes as a result of spawning-related male mortality (Magnuson & Smith 1963; House & Wells 1973).

Fecundity

Mature Sand Roller and Trout-perch females have a bimodal distribution of egg sizes (Magnuson & Smith 1963; Gray & Dauble 1979; Kocovsky et al. 2014). Whether a female spawns once and recruits the next batch of eggs for additional spawns or spawns once and resorbs the smaller eggs is unknown, but female Trout-perch apparently spawn multiple times in a season.

Little is known about fecundity in Sand Rollers. Eight Sand Roller females (76–92 mm FL) had 1,106–3,369 total eggs (mature and immature) (Gray & Dauble 1979). Another female contained 4,748 eggs (presumably total eggs) (Carlander 1969), but length-fecundity relationships for Trout-perch (see next paragraph; Magnuson & Smith 1963) suggest total egg counts likely substantially overestimate batch or total annual fecundity. Size differences in eggs of Sand Rollers were most notable in late June and July, coincident with the inferred spawning period. Obvious relationships between size of female and number of eggs were not apparent (Gray & Dauble 1979), but the sample size and size range examined was small.

In the Trout-perch, the numbers of mature ova increase with increasing length of fish, but available egg counts suggest a high degree of interpopulational variation. The relationship of TL to number of mature eggs in Lower Red Lake, Minnesota, was given by $\log(N) = -3.247 + 3.029 \log(TL)$, where N is the total number of mature eggs in both ovaries ($n = 28$ females, 67–124 mm TL) (Magnuson & Smith 1975). Hence, a 67-mm TL female produces on average 192 mature eggs and a 124-mm TL female produces 1,242 mature eggs. Adjusting for year class strength and population structure, age-1 females in Lower Red Lake contributed on average 10% of the eggs spawned, age-2 females 73%, age-3 females 24%, and age-4 females 1%. Fecundity in other populations is apparently much lower than in Lower Red Lake. In western Lake Erie, the average number of mature eggs across all ages (0–3) was 233 ± 58 (95% confidence interval) (Kocovsky et al. 2014). In a West Virginia stream, females contained 145–1,112 mature eggs (mean 346; $n = 30$, 59–125 mm SL) (Muth & Tarter 1975), fecundities much less than that expected in same-size Lower Red Lake females (229–3,648 eggs; SL converted to TL). The fecundity-length relationship in the West Virginia stream was linear and given by $N = -699.8 + 12.64(TL)$. Females in southeastern Lake Michigan ($n = 12$, 94–146 mm TL) contained 126–1,329 mature ova (House & Wells 1973), again well below expected counts from Lower Red Lake females (536–2,036 eggs), but same-size females showed high variability in egg counts, and some may have already spawned. Likewise, a 65-mm SL female from Little Sandy River, Kentucky, contained only 86 mature eggs (Clay 1975), below the fecundity of all the other populations also suggesting the female had initiated spawning before capture. Counts of mature eggs likely significantly underestimate annual fecundity for females, because females apparently spawn multiple times over the summer (Nelson & Dick 2002). Apparent total ova counts (mature and immature eggs) from

females in Heming Lake, Manitoba, ranged from 210 to 728 eggs (mean 349; $n = 19$, 60–78 mm FL) (Lawler 1954).

Eggs and Larvae

The mature eggs of Sand Rollers are reportedly much smaller than those of Trout-perch, being only 0.14–0.17 mm diameter (Gray & Dauble 1979). We question the reported egg size as being much too small (e.g., perhaps 1.4–1.7 mm diameter). The measurements should be treated with caution until verified.

The yellow, mature eggs of the Trout-perch range in diameter from 0.8 to 2.0 mm (Lawler 1954; Magnuson & Smith 1963; Clay 1975; Muth & Tarter 1975). Fertilized eggs are demersal and adhesive, measure 1.3–1.9 mm in diameter, and have a single oil globule (Fish 1932). Egg volume is 3.4 mm³, of which 2.28 mm³ is yolk. Embryo hatch in 6.5 days at 20–27°C (Magnuson & Smith 1963). Newly hatched larvae range from 5.3 to 6.0 mm TL (illus-

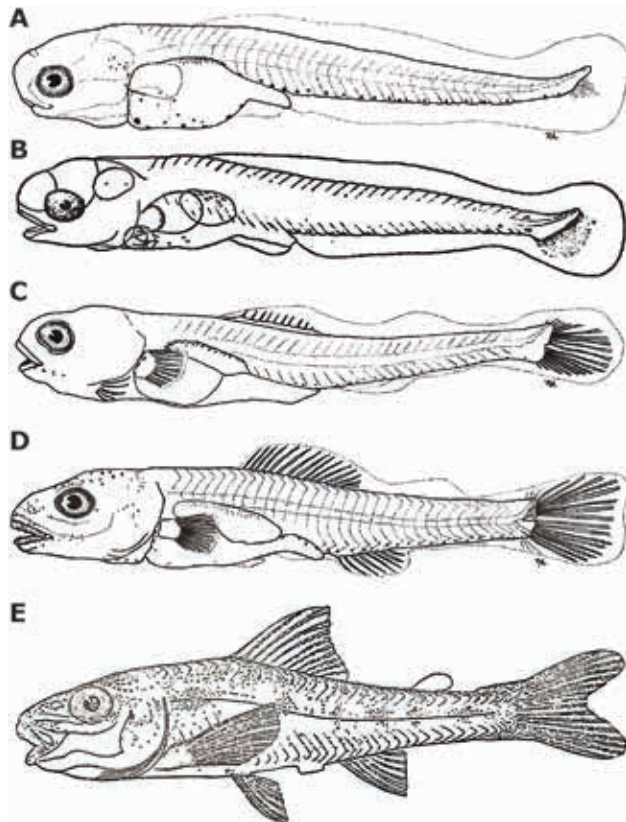


Figure 20.10. Development of young Trout-perch, *Percopsis omiscomaycus*. (A) Yolk-sac larvae, 6.7 mm TL; (B) post yolk-sac larvae, 7 mm TL; (C) post yolk-sac larvae, 7.6 mm TL; (D) post yolk-sac larvae, 11.5 mm TL; and (E) juvenile, 35.5 mm TL (redrawn from Baker & Wallus 2006; see original sources cited therein and in text).

trated and described by Fish 1932 and Auer 1982; Magnuson & Smith 1963; Fig. 20.10). The yolk sac is absorbed at about 6.2 mm TL (4–5 days at 20–23°C) (Magnuson & Smith 1963). At least in the Trout-perch, scale formation does not occur until the species reaches about 20 mm TL but is rapidly completed by 23 mm TL (Watkins 1974). At 39.5 mm TL, the Trout-perch is fully scaled and has assumed the adult appearance.

ECOLOGY

Adult Habitat

Sand Rollers and Trout-perch share an affinity for diurnal cover whether in the form of physical cover or deep water. Sand Rollers are secretive and spend most of the day in hiding. In small tributaries of the Columbia River, Washington, Sand Rollers occupied shallow water habitats with dense cover consisting of brush, tree roots, or undercut banks during the day but moved into stream riffles or the tail-end of pools at night (presumably to feed) (Wydoski & Whitney 2003). In tributaries of the Willamette River, Oregon, the species occurred most often in low-gradient stream segments over sandy substrates in association with large instream wood, undercut banks, and roots (Scheerer & Jacobs 2006). In the Columbia River, Sand Rollers exhibited diel periodicity in moving into deeper waters as cover during the day and returning to shallow waters at night. Nighttime SCUBA observations in the river revealed Sand Rollers in water 0.9–4.0 m deep (3–13.1 feet) (Gray & Dauble 1976). Divers never saw Sand Rollers during the day. The species occurs to depths of 22 m in the river mainstem (Wydoski & Whitney 2003). Nighttime seining of littoral habitats (April–August) in John Day Reservoir (Columbia River basin) revealed Sand Rollers as the most abundant species (of eight species, when adjusted for capture efficiencies). Their abundance over sand was 3.5 times greater than over gravel-cobble bottoms. The species was much more abundant at sites that lacked non-native fishes (Parsley et al. 1989).

Throughout its range, the Trout-perch inhabits lakes and small to large, upland streams, but it also occurs in flowing waters as large as the mainstem Mississippi River (e.g., Becker 1983). Stream-dwelling Trout-perch are captured frequently from clear, deep pools over a sand or mixed sand and gravel bottom (Fig. 20.11). In lakes, Trout-perch move from deep to shallow water at night, a habit which might make them an important factor in nutrient transfer, particularly in stratified lakes. Trout-perch occur



Figure 20.11. Example of stream habitat of Trout-perch, *Percopsis omiscomaycus*, at the southern edge of its range in Big Sinking Creek, Little Sandy River drainage, Kentucky (courtesy of MLW).

at depths ≤ 73 m in the Great Lakes (House & Wells 1973; McCullough & Stegemann 1992). In Lake Michigan, the species is restricted to shallow and intermediate depths (9.1–32.9 m) and occurs near shore in spring and summer and moves into deeper water during autumn (Wells 1968). In a multivariate study, Trout-perch were included in a group of fishes negatively associated with water transparency (Reyjol et al. 2008).

Larval Habitat

A preponderance of captures of Trout-perch larvae in sled net tows compared with plankton net tows in Lake Michigan (Madenjian & Jude 1985) indicates the larvae are demersal, staying on or near the bottom. Similarly, over the course of multiple samples in summer and early autumn in Lower Red Lake, Minnesota, age-0 Trout-perch occasionally occurred in shoreline seine hauls, but they were most commonly taken by bottom trawls in 3–6 m of water from about 20 days after hatching until the end of August (Magnuson & Smith 1963).

Diet

The Sand Roller apparently moves into shallow sandy areas at night to feed. The food items found in 55 individuals indicated no seasonal shifts in diet, but ontogenetic shifts were apparent (Gray & Dauble 1979). The overall diet was dominated volumetrically by dipteran larvae (58%), caddisfly larvae (24%), and microcrustaceans (15%). Eighty percent of yearlings (<41 mm FL, 1.6 inches) fed on zooplankton, which was about 31% of the diet by volume. Large caddisfly larvae, relative to the zooplankton, made up only a small part of the volume of yearlings but composed 32% of the volume of older fishes. Ten of 17 fish with empty guts were taken during winter (water temperatures 2.2–3.9°C), suggesting lack of food availability or reduced feeding at low water temperatures.

The diet of the Trout-perch is documented mostly in northern lakes. The species is primarily a benthic feeder. Average volumetric contribution to the diet was estimated as 61.5% benthic invertebrates (e.g., aquatic insect larvae, isopods), 16.7% amphipods, 13.2% plankton, and 8.6% mysid shrimp (various studies, $n = 787$ fish, Lakes Erie, Superior, and Nipigon; Vander Zanden & Rasmussen 1996). Chironomid larvae and pupae, amphipods, isopods, and Mysis shrimp often dominate the diet, but a variety of microcrustaceans, immature insects, small crayfish, other invertebrates, fish eggs (e.g., Walleye), and algae may be consumed (Nurnberger 1930; Wells 1980; Crowder et al. 1981; Bohr & Liston 1982; Muth & Busch 1989; Nelson & Dick 2002; Roseman et al. 2006; Nelson et al. 2010; Gamble et al. 2011ab; Blouzdis et al. 2013; Kocovsky et al. 2014; Fig. 20.12). The influence of prey size on diet appears less important than in many other fishes, although in Saginaw Bay, Lake Huron, significant but weak relationships occurred between Trout-perch size and size of amphipod and chironomid larval prey (Blouzdis et al. 2013). Age-1+ individuals in western Lake Erie ate a significantly higher proportion of benthic invertebrate prey (83%) and less zooplankton prey than did age-0 individuals (62%) (Kocovsky et al. 2014). Both age groups consumed benthic prey items in proportion to their availability in the environment (i.e., evidence of selectivity was lacking). At large sizes, the species eats darters (Percidae, Perches) and minnows (Cyprinidae) and may on occasion take young fishes of other species (Alewife, *Alosa pseudoharengus*; Rainbow Smelt, *Osmerus mordax*; Yellow Perch). Concentrated parasite loads and gut contents

indicate large Trout-perch opportunistically prey on small Yellow Perch (Nelson & Dick 2002).

Factors such as time of day, depth, season, and prey availability influence the diet of Trout-perch. Diel bottom-trawls in Lake Michigan revealed a preponderance of chironomids in Trout-perch ($n = 78$, mean 77 mm SL) stomachs during the day, but both chironomids and amphipods were numerically dominant in the nighttime diet ($n = 218$ fishes, mean 81 mm SL) (Crowder et al. 1981). Food of Trout-perch ($n = 288$) from southeastern Lake Michigan did not differ noticeably with size of fish (40–172 mm TL, mostly 80–139 mm TL), but the diet appeared to change with depth (Wells 1980). At depths of 9–13 m, the amphipod genus *Pontoporeia* made up 43% and immature midges 53% of diet volume. In deeper water (18–46 m), the relationship shifted with *Pontoporeia* dominating the diet volume at 80% and immature midge volume decreasing to 16%. At least five genera of immature midges were consumed, but most were *Chironomus* spp. Temporal diet differences in Trout-perch in Saginaw Bay, Lake Huron, were attributed to invertebrate emergence phenologies (timing and sequence) (Blouzdis et al. 2013; Fig. 20.12), and some seasonal changes were noted in Lake Erie (e.g., more copepods eaten in October than August) (Muth & Busch 1989). Even so, individuals in that system showed consistently strong selectivity of chironomids and at times amphipods and isopods but did not consume hyperabundant dresenid mussels.

Potential Resource Competition

The Trout-perch is a potential competitor with other lake-dwelling fishes because of its use of benthic food resources. Considerable dietary overlap with young Fresh-

water Drum was noted in western Lake Erie (Muth & Busch 1989). In a reservoir associated with Lake Michigan, diet overlap was greatest with another benthic fish, the Johnny Darter (*Etheostoma nigrum*) (Bohr & Liston 1982). The Trout-perch diet also shows high overlap (e.g., chironomids and amphipods) with age-0 Walleye and young Yellow Perch (*Perca flavescens*), the latter, like Trout-perch, positively selecting chironomids as prey (Roswell 2011; Blouzdis et al. 2013). Judging from the diet and feeding periodicity of a non-native percid, the Ruffe (*Gymnocephalus cernuus*), now established in Lake Superior, competition for food resources may develop with benthic-feeding fishes, including the Trout-perch and Yellow Perch (Ogle et al. 1995). Another Great Lakes invasive, the aggressive Round Goby (*Neogobius melanostomus*), is another likely resource competitor with Trout-perch, but at least in some areas that species does not appear to have displaced Trout-perch (e.g., Saginaw Bay, Lake Huron) (Blouzdis et al. 2013).

Abundance

Considerable local and annual variation occurs in Sand Roller distribution and abundance. Sand Rollers occurred in electrofishing samples in 11 of 45 randomly selected reaches of raftable rivers (sampled July–September) in Oregon but never was a dominant species in the samples (Hughes et al. 2002). Among various dam pools in the Columbia River, Washington, Sand Roller density estimates for July and August trawl samples (1987–1991) ranged from 0.04 to 11.6 individuals/ha. Annual density measurements were highly variable (Wydoski & Whitney 2003). Mark-recapture population estimates indicate Sand Rollers can be quite abundant in some situations. In 240-m reaches of Willamette River tributaries, Oregon, population estimates ranged from 451 to 1,093 individuals (95% confidence intervals, 183–2,049) (Scheerer & Jacobs 2006).

The Trout-perch can be one of the most abundant fishes in northern lakes but usually is less abundant in streams. For example, the species made up 52% of the otter trawl catch and 54% of the seine catch in a highly turbid, shallow prairie lake in Manitoba. It was in higher abundance than any other fish, even the pelagic and often hyperabundant Emerald Shiner (*Notropis atherinoides*) (Craig & Babaluk 1989). Similarly, mark-recapture work on Trout-perch (46–103 mm TL) in Heming Lake, Manitoba (August–September), yielded estimates of 482–598 individuals/ha (Lawler & Fitz-Earle 1968). Bi-annual bottom

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Figure 20.12. Trout-perch, *Percopsis omiscomaycus*, diet proportions by biomass in 2009 (a, c) and 2010 (b, d) from bottom trawl sampling in Saginaw Bay, Lake Huron. Diet contents are compared across TLs (a, b), and among months (c, d) for individuals 40–110 mm TL (redrawn from Blouzdis et al. 2013).

trawling (June and September 2010) in western Lake Erie at 56 sites yielded catches of 0 to 1,524 Trout-perch/h. The Trout-perch occurred at higher abundances than all other benthic species in those samples, except the White Perch (*Morone chrysops*) (Kocovsky et al. 2014). Out of 15 species captured, Trout-perch comprised 16.7% of the offshore experimental bottom-trawl catch (20,352 individuals, September) in Lake Michigan, being similarly abundant to the Rainbow Smelt (16.3%) and ranking second in overall abundance to the Alewife (38%) (Brandt et al. 1980). Repeated, monthly (May to November) trawling in Saginaw Bay, Lake Huron, Wisconsin, revealed Trout-perch represented 13.5% (by number) of all species captured, third behind Yellow Perch (38.0%) and Rainbow Smelt (19.1%) (Blouzdis et al. 2013). In contrast, the species was consistently a minor component of the systematic annual bottom-trawl catch in the main basin of Lake Huron from 1970–1999 (Dobiesz et al. 2005), but annual variability was high ranging from about 50 to >800 fish/ha (Riley et al. 2008). In that lake, the population peaked in about 1995, only to experience a 98% decrease from 1994–2006 (Riley et al. 2008; Roseman & Riley 2009; see conservation section).

In streams, Trout-perch abundance is generally low and its distribution sporadic. The species is widespread in tributaries of the Red River of the North (North Dakota and Minnesota), occurring in 17 of 25 major tributaries. However, over multiple surveys from 1962–1994, the Trout-perch usually occurred at only 0.05–20% of sampled sites within the 22 large-scale reaches from which it is known (Koel & Peterka 2003). Density of Trout-perch captured with 160-m² beach seine hauls at 171 sites in 11 Ottawa River tributaries (late July-early August) was only about 1.3 fish / 100 m² (Reyjol et al. 2008). Second-order streams (n = 24) on the south shore of western Lake Superior in summer yielded on average 0.16 individuals / 100 m² compared with 1.43 / 100 m² in third-order streams (n = 10). Nearly all individuals in the third-order streams were immature. Interestingly, no Trout-perch were taken in second- or third-order streams draining the steeper gradient north shore (Brazner et al. 2005). Similarly, researchers captured 30–85 specimens monthly for a year from a 1,532-m² pool in Twelvepole Creek, West Virginia (Watkins 1974) also suggestive of relatively low densities (i.e., <0.1 fish/m²). Some of these abundance estimates may be biased downward because of the secretive daytime habits of the species and gear selectivity, but, except for the highest numbers in spring, no patterns in seasonal abundance were apparent.

Age and Growth

Demographics of the Sand Roller and Trout-perch are somewhat similar in terms of size at age 1, population age structure, and average longevity, but the Sand Roller reaches smaller maximum size. Age and growth characteristics of Sand Rollers are based on a sample from the Columbia River, Washington (Gray & Dauble 1979). Age determinations from dorsal spine and scale annuli disagreed in 12 of 21 specimens; scales tended to show one less annulus than spines. In contrast to the Trout-perch (see next paragraph), no difference was noted in growth rate between males and females. Growth was greatest in the first year, declining rapidly after age 2. Of 51 Sand Rollers used to estimate length at age, 91% were age 1–3 and ranged from 39–77 mm FL. The largest Sand Roller recorded was an age-6, 103-mm FL female, but few fish apparently live beyond age-3. The average FL of Sand Rollers at the end of each year of life was: age-1, 45 mm; age-2, 67 mm; age-3, 77 mm; age-4, 84 mm; age-5, 93 mm; and age-6, 94 mm (presumably based on scale annuli).

Age and growth rates vary among populations and between the sexes of Trout-perch, but as in Sand Rollers, aging studies should be interpreted cautiously. Scales and otoliths were used for aging Trout-perch from Lake Champlain (n = 459) and only 50% of ages determined from otoliths agreed with scale ages. Otoliths tended to yield older ages than scales, but the authors had no basis to claim more accuracy for either method (Pereira & LaBar 1983). Six age classes were recognized with most specimens (89%) being age 1–3. Females averaged 2.5 years and males 1.5 years. Females were much more abundant in older age groups. All age-5 and -6, and most age-4 fish, were females. Studies of other lake populations also revealed disproportionate numbers of older females (Magnuson & Smith 1963; House & Wells 1973; Kocovsky et al. 2014). In western Lake Erie, males experienced 58% mortality between ages 0–1 compared with only 24% for females (Kocovsky et al. 2014). In southeastern Lake Michigan, ages 1–8 were recognized from scale annuli (House & Wells 1973), but Trout-perch populations in Twelvepole Creek, West Virginia (scale-aged), Heming (scale-aged) and Dauphin (otolith-aged) lakes, Manitoba, and Lower Red Lake (scale-aged), Minnesota, comprised only ages 1–4, 1–3, 1–4, and 1–4, respectively (Lawler 1954; Magnuson & Smith 1963; Nelson & Dick 2002). Most Trout-perch from the Lake Michigan study were age 1–4 and showed about equal sex ratios to age-4, when females began to outnumber males. Age-2 males and age 2–3 females

dominated the Dauphin Lake samples; again, age-3 males were rare, and none were age-4. The Lower Red Lake population consisted primarily of age-1–2 males and age-1–3 females. Females outgrew males in the second summer of life in Lower Red Lake, but growth rates for both sexes were similar in Lake Michigan. Mean TL in June for each age 1–8 of the Lake Michigan fish was 58.5 mm, 79.0 mm, 105.0 mm, 115.5 mm, 123.0 mm, 134.0 mm, 137.0 mm, and 152.0 mm TL, respectively. The maximum size of the Trout-perch is about 200 mm TL (Page & Burr 2011). Other populations may show higher or slower growth than these examples at least initially. For example, size of age-0 Trout-perch in October over a 20-year period showed remarkably little variability in Lake Winnebago, Wisconsin, with an average size of 81.6 mm (SE = 1.02) and a coefficient of variation of only 5.6% (Staggs & Otis 1996), well above age-1 size of the Lower Red Lake populations (51 mm TL). Average sizes at age-1 in Lake Superior and Twelvepole Creek were lower, being only about 39 and 43 mm TL (House & Wells 1973; Watkins 1974).

Several factors have been linked to first-year survival and growth in lake-dwelling Trout-perch, including temperature (see next paragraph), wind velocity, density dependent mortality, competition, and predation. Annual variability in young-of-the-year density can be dramatic. For example, age-0 Trout-perch densities calculated from bottom trawling in Oneida Lake, New York, ranged from 0 to >1,000 fish/ha from 1961–1999. Over this period, peaks of age-0 abundance (>500 fish/ha) generally were followed by ≥ 1 year of often dramatically decreased age-0 catches (Hall & Rudstam 1999). Although not as strongly associated as temperature, average wind velocities can also negatively affect year-class strength. Wind velocity associated mortality probably resulted from wave actions acting on eggs and newly hatched larvae in shifting sand bottoms. Another factor operating on year-class strength was density-dependent mortality possibly arising from higher rates of fungal infection in dense egg mats and attraction of predators in years of high abundance. Long-term trawling data in western Lake Erie (1961–2011) revealed on average a minor 4-year periodicity in age-0 Trout-perch abundance imposed over a longer-term dominant periodicity in abundance of 17 years on average (Kocovsky et al. 2014). The authors suggested the periodicity in that system might be evidence of intrinsic population regulation through mechanisms such as skewed sex ratios.

Temperature regime also affects early growth and year-class strength of Trout-perch. In Lower Red Lake, 70–91%

of the variation in first and second season's growth was associated with the total temperature experience (degree-day summations) of fish during early summer and autumn. Growth compensation also occurred in the Lower Red Lake population such that the longer a fish was at the end of its first summer, the less it grew the next summer (Magnuson & Smith 1963). Similarly, populations in Lake Winnebago, Wisconsin, showed a strong positive relationship with spring and summer temperatures and weaker negative relationships with age-0 abundance of the Trout-perch (i.e., density dependence) as well as age-0 abundances of the Freshwater Drum, a potential competitor, and the Saugey (*Sander canadensis*), a potential predator (Staggs & Otis 1996; see also Hall & Rudstam 1999). Year-class strength in Lower Red Lake, Minnesota, was associated positively and strongly with degree-days >10°C in the growing season. Temperature associated mortality may be related to extended egg or larval development times in a cool summer and increased predation due to slower growth.

Predation

Northern Pikeminnows (*Ptychocheilus oregonensis*) as well as three non-native predators, the Walleye, Channel Catfish (*Ictalurus punctatus*), and Smallmouth Bass (*Micropterus dolomieu*), preyed on Sand Rollers in the lower Columbia River, Washington. Walleyes were the main predators; 25–27% of the Walleye examined had consumed Sand Rollers, which was equivalent to about 17% of Walleye diet by weight. Sand Rollers were a minor component of the diet of the other three predators (Poe et al. 1991; Zimmerman 1999). To estimate the size of decomposed prey fishes in predator stomachs Hansel et al. (1988) identified and measured bony parts of prey fishes from the Columbia River. The FL of Sand Rollers was estimated from the size of the cleithral and opercular bones. The analysis revealed a wide range of sizes (29–106 mm FL) of Sand Rollers were eaten by piscine predators (species not specified).

The Trout-perch apparently is not a preferred prey species by some piscivorous fishes, although it is eaten if preferred prey is not available. In predation trials, where near equal-size individual fishes were tethered in similar habitats and monitored for predation from piscivores (e.g., Smallmouth Bass, *Micropterus dolomieu*; Largemouth Bass, *Micropterus salmoides*; Northern Pike, *Esox lucius*; Walleye, *Sander vitreum*) in a Canadian lake, Trout-perch showed intermediate vulnerability to predators (along with Blacknose Shiner, "*Notropis*" *heterolepis*, and Yellow

Perch) relative to Brown Bullheads (*Ameiurus nebulosus*; lowest predator vulnerability) and an array of silvery colored minnow species (highest vulnerability). The intermediate vulnerability of the Trout-perch may be explained by their more cryptic coloration (relative to the silvery-colored minnows) and perhaps their fin spines (Laplante-Albert et al. 2010). Interestingly, in a Lake Huron study, Trout-perch made up only 0.4% of the piscine diet of age-0 ($n = 1590$) and age-1+ ($n = 335$) Walleye and Yellow Perch (79–321 mm TL, $n = 168$) (Blouzdis et al. 2013) apparently avoiding predation by these species or being negatively selected against as in other systems (e.g., Walleye, Parsons 1971; Knight et al. 1984; Craig & Babaluk 1989). The mechanism for negative selectivity on Trout-perch by some fish predators is unknown.

In many northern lakes, Trout-perch are important forage for piscivorous fishes as well as terrestrial vertebrates. Fish predators include the Lake Trout (*Salvelinus namaycush*), Brook Trout (*Salvelinus fontinalis*), Northern Pike (*Esox lucius*), Burbot (*Lota lota*), Yellow Perch, Sauger, Walleye, and Freshwater Drum (Lawler 1954; Magnuson & Smith 1963; House & Wells 1973; Craig & Babaluk 1989; McCullough & Stegemann 1992; Knight & Vondracek 1993). The species also is eaten by the Smallmouth Bass, bullhead Catfishes (*Ameiurus* spp.), and the White Bass (*Morone chrysops*) (Priegel 1970; Ogle et al. 1996). In Ontario and Quebec lakes, Trout-perch supplied 10.7–34.4% of the dietary volume of Northern Pikes and Chain Pickerels (*Esox vermiculatus*) and $\leq 58\%$ of the diet of Walleyes (average 11.9%) (Vander Zanden et al. 1997). Age-1 Trout-perch appear to be most vulnerable to Walleye predation (Magnuson & Smith 1963). In Heming Lake, Manitoba, Trout-perch constituted the major food item in May and June for Northern Pike, when ≤ 63 Trout-perch occurred in individual Northern Pike stomachs (Lawler 1954). Freshwater Drum stomachs contained ≤ 19 Trout-perch, which were exploited when Trout-perch massed for spawning in lake tributaries (Magnuson & Smith 1963). Remains of the Trout-perch were present in River Otter (*Lutra canadensis*) scat around lakes in northeastern Alberta, Canada. The remains occurred in 6.9–9.8% of all scats examined in early summer months but were absent the remainder of the year (Reid et al. 1994). The timing of River Otter predation suggests the Trout-perch may have been exploited during spawning runs in shallow water. Trout-perch also are eaten by Northern Water Snakes (*Nerodia sipedon*), by Double-Crested Cormorants (*Phalacrocorax auritus*), and at least during courtship and chick feeding, by Common Terns (*Sterna hirundo*) (e.g., Court-

ney & Blokpoel 1980; Ernst & Ernst 2003 and references therein; Rudstam et al. 2004).

Parasitism

The Trout-perch is infected by a large variety of parasites (≥ 42 species), including protozoans, trematodes, cestodes, nematodes, acanthocephalans, leeches, and crustaceans (Bangham & Hunter 1939; Hoffman 1999; Nelson & Dick 2002; Nelson et al. 2010), but we could not locate any records of parasites in Sand Rollers. Although most of the parasites of Trout-perch infest many North American fishes, at least two are host-specific: the flatworms *Urocleidus baldwini*, which infects the gills, and *Crepidostomus percopsis*, an intestinal parasite (Nelson et al. 1997, 2010; Nelson & Dick 2002). The myxosporean phase of the parasitic protozoan, *Myxobolus intramusculi*, which occurs in striated muscle tissue, also is apparently restricted to the Trout-perch (Cone et al. 1997; Easy et al. 2005). The ecology and biogeography of parasite communities of the Trout-perch were examined in Dauphin Lake, Manitoba, and compared with parasite communities of Trout-perch in eight other areas across the Great Lakes and central Canada (Nelson & Dick 2002). Trout-perch in Dauphin Lake were infected by 14 species of parasites; the regional assessment revealed 42 species. Parasites infected the skin, gill lamellae and arches, muscles, eyes, body cavity, liver, and gut. Average intensity of infection was low for most parasitic species (< 5 individuals/fish), but larval forms of the trematode *Centrovarium lobotes* (vitreous humor and body musculature) averaged > 44 individuals/fish (range 1–175) throughout the summer ($n = 50$ –51 fish), and the adult trematodes *Crepidostomum cooperi* (gut) averaged 78 individuals/fish (range 1–432) in June ($n = 50$). Predictable, nonrandom parasite communities occurred at the local and regional scales. Factors influencing communities were phylogeny (ubiquitous, host-specific parasites), parasites associated with Trout-perch predators (Northern Pike, Walleye, and White Bass); habitat-driven parasites from piscivorous birds using shallow water and from snails in shoreline vegetation; and niche sympatry or resource sharing with darters (Percidae) and Suckers (Catostomidae). Host-behavior links from Trout-perch to the various parasites included schooling (e.g., yielding near homogeneous communities within a population), use of inshore habitats (e.g., acquisition of bird and snail-associated parasites), and feeding (e.g., mayfly associated parasites). In these systems, the Trout-perch serves as key intermediate host for the tapeworms *Triaenophorus*

stizostedionis and *T. crassus*, the nematode *Raphidascaris acus*, and the trematode *Centrovarium lobotes*. These parasites use the Walleye and Northern Pike, primary Trout-perch predators, as hosts.

Other studies also revealed high parasite loads in the Trout-perch. In Heming Lake, Manitoba, 48–64% of fish were parasitized by cysts of the tapeworm *Triaenophorous stizostedionis* in the liver and gonads (Lawler 1954). Intense infections of the protozoan *Myxobolus* spp. occurred in muscle of Trout-perch from heavily polluted Duluth Harbor, Lake Superior, with little evidence of damage to the tissue (Cone et al. 1997; Easy et al. 2005). Diplostomatid eye flukes occurred in the vitreous humor of 44% of 50 young-of-the-year Trout-perch in the St. Lawrence River (Marcogliese & Compagna 1999). Apparently, cataracts did not develop in the eyes, but the parasite load could be heavy enough in some populations in the Great Lakes and elsewhere to cause mortality. The parasite community of Trout-perch in the Athabasca River system, Alberta, Canada, consisted of 14 metazoan taxa, of which five were previously unreported (the digeneans *Hysterozoon* sp., *Ornithodiplostomum* sp., and *Rhipidocotyle* sp., and the larval nematodes *Ichthyobronema hamulatum* and *Raphidascaris acus*). Similarity of parasite communities along the river were correlated with sediment hydrocarbons (alkanes and polycyclic aromatic hydrocarbons) and land use ≤5 km of sampling sites (Blanar et al. 2016).

Among freshwater mussel species the Creek Heel-splitter, *Lasmigona complanata*, and Flutedshell, *Lasmigona costata*, use the Trout-perch as a host according to two unpublished reports (Hove et al. 2014; Marr et al. 2016). However, these mussel species are apparently host generalists infecting and successfully metamorphosing to juveniles on several other non-related fish species.

CONSERVATION

Percopsids are unique to North America both as fossils and as extant representatives. The Sand Roller is endemic to a relatively small area of North America and is restricted to one drainage, the Columbia River. Although regarded as common in the Columbia River mainstem (Wydoski & Whitney 2003) and not considered imperiled nationally (Jelks et al. 2008), the species is ranked as Vulnerable to Apparently Secure in Washington and Possibly Extirpated in Idaho (NatureServe 2012). Precautions are

warranted in shallow streams where flows are regulated to maintain the cover (e.g., undercut banks, submerged tree roots, and other structures) that provides essential habitat during the day for this species (Wydoski & Whitney 2003). Habitat protection is vital for Sand Roller survival in shallow tributaries of the Columbia River. The Sand Roller has apparently declined in the mainstem Willamette River, Oregon. In 1945 the species was distributed over 93 river km. Resurveys located the species at only a single mainstem locality, although the species persists in numbers in tributaries across the basin (Hughes & Gammon 1987; Scheerer & Jacobs 2006).

In most of the northern parts of its range the Trout-perch is Apparently Stable (e.g., Jelks et al. 2008), but on the eastern and southern edges of its range the species appears to be disappearing (Warren et al. 2000). Along the eastern edge of the range the species is considered Extirpated or Presumed Extirpated in Massachusetts, Connecticut, New Jersey, Maryland, and Virginia and is considered Vulnerable in Vermont and New York. Along the southern tier of states, the species is considered Critically Imperiled, Imperiled, or Vulnerable in Montana, South Dakota, Nebraska, Iowa, Missouri, Illinois, Indiana, and Kentucky (NatureServe 2012). The declines happened over the past 50–100 years. For example, the species was last taken in the mid-1960s in the Green River, Kentucky, the southernmost occurrence for the species (Burr & Warren 1986). Despite literally hundreds of collections in the Green River, made during both day and night, no one has captured another Trout-perch from that drainage. Similarly, the records in the 1960s of the Trout-perch from small tributaries of the Ohio River in Oldham and Jefferson counties, Kentucky, are the last of their kind from those streams. In Virginia, the species is on the southern edge of its range in the Potomac River drainage and has not been taken there since 1911 (Jenkins & Burkhead 1994). It also has disappeared from the entire Susquehanna River drainage. In Illinois, the species is gone from the entire Big Muddy River drainage, the last records from that system date to 1939 (Burr et al. 1988). Additionally, few contemporary occurrences are available from the Illinois River, Illinois, where Smith (1979) had a number of records dating to the 1960s. The Trout-perch has disappeared in Missouri from many locations where it occurred 30–50 years ago. In fact, no recent documentation exists for many Missouri populations, and the species is not common anywhere in Missouri. The Trout-perch is likely on the verge of disappearing

from the state (Pflieger 1997). Heavy predation pressure and poor agricultural practices that place emphasis on the use of pesticides for erosion-promoting row crops are blamed for the disappearance of this species on the southern edges of its range (Jenkins & Burkhead 1994; Pflieger 1997). Other abiotic factors such as warmer summer water temperatures associated with climate change or riparian degradation may also have played a role in disappearance.

Populations in some northern lakes also show decreases in abundance. A study in northeastern Lake Ontario based on three different time periods (1970s, 1980s, 1990s) demonstrated a sharp decline in Trout-perch abundance by the 1990s (O’Gorman & Burnett 2001). The decline was attributed to increased predation from Walleyes and Double-Crested Cormorants, and oligotrophication of that part of the lake studied. Similarly, abundance trends for common demersal fishes (>25 m depth) in Michigan waters of Lake Huron indicated no trends in Trout-perch population numbers between 1976–1991, but a 98% decrease in abundance over the period 1994–2006. The causes are likely multiple and complex, but the timing is coincidental with introductions and proliferation of several non-native aquatic species with capabilities to drastically alter the lake ecosystems (e.g., Round Goby, *Neogobius melanostomus*, dreissenid mussels) (Riley et al. 2008; Roseman & Riley 2009). Declines of Trout-perch in Lake St. Clair (Reid & Mandrak 2008 citing Thomas & Haas 2004) and along shallows of the north shore of Lake Erie (Reid & Mandrak 2008) were coincident with proliferation of the Round Goby.

The non-native Ruffe, an invasive Eurasian percid, may compete with Trout-perch and potentially cause population declines in areas of the Great Lakes, in which they co-occur. The Ruffe is now a dominant fish in the St. Louis River estuary of Lake Superior and is spreading across the Great Lakes (Fuller et al. 1999; Fuller & Jacobs 2011) and perhaps beyond. The diet, movement patterns, and sensory capabilities of Ruffe appear to overlap substantially with the Trout-perch. Competition between the two species may be especially high in dark-water habitats (Ogle et al. 1995).

COMMERCIAL IMPORTANCE

Both species are generally too small to be of genuine direct commercial importance, even though both are common food items in the diet of large piscivores (e.g.,

Walleye; Northern Pikeminnows; Lake Trout; see ecology section). They almost certainly are used as bait by local anglers but are rarely sold in bait shops or shipped to other locations for bait purposes. In Manitoba, Trout-perch show up infrequently in the bait fish trade in tubs of frozen or salted minnows (Stewart & Watkinson 2004). Other than occasional, almost experimental use as food by humans, neither species is attributed a particular economic value. McPhail & Lindsey (1970) pointed out that Trout-perch in thermally stratified lakes may serve as nutrient transporters by feeding at night in the shallows and then moving during daylight into deeper water where Lake Trout confined to the cooler depths consume them.

LITERATURE GUIDE

Page & Burr (2011) gave key characters for differentiation of the two species, provide color plates of each, and delineate their geographic ranges. In their *Inland Fishes of Washington*, Wydoski & Whitney (2003) provided the best available summary of the biology of the Sand Roller (Fig. 20.13), including some original observations and data. Excellent



Figure 20.13. Rosa Smith Eigenmann (1858–1947) was the first and most prominent female ichthyologist in North America. She and her husband Carl Eigenmann described about 150 fish species as new to science, many from South America. In 1892, they published a description of *Columbia transmontana*, which we know today as *Percopsis transmontana*, the Sand Roller (courtesy of the ichthyologist photograph collection of Brooks M. Burr).



Figure 20.14. The *Fishes of Wisconsin*, a 1,502-page book, with perhaps the most complete literature review and detail ever written for a North American state or province, was published in 1983 by George C. Becker (1917–2002), a professor from University of Wisconsin–Stevens Point. Becker’s masterful treatment of the 157 species found in his home state is exemplified here by his thorough review of the Trout-perch, *Percopsis omiscomaycus* (courtesy of the ichthyologist photograph collection of Brooks M. Burr).

summaries of Trout-perch natural history are included in several state and regional fish books: Scott & Crossman (1973; Canada); Becker (1983; Wisconsin) (Fig. 20.14); Jenkins & Burkhead (1994; Virginia); and Pflieger (1997; Missouri).

Acknowledgments

We thank A. Commens-Carson and Gayle Henderson for redrawing of figures. Ken Sterling assisted in proofing the chapter. Z. Barnett, M. Bland, A. Commens-Carson, E. McGuire, G. McWhirter, and V. Reithel assisted with proofing of literature cited and other copyediting tasks. M. Bland and A. Commens-Carson assisted in acquiring critical literature. Lance Grande kindly provided a photograph of a fossil percopsid.