

Chapter 19 Esociformes: Esocidae, Pikes, and Umbridae (Mudminnows)

Frank H. McCormick, Terry Grande, Cheryl Theile,
Melvin L. Warren, Jr., J. Andrés López, Mark V. H. Wilson,
Roger A. Tabor, Julian D. Olden, and Lauren M. Kuehne

By blue lake marge, upon whose breast
The water-lilies love to rest,
Lurking beneath those leaves of green
The fierce pike seeks his covert screen,
And thence with sudden plunge and leap,
Swift as a shaft through the air may sweep,
He seizes, rends, and bears away
To hidden lair his struggling prey.

—*Fishing in American Waters* by Genio C. Scott

I saw, dimly,
Once a big pike rush
And small fish fly like splinters . . .

—*Fish* by D. H. Lawrence

The order Esociformes (Pikes and Mudminnows) comprises two families, Esocidae (Pikes) and Umbridae (Mudminnows). The Pikes are a small Holarctic (Northern Hemisphere) family, that includes large, elongate predators with duckbill-like snouts full of sharp teeth. Popular with sport fishers, the largest Pikes fight fiercely on hook and line. As piscivorous, voracious, ambush predators, the Pikes play an important functional role in the trophic ecology and fish assemblage structure of many aquatic systems, especially in northern lakes. Other esocids, such as the Olympic Mudminnow, *Novumbra hubbsi*, and Blackfishes, genus *Dallia*, are interesting because of their tolerance of low dissolved oxygen and pH. The Alaska Blackfish, *Dallia pectoralis*, and the Northern Pike, *Esox lucius*, can also withstand the extremely cold conditions of the Arctic and subarctic waters of Canada, Alaska, and Siberia. The name Esocidae is derived from Linnaeus's (1758) generic name for Pike, *Esox*,

from the Latin word *esox* meaning Pike, which came originally from the Greek *isox* or possibly the Gaelic *eog*, *ehawe* (= salmon) (Boschung & Mayden 2004).

The three members of the Umbridae (genus *Umbra*) are small, secretive species living primarily in vegetated wetlands, sloughs, and ditches; slow-moving creeks and river margins; and off-channel habitats such as oxbows. Occasionally used as baitfish or sporadically popular in the aquarium trade, they are rarely seen except by fishery biologists and ichthyologists sampling such habitats. They can breathe atmospheric oxygen using a modified swim bladder, which allows them to survive in hypoxic (low dissolved oxygen) conditions in the lowland habitats they usually occupy. They also feed and digest food under relatively cold winter temperatures in their northern haunts. The family name is derived from the Latin word for shade or shadow, *umbra*, apparently in reference to the propensity of the group to inhabit darkly stained waters with abundant cover (Scott & Crossman 1973; Etnier & Starnes 1993).

DIVERSITY AND DISTRIBUTION

The number of living species of Esociformes is relatively small (Table 19.1). Worldwide, 14 species are recognized; eight of these are native to North America. All fossil and extant species assigned to this order are restricted to continents in the Northern Hemisphere. Extant esociform species are assigned to four genera: *Esox*, *Novumbra*, *Dallia*, and *Umbra*. All are represented in North America. These four genera are recognized either as one family, the Esocidae (Page & Burr 2011; Campbell et al. 2013; Page et al. 2013) or as two families, Esocidae (including

Table 19.1. Classification of the Mudminnows (Umbridae) and Pikes (Esocidae) based primarily on genetic evidence (López et al. 2000; Grande et al. 2004; Near et al. 2012b, 2013; Betancur-R. et al. 2013ab; Grande et al. 2013). After each genus name the number of extant, recognized species is given in parentheses.

Classification

Order Esociformes

Family Umbridae (Mudminnows)

Genus *Umbra* (3)

Family Esocidae (Pikes)

Subfamily Dallinae (Blackfishes)

Genus *Dallia* (3)

Subfamily Esocinae (Pikes)

Genus *Novumbra* (1)

Genus *Esox* (7)

Subgenus *Esox* (5)

Subgenus *Kenoza* (2)

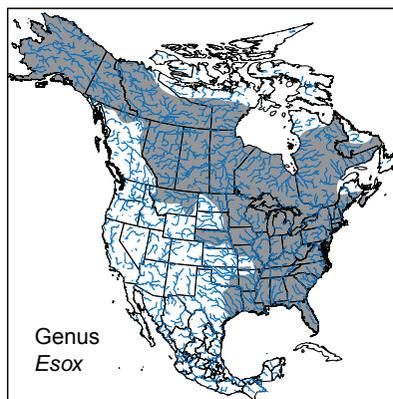


Figure 19.1. Geographic range of *Esox* in North America.



Figure 19.2. Northern Pike, *Esox lucius*, this group in the Yellowknife River, Northwest Territories, has the largest geographic range of any esociform in North America (photograph in May 2012 by and used with permission of © Paul Vecsei / Engbretson Underwater Photography).



Figure 19.3. The Chain Pickerel, *Esox niger*, one of two species in the subgenus *Kenoza*, the other being the Grass Pickerel, *Esox americanus*. *Kenoza* contains the smallest North American Pikes (photographs taken in Nov 2013 by and used with permission of Lance Merry).

Esox, *Novumbra*, and *Dallia*) and Umbridae (including *Umbra*). We adopt the latter approach herein (see phylogenetic relationships section) (López et al. 2000; Grande et al. 2004, 2013; Betancur-R. et al. 2013ab, 2017; Nelson et al. 2016).

Genus *Esox*

The genus *Esox*, the Pikes (and pickerels), is the most diverse and has the widest geographic distribution among esociform genera. Seven living species are currently rec-

ognized in *Esox*; three are endemic to North America, one has a Holarctic distribution (Table 19.1; Fig. 19.1), one is native to Asia, and two are endemic to southern Europe.

The species of *Esox* are divided between the subgenera *Esox* and *Kenoza*. The subgenus *Esox* comprises of the Northern Pike (*Esox lucius*), Holarctic distribution (Fig. 19.2); Muskellunge (or musky), *Esox masquinongy*, endemic to North America; Amur Pike, *Esox reichertii*, of Asia; and Southern Pike, *Esox cisaplinus* = *E. flaviae* and Aquitanian Pike, *Esox aquitanicus*, of southern Europe (Launey et al. 2006; Berra 2007; Bianco & Delmastro 2011; Lucentini et al. 2011; Bianco 2014; Denys et al. 2014; Gandolfi et al. 2015; Nelson et al. 2016). The subgenus *Kenoza* comprises the Chain Pickerel, *Esox niger* (Fig. 19.3), and Grass Pickerel, *Esox americanus* (Fig. 19.4), both of which are endemic to North America. The Grass Pickerel has two subspecies, the Redfin Pickerel, *E. a. americanus*, and the Grass Pickerel, *E. a. vermiculatus* (Page & Burr 2011; Fig. 19.4). The eastern Asian endemic, Amur Pike, and the European endemics, Southern Pike (native to Padano-Veneto, Tuscany and Lazio, Italy, and apparently historically to Lake Geneva, Switzerland, and

France), and Aquitanian Pike (endemic to southwestern France) are the only extant species in the genus that are not native to North America (Bianco & Delmastro 2011; Lucentini et al. 2011; Denys et al. 2014).

The Northern Pike exhibits the widest distribution of any esociform species, occurring at temperate latitudes in Asia, Europe, and North America (Crossman 1996; Berra 2007; see Bianco & Delmastro 2011; Denys et al. 2014). In North America, the native range of the species includes most of Canada except the Maritime Provinces, most of western and southern British Columbia, and the Arctic Archipelago. In the United States, the native range of the Northern Pike includes the northern half of the country (as far south as Missouri) between the Rocky and Appalachian Mountains, a range covering 23 states (Page & Burr 2011). Generally, the Northern Pike is restricted to fresh water, but some European populations regularly enter brackish water and spawn in coastal areas of the Baltic Sea (Scott & Crossman 1973). The present distribution of the species and apparent genetic homogeneity throughout its range probably resulted from a rapid range expansion of some small number of populations, which took place after receding glaciers made habitat available; however,



Plate 19.1. Muskellunge, *Esox masquinongy*.



Figure 19.4. Grass Pickerel, *Esox americanus vermiculatus* (adult, upper, and juvenile, lower), another member of the subgenus *Kenoza* (photographs taken in Kankakee County, Illinois, upper, and Newton County, Indiana, lower, in April 2008 by and used with permission of Uland Thomas).

debate is ongoing over the number and location of the populations of the Northern Pike that survived the glacial maxima and gave rise to living populations (see genetics section).

The other three North American species of *Esox* are more limited in native distribution than the Northern Pike. They are restricted to the Great Lakes, Mississippi River, and Atlantic Coast drainages of central and eastern North America. The Muskellunge (from the Ojibwa word *maashkinoozhe*) is native to the Great Lakes and the upper Mississippi River system from southern Canada to Tennessee. The native range of the Muskellunge is sometimes divided into three geographic regions reflecting variation in color pattern among populations, which may be indicative of incipient taxonomic differentiation. The three regions are Wisconsin, Minnesota, southwestern Ontario, and southeastern Manitoba; Great Lakes and St. Lawrence River; and the Ohio River system (Scott & Crossman 1973) with possibly a fourth variant in the Tennessee and Cumberland Rivers (Etnier & Starnes 1993). The taxonomic status of the color variants prevalent in these regions is the subject of debate (e.g., Hourston 1955; Crossman 1978; Trautman 1981; Etnier & Starnes 1993). Dramatic population declines in much of the Ohio River system (e.g., Cumberland and Tennessee River populations) and introductions and artificial hybridization confound understanding of these variants (Casselman et al. 1986; Etnier & Starnes 1993; Jenkins & Burkhead 1994).

The native range of the two species in the subgenus *Kenoza* (Chain Pickerel and Grass Pickerel) extends south into central Florida and includes the southernmost latitudes naturally inhabited by any esociform. The Chain Pickerel (Fig. 19.3) inhabits Atlantic Coastal Plain drainages from southern Canada to Florida, in the lower reaches of the Mississippi River basin, and Gulf Coast drainages (Page & Burr 2011). The native range of the Grass Pickerel

(Fig. 19.4) includes Atlantic and Gulf Coast drainages as far north as the U.S.–Canadian border (Page & Burr 2011). The two species are morphologically distinct (e.g., *E. americanus*, unlike *E. niger*, exhibits an elongation of the maxillae beyond the midpoint of the eye, and reduction in the number of branchiostegal rays, pelvic-fin rays, and lateral-line scales) (Grande et al. 2004).

Populations of the Grass Pickerel in the Atlantic Coast drainages correspond to the subspecies *E. a. americanus*, Redfin Pickerel, which gradually intergrades with populations of *E. a. vermiculatus*, Grass Pickerel, in the southern part of its range between western Florida and western Mississippi (Crossman 1978). The Mississippi drainage populations consist mostly of Redfin Pickerel. Individuals of both subspecies occur in Coastal Plain drainages of Alabama and Georgia. Morphological analyses (i.e., morphometrics, cardioid scale frequencies) confirm distinctiveness of the two subspecies. In the intergrade zone fish show intermediacy in some characters and tendency to overlap with one subspecies or the other in other characters (Crossman 1966; Reist & Crossman 1987).

Mitochondrial DNA barcoding, using partial sequences of cytochrome *c* oxidase subunit I among geographically dispersed individuals of *E. americanus* revealed two unconfirmed candidate species with genetic divergences of >2% (April et al. 2011). A similar analysis of Canadian populations detected genetic differentiation between *E. a. americanus* from the St. Lawrence River to the east and *E. a. vermiculatus* from the Laurentian Great Lakes farther west (Hubert et al. 2008). DNA barcoding did not detect any unconfirmed candidate species in the Chain Pickerel, but the species did share DNA barcodes with the Grass Pickerel (April et al. 2011; see genetics section); other genetic analyses of these taxa produced similar results (Grande et al. 2004; Hubert et al. 2008).



Figure 19.5. The Olympic Mudminnow, *Novumbra hubbsi*, is the smallest and most range restricted esocid, reaching only about 80 cm TL, and being restricted to the Olympic Peninsula, Washington (photograph taken by and used with permission of Tom Baugh).

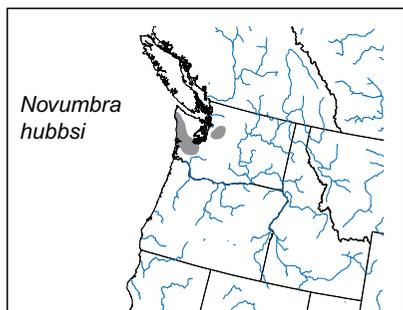


Figure 19.6. Geographic range of the Olympic Mudminnow, *Novumbra hubbsi*.

Genus *Novumbra*

The monotypic genus *Novumbra* includes the Olympic Mudminnow, *Novumbra hubbsi*, (Fig. 19.5), but one fossil species, †*Novumbra oregonensis*, is also assigned to the genus (Cavender 1969). The Olympic Mudminnow is conspicuous as the smallest, most range-restricted species of esocid. It occurs in the Chehalis River drainage, Washington, in direct tributaries of southern Puget Sound, and in lowland habitats of the Olympic Peninsula from North Bay of Grays Harbor to Ozette Lake (Harris 1974). The Olympic Mudminnow distribution reflects the glacial refugia that existed at the margins of the Vashon Glacier during the Pleistocene (1.8–0.01 mya) (Fig. 19.6). Morphological differences among populations suggest limited dispersal since that time (Meldrim 1968). Genetic evidence indicates that Olympic Mudminnow populations in eastern Puget Sound represent undocumented introductions of the species from an unknown location on the southern Olympic Coast (DeHaan et al. 2014). As with other Mudminnow species, the Olympic Mudminnow is strongly associated with shallow, sluggish water bodies, dense vegetation, and fine substrates (Meldrim 1968).

Fossil locations of *Novumbra* suggest bogs, swamps, and freshwater marshes were the preferred habitat since the Oligocene (33.9–23.03 mya) (Schultz 1929, 1930).

Genus *Dallia*

The three currently recognized species of *Dallia* are native to western Alaska and the northeastern Siberian Chukot, although controversy exists over the validity of the two forms restricted to Asia (Mecklenburg et al. 2002; Campbell & López 2014). The Alaska Blackfish, (can'giiq in the Yup'ik language) (Fig. 19.7), is the only member of the genus occurring in North America (Fig. 19.8). The complete geographic range of *D. pectoralis* covers the northeastern portion of the Chukotsky (Chukchi) Peninsula in Asia to the coastal areas of the Bristol Gulf in the far northeast of Russia, the coastal plains of the Arctic and Bering Sea drainages of western Alaska, and St. Lawrence, St. Matthew, and Nunivak Islands in the Bering Sea. The two other species in the genus, the Palkhykay Blackfish, *Dallia delicatissima*, and the Amguema Blackfish, *Dallia admirabilis*, are endemic to the northern coastal drainages of the Chukotka Peninsula, Amguyema River drainage, in far northeastern Siberia (Chereshnev & Balushkin 1981; Gudkov 1998).

From a zoogeographic perspective, the genus is unique among strictly freshwater fishes in being restricted to the Beringia Ice Age refugium. The distribution of the Alaska Blackfish is mysteriously circumscribed without evident barriers to its post-glacial dispersal along Arctic Coastal lowlands (toward the Mackenzie or Kolyna Rivers) or upstream in the Yukon River beyond its present limit near Fairbanks (Lindsey & McPhail 1986). Differences in chromosome numbers between populations of the Alaska Blackfish from



Figure 19.7. Male Alaska Blackfish, *Dallia pectoralis*, about 203 mm TL, captured from ditches near the vicinity of Anchorage, Alaska, by K. Stoops in 1982 (courtesy of John Brill).

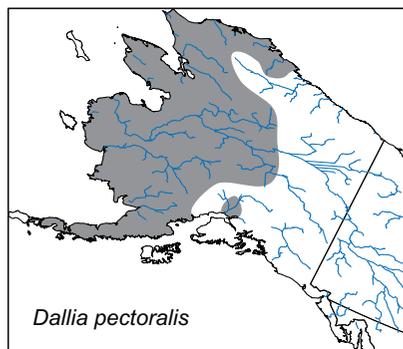


Figure 19.8. Geographic range of the Alaska Blackfish, *Dallia pectoralis*, in North America, including an introduced population near Anchorage, Alaska.

the Yukon and Colville River drainages and genetic structure revealed by mitochondrial DNA analyses suggest the presence of undescribed taxonomic units (see genetics section) (Crossman & Ráb 1996; Campbell & Lopez 2014).

Genus *Umbra*

The genus *Umbra* includes three extant species of Mudminnows; of these, two are endemic to North America (Fig. 19.9) and one to Europe (European Mudminnow, *Umbra krameri*). The Central Mudminnow, *Umbra limi* (Fig. 19.10), inhabits the Great Lakes region, Hudson Bay, the upper and middle Mississippi River drainage, mostly northern tributaries of the Ohio River, and sparsely occurs in the Missouri River drainage, Iowa, South Dakota, and Missouri. The Eastern Mudminnow, *Umbra pyg-*

maea (Fig. 19.11), occurs in Atlantic Coast drainages from New York to South Carolina (Page & Burr 2011). Problematic specimens of *Umbra pygmaea* from south of Okefenokee Swamp in Baker County, Florida, have higher dorsal- and anal-fin ray counts than either *U. pygmaea* or *U. limi* (Laerm & Freeman 2008).

Esociforms as Non-natives

The native distribution of species of *Esox* has been altered as a result of introduction and extirpation. The Northern Pike and Muskellunge are introduced extensively outside of their natural ranges because of their value to recre-

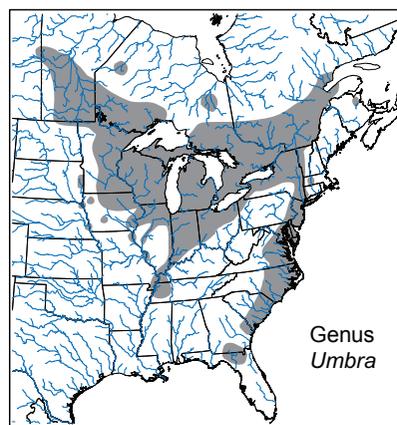


Figure 19.9. Geographic range of *Umbra* in North America.



Figure 19.10. Male (upper) and female (lower) Central Mudminnows, *Umbra limi*, during the breeding season (photographs taken April 2008, Kankakee County, Illinois, by and used with permission of Uland Thomas).



Figure 19.11. Adult female Eastern Mudminnow, *Umbra pygmaea* (60 mm SL), from Sussex County, Coppahaunk Swamp, Virginia, July 1984 (courtesy of N. Burkhead and R. Jenkins and courtesy of Virginia Division of Game and Inland Fisheries).

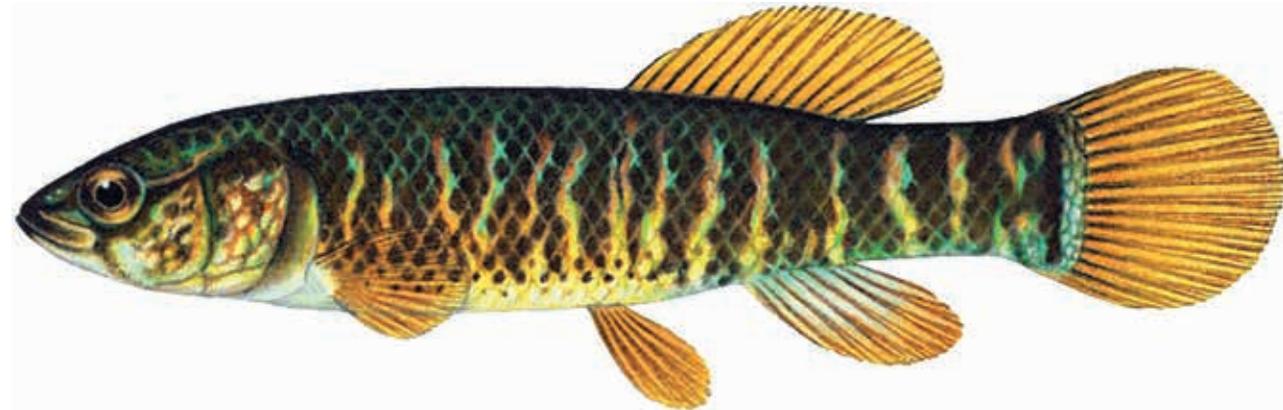


Plate 19.2. Central Mudminnow, *Umbra limi*.

ational anglers. Government-funded stocking programs maintain populations of these two species in water bodies where they did not occur naturally or from which native populations are extirpated or are in decline (e.g., Simonson 2003). In the United States, Northern Pike are introduced in 20 states and Muskellunge in 16 states outside of their natural distributions. The combined result of legal and illegal introductions is the presence of self-sustaining populations of all four North American species of *Esox* outside of their natural range (Fuller et al. 1999). The Asian-native Amur Pike was stocked in central Pennsylvania between 1968 and 1971, but its status is uncertain (Fuller et al. 1999). Cooper (1983) reported Amur Pike as established; however, Robins et al. (1991) considered them as not established.

Introductions of top piscivores, such as the Northern Pike and Muskellunge, affect native fish assemblages and trophic relationships in aquatic ecosystems (Persson et al. 1996; Findlay et al. 2005; Eby et al. 2006). For example, introduced Northern Pike dramatically reduced native minnow (Cyprinidae, Carps and Minnows) richness in Adirondack lakes (Findlay et al. 2000) and reduced the abundance of native salmonids in Flathead Lake, Montana (Muhlfeld et al. 2008). Northern Pike replaced Arctic Char, *Salvelinus alpinus* (Trouts, Salmons, and White-

fishes, Salmonidae), as the top predator in a subarctic lake in northern Sweden and produced strong cascading effects on both prey abundance and trophic structure (Bystrom et al. 2007).

State and federal programs have undertaken vigorous control programs for the Northern Pike, which include penalties for illegal introduction, monitoring, and active removal to protect native and recreationally and commercially important fishes. The Upper Colorado River Endangered Fish Recovery Program includes an eradication program for Northern Pike in an attempt to reduce their impact on native minnows and Suckers (Catostomidae) (USFWS 2008; Zelasko et al. 2016). The state of Washington similarly regards the Northern Pike as an invasive species in the Pend Oreille and Spokane Rivers, Columbia River drainage, and of grave concern to fisheries management agencies throughout the Pacific Northwest. Predation by non-native Northern Pike in that region has contributed to reduced recruitment in adfluvial Westslope Cutthroat Trout, *Oncorhynchus clarkia lewisi*, in Coeur d'Alene Lake, Idaho, and declines in Cutthroat Trout populations across much of the Pacific Northwest (Muhlfeld et al. 2008; Walrath et al. 2015). The Alaska Department of Fish and Game identifies Northern Pike as an invasive species in south central Alaska. In that region the species is decimating native

populations of Pacific salmon, *Oncorhynchus* spp., poses an economic threat to recreational and subsistence fishing, has resulted in the extirpation of Coho Salmon, *Oncorhynchus kisutch*, Rainbow Trout, *O. mykiss*, and Arctic Grayling, *Thymallus arcticus* (Salmonidae), from lakes in the Susitna River drainage, and has caused declines in Suckers (Catosomidae) and whitefishes (*Coregonus* spp., Salmonidae) (ADFG 2002; Southcentral Alaska Northern Pike Control Committee 2007; Sepulveda et al. 2013, 2015).

Several western states have begun introducing the hybrid tiger muskellunge (Northern Pike, *Esox lucius* × Muskellunge, *E. masquinongy*) into aquatic systems to ostensibly control perceived nuisance species (e.g., Northern Pikeminnow, *Ptychocheilus oregonensis*, in some reservoirs in western Washington) and overabundant nongame fishes to aid in establishing a recreational fishery. The use of the tiger muskellunge as biological control agents to benefit sport fish populations, however, may be counterproductive to management goals. Stable isotope analyses in Colorado reservoirs where tiger muskellunge were stocked indicated that it primarily consumed stocked salmonids (53–84% by mass) (Lepak et al. 2014).

Other species of umbrids and esocids also occur outside their native ranges. Olympic Mudminnow populations in several drainages east of Puget Sound are apparently the result of introductions (Mongillo & Hallock 1999; DeHaan et al. 2014). Introduced populations of the Alaska Blackfish thrive in lakes near Anchorage, Alaska, where it creates a serious problem in the management of the Rainbow Trout, *Oncorhynchus mykiss*, fishery, and on St. Paul Island in the Pribilofs (Morrow 1980; Lindsey & McPhail 1986; Fuller et al. 1999).

Several populations of the Eastern Mudminnow are established in Europe, likely resulting from the release of aquarium specimens (Fuller et al. 1999; Verreycken et al. 2007). Although introduced in the early 1900s, the Eastern Mudminnow is currently found in only six European countries: Belgium, Denmark, France, Germany, Poland, and The Netherlands. Assessments of invasive potential vary, but Verreycken et al. (2010) ascribed low to medium risk of invasiveness to Eastern Mudminnows. However, Copp et al. (2009) applied the Fish Invasiveness Scoring Kit (FISK) analysis to 67 fish species including the Eastern Mudminnow and determined it was a high-risk species for the United Kingdom. In North America, accidental release of laboratory specimens gave rise to a self-sustaining population of the Central Mudminnow in the Connecticut River system, Connecticut and Massachusetts (Fuller et al. 1999; Hartel et al. 2002). Introductions

are also documented in Montana, Oklahoma, and Texas (Fuller et al. 1999). The Central Mudminnow has dispersed into Atlantic Slope drainages, New York, presumably via the old Erie Canal and has expanded its range along the Mohawk River watershed from Fort Hunter to the Hudson River (Smith 1985; Daniels 2001; Waldman et al. 2006) where it appears to be hybridizing with the Eastern Mudminnow (Schmidt & Daniels 2006). It has recently been reported from the Saint John River near Edmundston, New Brunswick, presumably as a result of a bait bucket transfer by fishermen (Curry et al. 2018).

PHYLOGENETIC RELATIONSHIPS

Early Views of Esociform Relationships

The position of esociforms among the classification of fishes has undergone many changes. At the onset of formal classification schemes, Linnaeus accepted Peter Artedi's work on fishes in which the only esociform recognized at the time, *Esox lucius*, was placed among the malacopterygians (fishes with soft fins). Much later, the genera *Esox* and *Umbra* were grouped in the order Haplomi, which was thought to have close affinities to the orders Isospondyli and Cyprinodontes of the superorder Teleostei. In the original description of *Dallia pectoralis*, Bean (1880) provisionally placed the species with *Umbra* in the family Umbridae of haplamous fishes. Distinct features of the anatomy of the pectoral girdle and maxillary skeleton in *Dallia* led Gill (1885) to place the genus in its own order, Xenomi. Schultz (1929) in the description of *Novumbra hubbsi*, erected a new family, Novumbridae, as part of the Haplomi related to Umbridae and Dalliidae. Gill's evidence in support of Xenomi was later reinterpreted and eventually *Dallia*, *Novumbra*, and *Umbra* were grouped in the family Umbridae (Berg 1931). Chapman (1934) proposed an alternative arrangement of haplamous fishes in which *Novumbra*, *Umbra*, and *Dallia* were each placed in its own family. Gradually, the order Haplomi, which also included *Esox*, was replaced by either the suborder Esocoidei or the order Esociformes without changes in membership. Berg (1948) placed the Esocoidei in the order Clupeiformes, which he recognized as an artificial assemblage. In his classification, Esocoidei contained the families Dalliidae (*Dallia*), Umbridae (*Novumbra* and *Umbra*), and Esocidae (*Esox*). In mid-20th century classifications, esociforms were recognized as a basal lineage of the higher Division III teleosts beginning with the seminal work of Greenwood et al. (1966), who placed esociforms in

the Protacanthopterygii with groups such as argentinids (Herring Smelts), salmonids, and osmerids (Smelts).

Esociform Interordinal Relationships

Into the late 20th century the relationships of the order continued to be debated (summaries by Nelson 2006; Nelson et al. 2016). Some considered esociforms to be a primitive sister-group to osmeriforms (Freshwater Smelts) + salmoniforms (Trouts, Salmon, and Whitefishes). Others viewed them as the primitive sister-group to the euteleosts (Fink & Weitzman 1982; Lauder & Liem 1983; Fink 1984). A morphological study of lower euteleostean relationships supported placement of esociforms as the closest relatives of the Neoteleostei based on four synapomorphic (shared, derived) characters, including Type 4 tooth attachment, acellular skeleton, loss of the third uroneural (a bone in the caudal skeleton), and scaling of the cheek and operculum (Johnson & Patterson 1996). In contrast, Williams (1987) considered osmeroids and argentinoids (Marine Smelts) as the primitive sister-group of the neoteleosts and suggested salmonids and esocoids were closest relatives (see also Arratia 1997, 1999; Wilson & Williams 2010) and more primitive than osmeroids and other higher forms. Reaching agreement on the lineage among basal euteleosts closest to Esociformes proved to be difficult. Morphologically based phylogenetic studies of relationships among the basal lineages of the Euteleostei did not lead to a consensus view on the placement of esociforms perhaps because of a scarcity of shared, derived morphological traits between this group and other basal euteleost lineages (e.g., Rosen 1974).

Sister-group to the Esociforms

DNA sequence-based studies that included representative esociforms and salmonids agree among themselves in placing these two groups as closest relatives. The sister relationship of esociforms and salmoniforms was morphologically supported earlier by evidence from the suspensorium (cartilage and bone supporting lower jaw) and associated musculature, including presence of an anteroventral wing of the hyomandibular bone that overlaps the metapterygoid and by loss of the supramaxillary ligament in both groups (Williams 1987). In sequence-based studies, the salmonids and esociforms are resolved consistently as a strongly supported sister pair by multiple lines of evidence (summarized by Zaragüeta-Bagils et al. 2002; mitochondrial genome: Ishiguro et al. 2003; Li et al. 2010; Campbell et al. 2013; nuclear sequence data: López et al. 2004; Santini et al. 2009;

combined mitochondrial and nuclear data: López et al. 2004; Burrige et al. 2012), some of which used broad taxon sampling and numbers of nuclear genes (Near et al. 2012b, 2013; Betancur-R. et al. 2013ab, 2017). However, unlike the strong support for a salmoniform-esociform clade, the position of this clade among other groups of teleosts is less certain. The salmoniform-esociform clade is resolved with the Argentiniformes (Near et al. 2012b, 2013) or with poor support closest to the Galaxiidae (Galaxids) (minus *Lepidogalaxias*) with the argentiniforms basal to these two clades (Betancur-R. et al. 2013ab, 2017). Complete mitogenomic analyses yielded a fossil-calibrated divergence time between esociforms and salmoniforms in the Early Cretaceous (113.02 mya, 96.34–134.11 mya highest probability density) (Campbell et al. 2013), although these dates should be interpreted cautiously because no fossils of either group are available before the early Campanian (Late Cretaceous; about 84 mya) (Wilson et al. 1992; Grande 1999).

Esociform Intraordinal Relationships

In the past, two esociform families were recognized: Esocidae containing only *Esox*, and Umbridae containing *Dallia*, *Novumbra*, and *Umbra*. This classification neatly divided the larger, piscivorous esocids from the smaller umbrids and seemed to explain the evolution of their different body forms parsimoniously. Cavender (1969) examined umbrid osteology, finding evidence to support a close relationship between *Dallia* and *Novumbra* (Fig. 19.12A) (e.g., an elongation of the subopercle, presence of a single row of well-developed incurved teeth on the dentary, presence of a crescent ridge of bone on the posterior part of each frontal forming the anterior limit of the posttemporal fossa) but also found characters to unite *Umbra* and

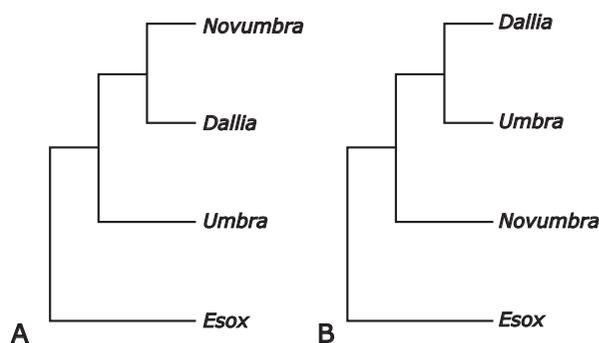


Figure 19.12. Historically proposed hypotheses of relationships among genera within Pikes (Esocidae) and Mudminnows (Umbridae): (A) Cavender (1969); (B) Nelson (1972) (redrawn from López et al. 2000).

Novumbra (e.g., presence of an inframandibular bone, presence of a transverse process on vertebra one with a ligamentous connection to the cleithrum). In a cladistic study based on characters of the cephalic (head) sensory system, Nelson (1972) cited evidence that supported uniting *Novumbra*, *Dallia*, and *Umbra*, which were at that time in Umbridae (e.g., reduction or loss of the mandibular, jaw, sensory canal), placing *Novumbra* as the most basal of the three umbrid genera based on loss of the infraorbital and extrascapular (dorsal posterior head) canals in *Dallia* and *Umbra* (Fig. 19.12B) and supporting division of *Esox* into the subgenera *Esox* for the Pikes (including the Muskellunge) and *Kenoza* for the pickerels. In *Kenoza*, for example, the infraorbital canal is discontinuous and the extrascapular canal is lost. In a broad study of the salmoniforms, Rosen (1974) discovered characters of the axial skeleton (skull and vertebral column) (e.g., reduced height of the fourth epibranchial and loss of the fifth epibranchial, epurals reduced to one, a full neural spine on preural centrum one, and an anteriorly foreshortened uroneural) supporting a *Dallia* + *Novumbra* clade as sister to *Esox* with this group being sister to *Umbra*. Further evidence from osteological traits (Wilson & Veilleux 1982) supported Nelson's (1972) hypothesis of umbrid relationships. López et al. (2000), however, later critiqued the morphological evidence as being mostly based on skeletal reduction, a process that could happen convergently or as expressed in a mosaic fashion in the taxa in question. Their mitochondrial DNA sequence evidence suggested the following relationships: *Umbra* (*Dallia* (*Novumbra* + *Esox*)). López et al. (2004) provided additional molecular support for that view. A morphological and molecular cladistic analysis of the species of *Esox* using *Novumbra* and *Umbra* as outgroups, found 38 synapomorphies, which supported the following set of interrelationships: (*Esox masquinongy* (*E. lucius* + *E. reicherti*) + (*E. niger* + *E. americanus*)) (Grande et al. 2004). Monophyly of the genus *Esox* was supported by the presence of a posttemporal canal; the anterior part of the palatine articulating with the premaxilla forming a toothed biting surface; the mandibular length being >50% of the head length; a process on the anterolateral margin of the palatine that articulates with the maxilla; the presence of depressible teeth on the dentary, vomer, and palatine; the presence of toothplates on basibranchials one and two; expansion of the anterior supraneural; and the presence of notched or cardioid (heart-shaped) scales along the lateral line. The monophyly of the subgenus *Esox* was supported by eight derived character states, including a continuous and complete infraorbital canal, a vomer length <50% of

the parasphenoid length, number of abdominal vertebrae 39–48, caudal vertebrae 17–21, and the presence of three epurals. The subgenus *Kenoza* was diagnosed by 12 derived character states, including the presence of four mandibular canal pores, a discontinuous infraorbital canal, a vomerine tooth patch <50% of the vomer length and consisting of small teeth and with only a few teeth along the neck of the vomer, a close connection between epicentral and epineural intermuscular bones, an expansion of the second neural arch in the transverse plane, two epurals in the caudal skeleton, and the presence of cardioid scales between the pelvic fins. Denys et al. (2014), using partial mtDNA sequences, investigated the relationships of the two recently named European species of Pikes. They concluded that *Esox cisalpinus* and *E. flaviae* are more closely related to *E. lucius* than to any other species of *Esox*.

Molecular evidence also strongly supports the subgenera *Esox* and *Kenoza* as monophyletic (Grande et al. 2004; López et al. 2004) in agreement with the morphological evidence of Grande et al. (2004) cited above. Evidence from gene sequences also supports a sister relationship between *Novumbra* and a monophyletic *Esox* (López et al. 2000, 2004; Campbell et al. 2013; Near et al. 2012b, 2013; see Betancur-R. et al. 2013ab, 2017; Fig. 19.13). Complete mitogenomic analyses yielded a fossil-calibrated divergence time between the two genera at the Paleocene-Eocene boundary (56.31 mya, 48.48–64.44 mya highest probability density) (Campbell et al. 2013); however, this is after the first appearance of *Esox* in the fossil record 66–59 mya (Wilson 1980, 1984). The clade *Esox* + *Novumbra* is resolved as sister

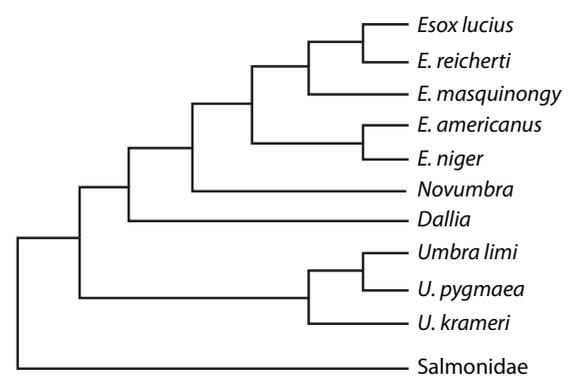


Figure 19.13. Phylogeny of species of the Pikes (Esocidae: *Esox*, *Novumbra*, *Dallia*), and Mudminnows (Umbridae: *Umbra*) including the sister family to these two clades, the Trouts and Salmon (Salmonidae), as resolved from extensive taxon sampling and analyses of multiple nuclear and mitochondrial gene sequences (modified from López et al. 2000, 2004; Grande et al. 2004; Near et al. 2012b, 2013; Betancur-R. et al. 2013ab).

to *Dallia*, leaving a monophyletic *Umbra* as the most basal extant esociform lineage and the only member of its family. The mean divergence estimate between *Umbra* and the other two genera is 88.61 mya (Late Cretaceous). We follow Nelson et al. (2016) using the best available evidence and recognize Umbridae as containing only the genus *Umbra* and place the remaining genera (*Dallia*, *Novumbra*, and *Esox*) in the family Esocidae (Table 19.1; Fig. 19.13).

FOSSIL RECORD

The oldest fossils assigned to the Esociformes lived in the Late Cretaceous in Western North America beginning with fossils from the Campanian (84–72 mya) (Wilson et al. 1992; see also the review of fossil Esocidae by Grande 1999). The Cretaceous fossils consist of palatine and dentary bones with distinctive C-shaped tooth bases on their tooth-bearing surfaces. The shape and orientation of the tooth bases are diagnostic of a particular type of depressible teeth (teeth that fold back toward the throat) seen, among extant fishes, only in the modern genus *Esox* (Cavender et al. 1970; Wilson et al. 1992). All of the Cretaceous esociform fossil remains come from small fishes about the size of living species of Mudminnows. Wilson et al. (1992) erected two genera for the pre-Cenozoic (>66 mya) esociform fossils: †*Estesox* and †*Oldmanesox*. †*Estesox* is the more abundant and more ancient of the two with fossils as old as early Campanian (about 83.6–72.1 mya); its jaws and palatines had only depressible teeth. †*Oldmanesox* had jaws with depressible and fixed canine teeth as in the extant and fossil members of *Esox*. As in all species of *Esox*, the depressible teeth on the lower jaw are located near the front of the mouth, and the fixed canine teeth are farther back, closer to the angle of the jaws (Wilson et al. 1992). Extant *Umbra*, *Novumbra*, and *Dallia* have neither depressible teeth nor fixed canine teeth similar to those of *Esox* (Wilson & Veilleux 1982). Thus, the fixed teeth of *Esox* possibly evolved from depressible teeth by secondary loss of the depression mechanism coupled with enlargement of the teeth. If this is correct, the Cretaceous †*Oldmanesox* may well be more closely related to *Esox* than it is to *Novumbra*, *Dallia*, or *Umbra*. The earliest fossils assigned to an extant esociform genus were discovered in deposits of mid-Paleocene age (66–59 mya) in Alberta, Canada. From these deposits Wilson (1980, 1984) described †*Esox tiemani*, based on one well-preserved and nearly complete fossilized skeleton and about a dozen partial skeletons of different sizes;

these display many of the characteristics that identify extant species of *Esox*, including the duckbill-like snout, depressible teeth and fixed canine teeth, the elongate body with posteriorly situated dorsal and anal fins, and the distinctive, tri-lobed body scales (Wilson 1980). Another noteworthy extinct species assigned to this genus is †*Esox kronneri*, which was described from a single fossil in good condition from the Green River Formation and dating to the early Eocene (about 52–50 mya) (Grande 1999; Fig. 19.14). The significance of †*E. kronneri* is due in part to its hypothesized close relationship to the subgenus *Kenoza*. Characters placing †*E. kronneri* in *Kenoza* include a smaller number of vertebrae and having only two epurals in the caudal skeleton (Grande 1999). If it indeed belongs in *Kenoza*, the fossil is evidence for an ancient divergence between the two subgenera of *Esox* (>50 mya).

Abundant fossils of *Esox* are known from the Oligocene to the Pleistocene occurring throughout the Holarctic (reviewed by Grande 1999). Notably, a fossil of a Pike from the Miocene of Oregon (23.0–5.33 mya) (Cavender et al. 1970) had fixed canine teeth as well as depressible teeth on its palatine bones, a characteristic of the extant Muskellunge. Another fossil relative of the Muskellunge is †*E. columbianus* from the Pliocene (5.3–2.6 mya) of southern Washington, which also had fixed canines on its palatines and vomer (Smith et al. 2000). This rich fossil record has the potential to inform our understanding of the biogeographical factors influencing the distribution of the living members of the genus once the relationships among the fossil and living forms are better understood.



Figure 19.14. Holotype of †*Esox kronneri* (118 mm TL; FMNH PF14918) from the Fossil Butte Member of the Green River Formation (early Eocene, about 52 mya), the only known specimen of an esociform from the fish-fossil rich Green River Formation. Although small, the specimen is one of the best-preserved fossil esociforms ever found (from Grande, Lance, 2013. *The Lost World of Fossil Lake: Snapshots from Deep Time*. University of Chicago Press, 425 pp.) (courtesy Lance Grande.)

A new species from the early Pleistocene of the Ukraine, †*Esox nogaicus*, has a massive dentary with deep symphysis (fibrocartilaginous fusion between two bones) and the possible presence of a pair of fixed canine-like teeth near the anterior end of the vomer. Such canine teeth are also seen in a few species known only from North America, the extant Muskellunge, the fossil species †*E. columbianus*, and an unnamed Miocene form (Grande et al. 2017). Fixed canines also occur anteriorly on the palatines in the three North American species.

In contrast to *Esox*, the other extant esociform genera are poorly represented in the fossil record. †*Novumbra oregonensis* from middle Oligocene deposits (about 31.1 mya) of the John Day Formation of Oregon is the sole fossil species presently assigned to *Novumbra* (Cavender 1969, 1986). Similarly, a single fossil consisting of a partial skeleton from late Miocene deposits (about 7.2 mya) in the Kenai Peninsula, Alaska, is assigned to the genus *Dallia*. Lastly, otoliths assigned to *Umbra* from Oligocene (33.9–23 mya) and Pliocene (5.3–2.6 mya) deposits in Europe form part of the fossil record of this genus. Additional Paleocene through Oligocene (66–23 mya) esociform fossils from Europe (e.g., Sytchevskaya 1976; Gaudant 2012) are potentially important for future understanding of the origins and radiation of this order. Fossils with combinations of derived and primitive traits not seen in living forms are potentially informative in the development of evolutionary hypotheses. Apart from Cretaceous material (Wilson et al. 1992), several extinct esociform genera are thought to represent transitional forms or intermediate lineages between extant esociform genera. Gaudant (2012) reviewed European fossil umbrids and included †*Boltyschia* from the early late Paleocene (58 mya) of Ukraine, †*Palaeoesox* from the Eocene (56.0–33.9 mya) and Oligocene (33.9–23.0 mya) of Germany and Switzerland, and †*Umbra prochazkai* from the Oligocene of the Czech Republic. These were all placed within the Umbriidae as currently conceived (i.e., closer to *Umbra* than to other esociforms). †*Boltyschia* has a combination of characters seen in umbrids (e.g., several rows of small teeth on the dentary and premaxillary) and esocids (e.g., a narrower frontal, a face bone); even so, Gaudant (2012) suggested that it is a primitive umbrid.

†*Palaeoesox fritzchei*, described from middle Eocene deposits (about 45 mya) of Geiseltal, Germany, has proven particularly difficult to classify. Until the description of more ancient fossils of *Esox*, †*P. fritzchei* was thought to represent a close relative of the stem lineage of *Esox*. Others placed it among the umbrids (Cavender 1969; Nelson 1972; Gaudant 2012).

†*Proumbra* is another extinct esociform genus displaying combinations of traits not observed in living members (Sytchevskaya 1968; Gaudant 2012). The genus was described from fossils dating to the late Oligocene of western Siberia, and its affinities are the subject of debate. The genus was proposed as a close ally of the lineage leading to *Dallia* or of the lineage leading to *Umbra*, although Gaudant (2012) suggested †*Proumbra* is intermediate between †*Palaeoesox* and the most primitive species of *Umbra*.

MORPHOLOGY

External Morphology

All esociform fishes are characterized by the placement of the dorsal fin far back on the body opposite the anal fin (Figs. 19.2–19.5, 19.7, 19.10, 19.11, and 19.14). The bodies of esociforms are elongate with a round to oval cross section. The caudal peduncle is robust, and the caudal fin ranges in shape from rounded (i.e., *Dallia*, *Umbra*; Figs. 19.7, 19.10, and 19.11; Table 19.2) to truncate (i.e., *Novumbra*; Fig. 19.5) to forked (i.e., *Esox*; Figs. 19.2–19.4). The pelvic fins are abdominal in position, but poorly developed in Alaska Blackfish (Fig. 19.7). The pectoral fins originate ventrally immediately behind the opercular opening. A well-developed fleshy base supports large, rounded pectoral fins in the Alaska Blackfish (Fig. 19.7). In all esociforms, both paired and median fins are without spines. Members of *Esox* stand out by their flattened, elongated snouts that resemble a duck's bill (Figs. 19.2–19.4 and 19.15). Other esociform species have robust, rounded to square heads, and terminal mouths (Figs. 19.5, 19.7, 19.10, and 19.11). *Esox* spp. possess a complete, straight lateral line (weakly developed in the Muskellunge); the lateral line is inconspicuous in *Dallia*, incomplete or lacking in the Eastern Mudminnow, and lacking in *Novumbra* and the Central Mudminnow (Page & Burr 2011; Table 19.2). Although lacking a lateral line per se, the Central Mudminnow has an elaborate development of superficial neuromasts on the head and body. Notably, groups of 3–18 vertically and horizontally alternating neuromasts occur along the sides in the position of the lateral line and elsewhere on the trunk (Fig. 19.16) and head (see sensory morphology and biology subsection, this section). The body and head of esociforms are covered with cycloid scales. The cycloid scales of *Dallia* and *Novumbra* resemble those of *Esox* in size; the scales in *Umbra* are large (i.e., relatively low scale counts) (Table 19.2). Species of *Esox* have distinctive tri-lobed body scales (Casselman et al.



Figure 19.15. Close-up of the head of the Grass Pickerel, *Esox americanus vermiculatus*, emphasizing the duckbill-like snout and relatively large mouth that characterizes all members of *Esox*. The individual was in Lake Tomahawk, Oneida County, Wisconsin (photograph in July by and used with permission of © Eric Engbretson / Engbretson Underwater Photography).

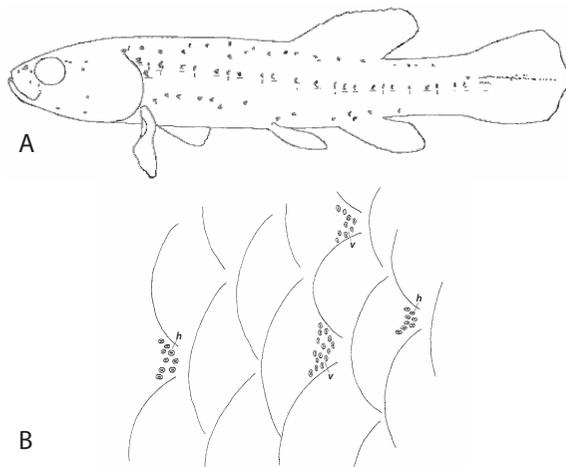


Figure 19.16. (A) Distribution of groups of neuromasts along the sides and back of the Central Mudminnow, *Umbra limi*. Although the lateral line canal is lacking, note the groups (about 23–26) of 3–18 superficial neuromasts extending from the upper angle of the gill cleft to the caudal fin and then extending in two rows onto the caudal fin (one short and one long extending to the end of the fin). (B) Close-up of groups of oval-shaped neuromasts along the sides with groups aligned vertically (v) and horizontally (h). In laboratory experiments, enucleated individuals (eyes removed) conditioned to food responded to water currents ≥ 1.6 mm/s, including orientation to surface waves, apparently using at least in part the elaborate system of neuromasts to detect the currents (Schwartz & Hasler 1966) (redrawn from Schwartz & Hasler 1966).

1986) and modified (cardiform or cardioid) scales with notched posterior margins (Fig. 19.17). Notched scales are randomly scattered and intermixed with tri-lobed cycloid scales along the lateral line in all *Esox* species. In the Grass Pickerel, the notched scales are more numerous and far outnumber the typical lateral-line scales. Notched scales positioned between the pelvic fins occur in all species of *Kenoza*, but are absent in the subgenus *Esox* and *Umbra* (Grande et al. 2004). The Redfin Pickerel has the

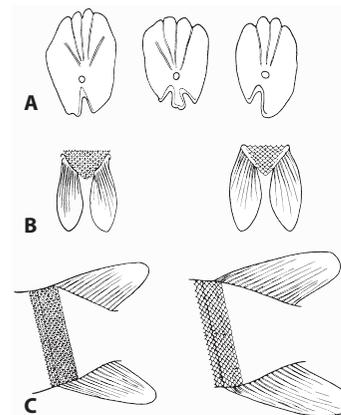


Figure 19.17. Some of the cycloid scales of Pikés (Esocidae; genus *Esox*) are (A) singly or doubly notched at the posterior margin (cardioid scales) or are tri-lobed (not shown). The relative numbers of cardioid scales (B) between the pelvic fins and (C) along the sides (dorsal to anal fin origin) are used to separate the Redfin Pickerel, *Esox americanus americanus* (more smaller scales, left), and Grass Pickerel, *E. a. vermiculatus* (fewer larger scales, right) (redrawn from Crossman 1966).

highest number of notched scales between the pelvic fins (Fig. 19.17), possibly being correlated with the numerous notched scales on the body. The higher number of notched scales on the body and the higher number of lateral-line scales of the Redfin Pickerel differentiates this subspecies from the Grass Pickerel (Crossman 1966; Grande et al. 2004).

Pigmentation

The pigmentation patterns of esociforms are varied and include mottling (Alaska Blackfish; Fig. 19.7), vertical bars (Olympic Mudminnow; Fig. 19.5), horizontal bars (Eastern Mudminnow; Fig. 19.11), spots (Northern Pike;

Table 19.2. Morphological comparison of Pikes, Esocidae, and Mudminnows, Umbridae (Esociformes) (from Crossman 1996).

| | <i>Dallia pectoralis</i> | <i>Novumbra hubbsi</i> | <i>Esoc lucius</i> | <i>Esoc masquinongy</i> | <i>Esoc a. americanus/ a. vermiculatus</i> | <i>Esoc niger</i> | <i>Umbr limi</i> | <i>Umbr pygmaea</i> |
|------------------------------|---------------------------|------------------------|--------------------|-------------------------|--|-------------------|------------------|---------------------|
| Dorsal-fin spines; soft rays | 0; 10-14 | 0; 12-15 | 0; 17-25 | 0; 15-19 | 0; 13-21 0; 14-17 | 0; 14-15 | 0; 13-17 | 0; 14-15 |
| Anal-fin spines; soft rays | 0; 12-16 | 0; 10-13 | 0; 10-22 | 0; 14-16 | 0; 13-18 0; 13-15 | 0; 11-13 | 0; 7-10 | 0; 8-11 |
| Caudal fin | Rounded | Truncated | Forked | Forked | Forked | Forked | Rounded | Rounded |
| Vertebrae | 40-42 | 37-38 | 57-65 | 64-66 | 42-51 42-47 | 52-54 | 35-37 | |
| Lateral series scales | 76-100 | 52-58 | 105-148 | 132-167 | 93-124 97-118 | 117-135 | 30-37 | 28-35 |
| Pored lateral-line scales | Present but inconspicuous | Absent | 55-65 | Weakly developed | Present | Present | Absent | 0-7 |
| Pectoral spines; soft rays | 0; 32-36 | 0; 18-25 | 0; 14-17 | 0; 14-19 | 0; 8-18 0; 14-15 | 0; 12-15 | 0; 11-16 | 0; 12-16 |
| Pelvic spines; soft rays | 0; 2-3 | 0; 6-7 | 0; 9-11 | 0; 11-12 | 0; 8-11 0; 9-10 | 0; 9-10 | | 0; 6 |
| Branchiostegal rays | 14-18 | 8 | 14-15 | 16-19 | 14-16 0-14 | 14-17 | 4-5 | |
| Submandibular pores | | | 5-6 | 5 (6-10) | 4 (3-5) 4 (3-5) | 3-5 | | |

Fig. 19.2), and netlike pigmentation (Chain Pickerel; Figs. 19.3 and 19.18). Three geographic color variants of the Muskellunge occur throughout its range (see diversity and distribution section): populations in the Great Lakes basin have spots on the body arranged in oblique rows (Scott & Crossman 1973); Muskellunge in the Ohio River system, Chautauqua Lake, Lake Ontario, and the St. Lawrence River tend to have a barred or striped pattern (Trautman 1981); and populations in the inland lakes of Wisconsin, Minnesota, northwestern Ontario, and southeastern Manitoba lack distinct markings (Becker 1983).

Species of *Esox* tend to have brighter or more iridescent body color than other esociforms, which are mostly drab olive-green to brown in color. Overall coloration in *Umbra* is dark olive-green to brown-black with vertical dark brown bars along the lateral surfaces (Figs. 19.10 and 19.11). Central Mudminnows and Eastern Mudminnows have a prominent, vertical, dusky bar at the caudal base. Notable exceptions to the subdued pigmentation patterns are the iridescent blue-green highlights on the anal and dorsal fins of Central Mudminnows and the breeding colors of male Olympic Mudminnows (see reproduction section).

All species of *Esox* have a suborbital (below the eye) bar or tear drop, which varies among species in prominence and length. For example, the suborbital bar in *Kenoza* is complete and extends from the ventral margin of the eye to the ventral margin of the head (Figs. 19.3, 19.4, 19.15, and 19.18). The suborbital bar in the Northern Pike extends from the ventral margin of the orbit to two-thirds the distance to the ventral margin of the head, but in the Muskellunge, the bar extends only halfway to the ventral margin of the head. The North American species of *Umbra* have an indistinct horizontal eye stripe (preorbital

stripe), which extends anteriorly to the snout (Figs. 19.10 and 19.11). Eye stripes and bars are lacking in *U. krameri*, *Dallia*, and *Novumbra*.

Size and Longevity: *Esox*

In general, Muskellunge live longer than Northern Pike and achieve larger size (Scott & Crossman 1973; Trautman 1981; Becker 1983; Burdi & Grande 2010; Fig. 19.19). The Muskellunge normally lives 5–15 years but can reach 30 years of age and achieves an average maximum size of about 130 cm TL and weight of about 30 kg. The normal life expectancy of the Northern Pike is about seven years but may reach 24–26 years, reaching an average maximum length of about 120 cm TL and weight of about 20 kg. Fish tales being what they are, the North American angling record for the Northern Pike is 21 kg, 133.3 cm TL and 31.8 kg, 163.8 cm TL for the Muskellunge (International Game Fish Association 2015; NYDEC 2016). Ultimate size in the Northern Pike and Muskellunge differs between sexes (females are generally larger than males) and varies regionally (Mann 1976; Casselman et al. 1999). A general trend is evident within species, such as the Northern Pike for the more northern populations to grow more slowly, achieve larger sizes, and live longer than southern populations of the same species (Scott & Crossman 1973).

Species of pickerels also show differential sizes and ages. The Chain Pickerel lives ≤ 9 years and can reach 99 cm TL and about 4 kg in weight (Scott & Crossman 1973; Trautman 1981; Becker 1983; Page & Burr 2011). The smaller Grass Pickerel reaches about 38 cm TL and 0.40 kg in weight (Trautman 1981; Scott & Crossman 1973; Rohde et al. 1994; Page & Burr 2011). Both subspe-



Figure 19.18. A Chain Pickerel, *Esox niger*, with typical chain-like lateral coloration, swims over an algae bed in Ponce de Leon Springs, Holmes County, Florida, in October. This species inhabits vegetated lakes, swamps, and backwaters and can also occur in quiet pools of creeks and small rivers (Page & Burr 2011) (courtesy of © Isaac Szabo / Engbretson Underwater Photography).



Figure 19.19. The Muskellunge, *Esox masquinongy*, here cruising near large logs in Sparkling Lake, Wisconsin, is a voracious, top predator. The fast-growing species is the largest member of the family and among North America's largest freshwater fishes (photograph in May 2006 by and used with permission of © Engbretson Underwater Photography).

cies of the Grass Pickerel live about 7–8 years (Murdy et al. 1997; Table 19.3), although Canadian populations are reported to live only 6–7 years and tend to be smaller, reaching only about 32 cm TL (Scott & Crossman 1973).

Size and Longevity: *Dallia* and *Novumbra*

Alaska Blackfish seldom are >200 mm TL and 30–35 g (Morrow 1980); however, maximum size varies across the range of the species. Individuals from near Point Barrow, Alaska, averaged about 71 mm and 4 g; the largest individual reported was 116 mm TL (Ostdiek & Nardone 1959). A 165 mm Alaska Blackfish in the 3+ age group was the longest fish collected from Big Eldorado Creek (Blackett 1962). Fish in the Yukon-Kuskokwim delta commonly reach 255 mm TL. Introduced populations near Anchorage, Alaska, yield larger specimens on average, and fish ≤304 mm and ≤366 g are recorded (Trent & Kubik 1974), including one specimen of about 330 mm (Morrow 1980). Alaska Blackfish live ≤8 years (Aspinwall 1965).

In *Novumbra*, the maximum size is seldom >90 mm TL (McPhail 1969) with most specimens being <77 mm TL (Mongillo & Hallock 1999). The average size of individuals from several populations was about 52 mm TL with females averaging slightly larger than males (Hagen et al. 1972; Mongillo & Hallock 1999). Olympic Mudminnows may live 4–5 years (A. Mearns, pers. comm.).

Size and Longevity: *Umbra*

The Central and Eastern Mudminnows appear to have similar growth rates, average sizes, and life spans, although data are rather scant. The average adult size of the Central Mudminnow is 60–80 mm TL with a range of 50–115 mm (Peckham & Dineen 1957; Robinson et al.

2010) and a maximum of 140 mm SL (Schilling et al. 2006). Eastern Mudminnow adult lengths are variable, ranging from 91 mm TL (Virginia; Jenkins & Burkhead 1994) to 149 mm TL (North Carolina; Pardue & Huish 1981) to 152 mm TL (Maryland tributaries to Chesapeake Bay; Mansueti & Hardy 1967). Longevity in these species is typically ≤4 years (Applegate 1943; Becker 1983).

In a study contrasting growth characteristics of New York State lake and stream populations of the Central Mudminnow, individuals in the lake population were larger and achieved a larger maximum size, especially at older ages, than individuals from the stream population of the same age (Robinson et al. 2010). Growth rate was also greater in the lake population. Females were larger at age than males in both populations; however, all individuals <age 3 were males.

Skeletal Morphology

The skeletal morphology of *Esox* differs in several key characteristics from that of other esociforms. The increased number of precaudal vertebrae (range, 32–48) in *Esox* yielding an elongate body shape is indicative of an ambush predator (Maxwell & Wilson 2013). Within *Esox*, Northern Pike exhibit greater numbers of precaudal vertebrae (39–48) than do Grass and Chain Pickerel (32–39) (Grande et al. 2004). *Esox* spp. also share a higher caudal vertebral count (17–21) than all other esociforms (13–18). Total vertebrae in the Central Mudminnow are 35–37 (Chapman 1934; Dineen & Stokely 1954); precaudal vertebral counts are 20–21. Total vertebral counts in larval Olympic Mudminnows are 37–39 and vary with SL (Kendall & Mearns 1996); adult counts are 37 or 38 with the total being divided about equally (18 or 19) in precaudal or caudal vertebrae.

Table 19.3. Life-history characteristics of Pikes, Esocidae, and Mudminnows, Umbridae (Esociformes) from references in the text. IUCN, International Union for Conservation of Nature; AFS, Jelks et al. 2008.

| Life-history attribute | <i>Esoc a.</i> | | | | | | | |
|---|---|---------------------------------|--|--|---|--|--|--|
| | <i>Dallia pectoralis</i> | <i>Novumbra hubbsi</i> | <i>Esoc lucius</i> | <i>Esoc masquinongy</i> | <i>americanus/a. vermiculatus</i> | <i>Esoc niger</i> | <i>Umbr a limi</i> | <i>Umbr a pygmaea</i> |
| Strictly fresh water (ppt) | Yes | Yes | Transient in brackish water | Yes | Yes, infrequent in brackish water | Yes | Yes | Yes, rarely in brackish water |
| Maximum length (cm TL) | 33 (usually <20) | 8.9 (usually ≤5.3) | 124 | 138 | 38 | 99 | 15 | 9–15 |
| Maximum weight | 366 g | Unknown | 28.4 kg | 31.8 kg | 1.0 kg | 4.25 kg | Unknown | Unknown |
| Maximum age (years) | 8 | 4–5 | 24–26 | 30 | 7–8 | 8–9 | 4–7 | 4–5 |
| Length at maturity (cm TL, unless noted) | 8.0 | 5.4 (range, 4.1–6.5) | 35–56 | 59–80 | Male, 15.0; female 14.0 | 17.0 | 5–10 SL | Unknown |
| Age at maturity (years) | 2–3 | Unknown | 1–6 | 3–5 | 1–4 | 1–4 | 2 | 1–2 |
| Iteroparous | Yes | Yes | Yes | Yes | Yes | Yes | Yes | Yes |
| Fecundity estimates range (average) | 40–300 | Unknown | 7,600–595,000 (32,000) | 6,000–265,000 (120,000) | 186–800 (3,700–15,000 eggs total; see text for explanation) | 300 to 8,000 (see text for explanation) | 220–2,286 (425–450) | 31–2,566 (342) |
| Mature egg diameter (mm) | 2.0 | 1.9 | 2.5–3.0 | 2.5–3.0 | 2.8 | 2–2.5 | 1.6 | 1.65 (1.4–2.2) (fertilized) |
| Egg deposition sites | Attached to vegetation | Attached to vegetation | Scattered on vegetation or debris in shallow water | Scattered on vegetation or debris in shallow water | Scattered on vegetation or debris in shallow water | Scattered on vegetation or debris in shallow water | Attached to vegetation | Attached to vegetation |
| Range of spawning dates and temperatures (°C) | May– August; 9.2–16.8 | 10.0–17.9 | Late March– April; 4.4–11 | Mid–April– May; 9–15 | March–April; 10 | Early spring; 6–11 | Mid–March– April; 12.8–15.6 | March–April or later; 9.0–15.0 |
| Habitat of spawning sites; water depth (cm) | Vegetation at the bottom of shallow ponds and quiet streams | Shallow, flooded stream margins | Shallow flooded marshes, 15–25 | Shallow bays, 15–75 | Vegetated stream margins and floodplains | Vegetated stream margins and floodplains | Vegetated margins of ponds, lakes, and stream floodplains; 12–20 | Vegetated margins of ponds, lakes, and stream floodplains; <10 |

(continued)

Table 19.3, continued

| Life-history attribute | <i>Esox a.</i> | | | | | <i>Umbra limi</i> | <i>Umbra pygmaea</i> |
|-----------------------------------|---|---|--|--|--|--|--|
| | <i>Dallia pectoralis</i> | <i>Novumbra hubbsi</i> | <i>Esox lucius</i> | <i>Esox masquinongy</i> | <i>americanus/a. vermiculatus</i> | | |
| Incubation period | 9 days at 12°C; 14 days at 10°C | 9 days at 15–17°C; 13 days at 10.1°C | 12–14 days at 7.2–15.6°C | 8–14 days at 12.2–16.7°C | 10–14 days at 10°C | 6 days; temperature not reported | Unknown |
| Mean size at hatching (mm TL) | 6.0 | About 5.0 | 6.0–10.0 | 7.9–9.2 | 5.0–6.2 | 5 | Unknown |
| Parental care | Unknown | No parental care; male defends territory after first spawning | No parental care | No parental care | No parental care | Guarding by male | Courtship; nest-building, guarding, fanning by female |
| Minimum dissolved oxygen (ppm) | 2.3 | 2.5 | 1.0 | 3.2 | Unknown | 1.6 | 2.0 |
| Minimum pH | 6.8 | 3.8 | 5.0 | Unknown | Unknown | 6.0 | 4.0 |
| Major dietary items | Aquatic invertebrates and fishes | Aquatic invertebrates | Fishes and other small vertebrates | Fishes and other small vertebrates | Aquatic insects, other invertebrates, small fishes | Aquatic invertebrates | Aquatic invertebrates |
| General year-round habitat | Heavily vegetated lowland swamps, ponds, and medium to large rivers and lakes | Vegetated portions of slow streams, sloughs, marshes, and off- channel habitats | Vegetated portions of lakes, ponds, slow rivers | Vegetated portions of lakes, pools, and slow rivers | Vegetated portions of slow streams, swamps, and lakes | Vegetated portions of slow streams, and swamps, and ponds, and sloughs | Vegetated portions of slow streams, swamps, ponds, and sloughs |
| Migratory or diadromous | Yes, in fresh water | Yes, in fresh water | Yes, in fresh water | Yes, in fresh water | Yes, in fresh water | Yes, in fresh water | Yes, in fresh water |
| Impairment status IUCN/AFS | Least concern/ no status | Least concern/ vulnerable | Least concern/ no status | Least concern/ no status | Least concern/ no status | Least concern/ no status | Least concern/no status |

Esociforms share several characteristics in the caudal skeleton, including one pair of uroneurals, two ural centra, and the presence of an autogenous (unfused) first preural centrum (Rosen 1974; Wilson & Veilleux 1982; Grande et al. 2004; Burdi & Grande 2010). In the caudal fin skeleton (Fig. 19.20), the subgenus *Esox* has three epurals and six hypurals, but the subgenus *Kenoza* and *Umbra* have two epurals (Grande et al. 2004). The adult caudal skeletons of Alaska Blackfish have one epural, Olympic Mudminnows have five or six hypurals, and *Umbra* spp. have five hypurals (Rosen 1974; Wilson & Veilleux 1982).

Esox is also distinguished from all other genera by an expansion of the anterior supraneural (Fig. 19.21). The position of the anterior supraneural relative to the corresponding neural arches is variable within *Esox* (Grande et al. 2004). In *Kenoza* the supraneural sits directly above neural arches two and three (Fig. 19.21); in the Northern Pike the supraneural is expanded and positioned above neural arches one through three; and in Muskellunge the supraneural is positioned above arches one through four.

Umbra spp. have four supraneurals positioned above neural spines 1–4 and *Novumbra* and *Dallia* have a single supraneural above neural spine 4 (Wilson & Veilleux 1982; Grande et al. 2004; Fig. 19.21).

Jaw (dentary and palatine) teeth in *Esox* spp. are completely mineralized at the point of attachment of the tooth base to the associated bone (Fink 1981). The large, fang-like teeth of Pikes (and pickerels) (Fig. 19.22) are typically attached by full ankyloses (rigid fusion of bones) and are related to a piscivorous (or at least carnivorous) diet (Type 1). Type 1 attachment also occurs in *Umbra*. In *Dallia*, the attachment is similar, but a narrow ring of unmineralized collagen lies between the dentine and the bone (Type 2). Pharyngeal (throat) teeth in *Esox* have a depressible, posteriorly hinged tooth attachment (Type 4) with the axis of rotation posterior to the tooth attachment site. Pharyngeal tooth attachment is more fixed in *Umbra* (Type 1) and *Dallia* (Type 2).

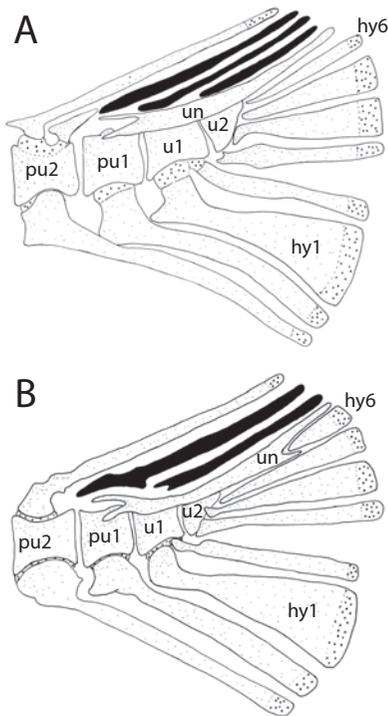


Figure 19.20. Caudal fin skeleton of the (A) Muskellunge, *Esox masquinongy* (133 mm SL, CU 9118) representing the subgenus *Esox* and (B) Grass Pickerel, *Esox americanus vermiculatus* (128 mm SL, FMNH 7187) representing the subgenus *Kenoza* (redrawn from Grande et al. 2004). Key: Epurals drawn in black; hy1 = hypural 1; hy6 = hypural 6; pu1 = preural centrum 1; pu2 = preural centrum 2; u1 = ural centrum 1; u2 = ural centrum 2; un = uroneural. Anterior to the left.

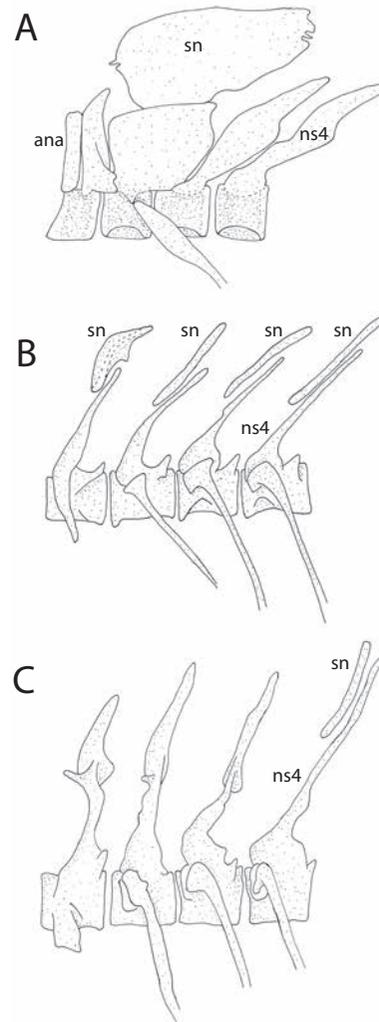


Figure 19.21. Anterior vertebral region of the (A) Chain Pickerel, *Esox niger* (105 mm SL, FMNH 21811), (B) Central Mudminnow, *Umbra limi* (74 mm SL, FMNH 99738), and (C) Olympic Mudminnow, *Novumbra hubbsi* (48 mm SL, composite of UMMZ 187427 and UAMZ 3714) (A by T. Grande, B and C redrawn from Grande et al. 2004). Key: ana = accessory neural arch; ns4 = neural spine 4; sn = supraneural. Anterior to the left.

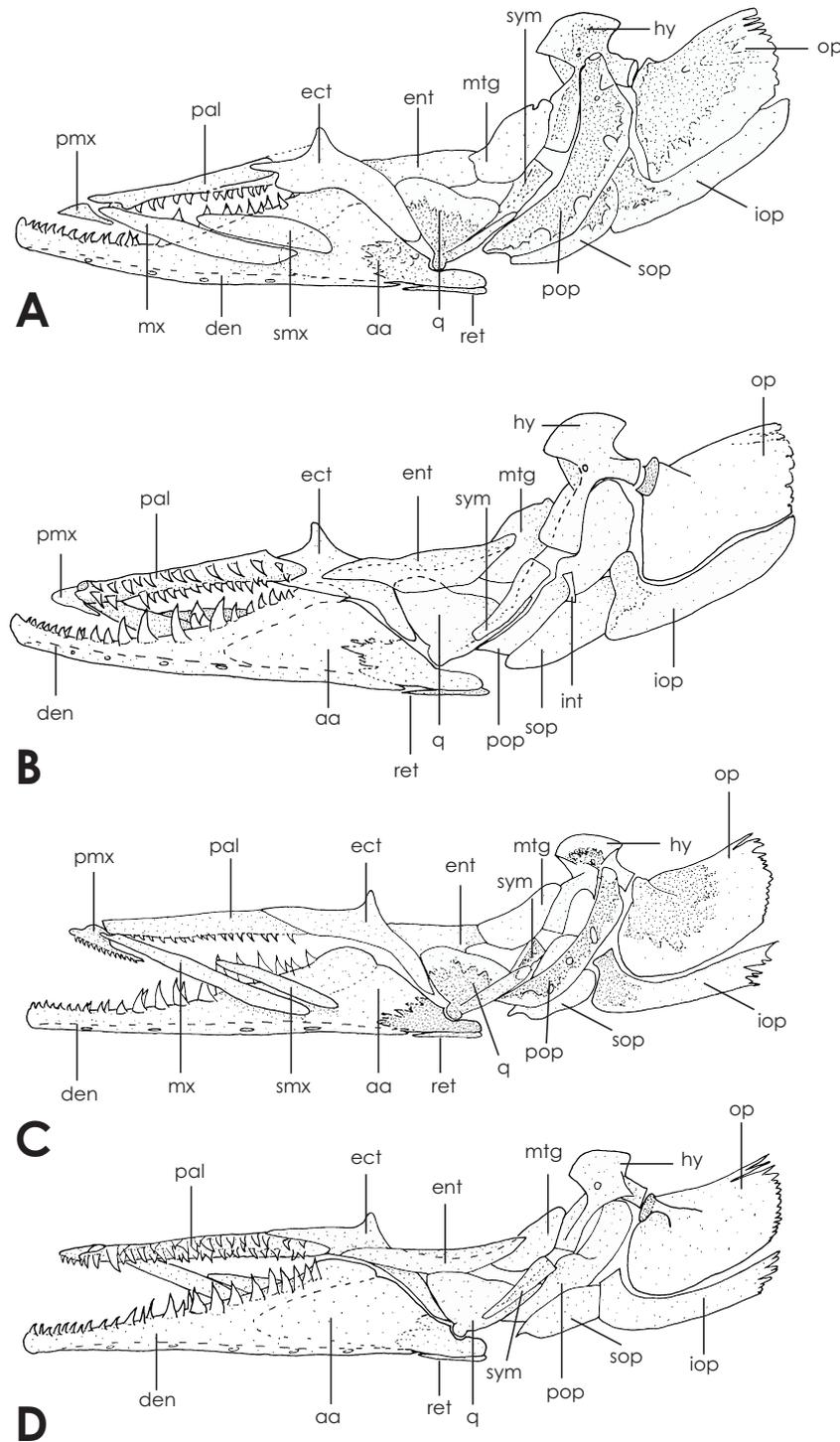
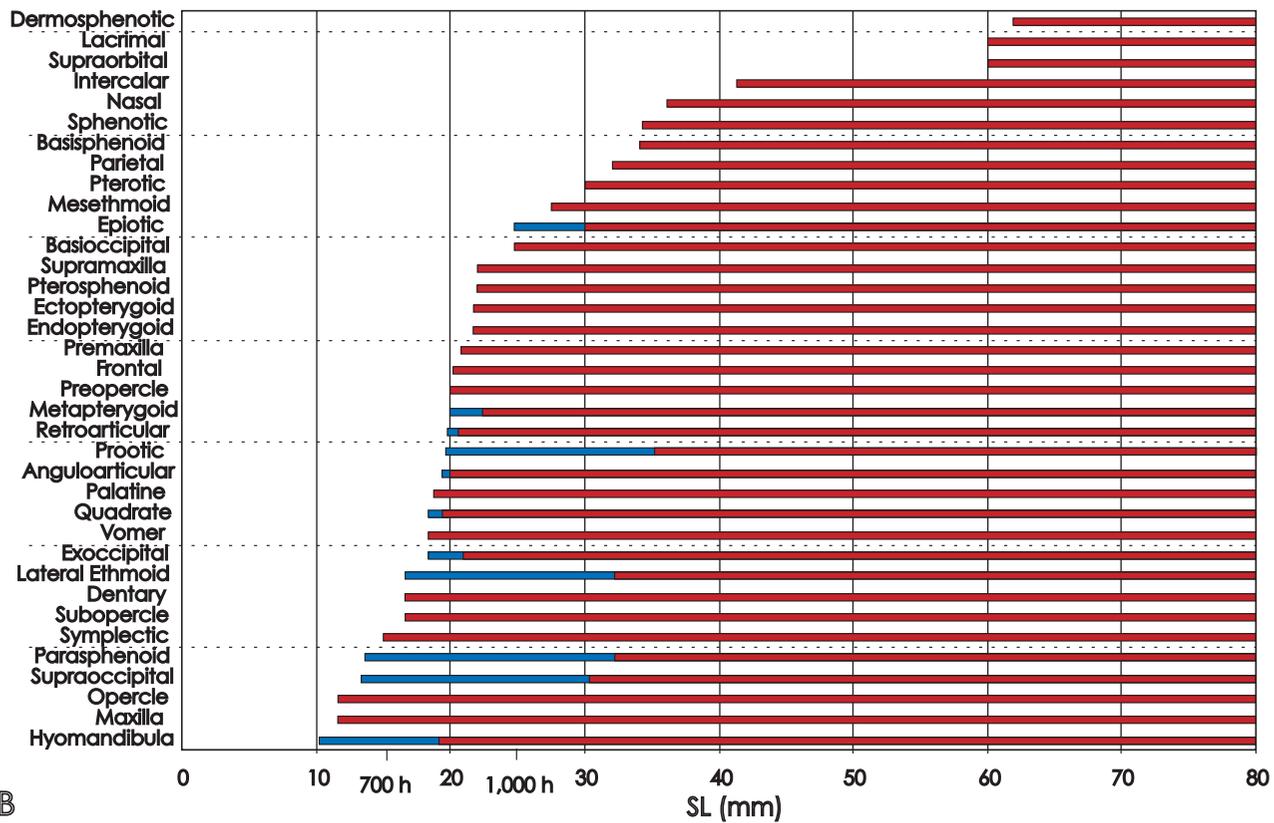
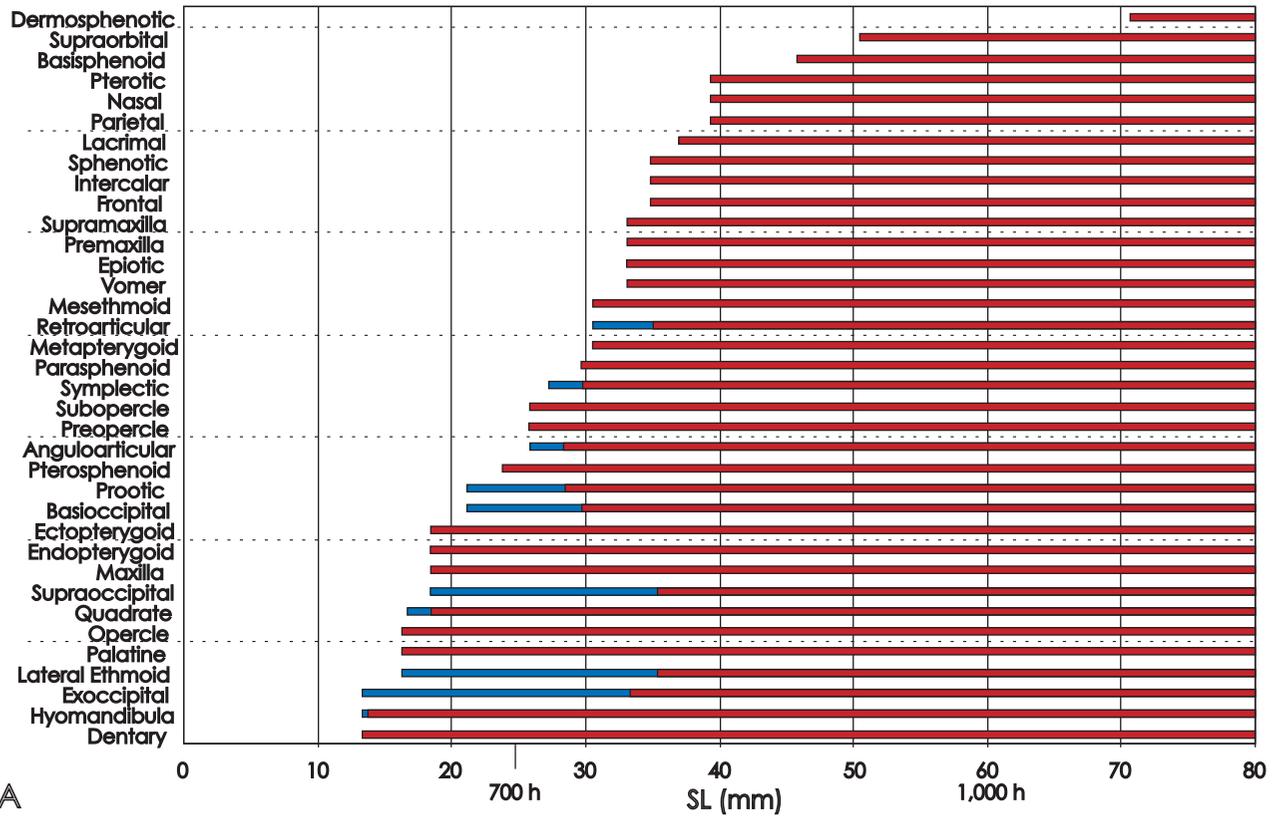


Figure 19.22. As top predators, the Pikes (Esocidae; genus *Esox*) characteristically bear large, fang-like teeth on the jaws and other bones as illustrated here on the dentary (lower jaw) and palatine (upper jaw) bones of the suspensorium (series of bones suspending lower jaw from skull) of the Northern Pike, *Esox lucius*, and Muskellunge, *Esox masquinongy*. Suspensorium of *Esox lucius*, lateral (A) and medial (B) view, LUD.F 241811, 78.4 mm SL; 41811; *E. masquinongy*, lateral (C) and medial (D) view, LUD.F 241812, 81.0 mm SL. Anterior to left (redrawn from Burdi & Grande 2010). Key: aa = anguloarticular; den = dentary; ect = ectopterygoid; ent = entopterygoid; hy = hyomandibula; int = interhyal; iop = interopercle; mx = maxilla; mtg = metapterygoid; op = opercle; pal = palatine; pmx = premaxilla; pop = preopercle; q = quadrate; ret = retroarticular; smx = supra-maxilla; sop = subopercle; sym = symplectic.

Larval Adaptations

Regardless of individual variation, the relative sequence in development of the axial skeleton bones is consistent between the Northern Pike and Muskellunge (Burdi & Grande 2010). The hyomandibular, dentary, and quadrate bones form first in cartilage, followed by the hypurals.

Mineralization of the hyomandibula and dentary occur first, followed by the maxilla, symplectic, and opercle. The last bones to mineralize are the supraorbitals and dermosphenotics (Jollie 1975; Burdi & Grande 2010). Although a consistent pattern of bone development occurs, the Northern Pike grows faster than the Muskellunge, yet bone formation and mineralization at a given size is



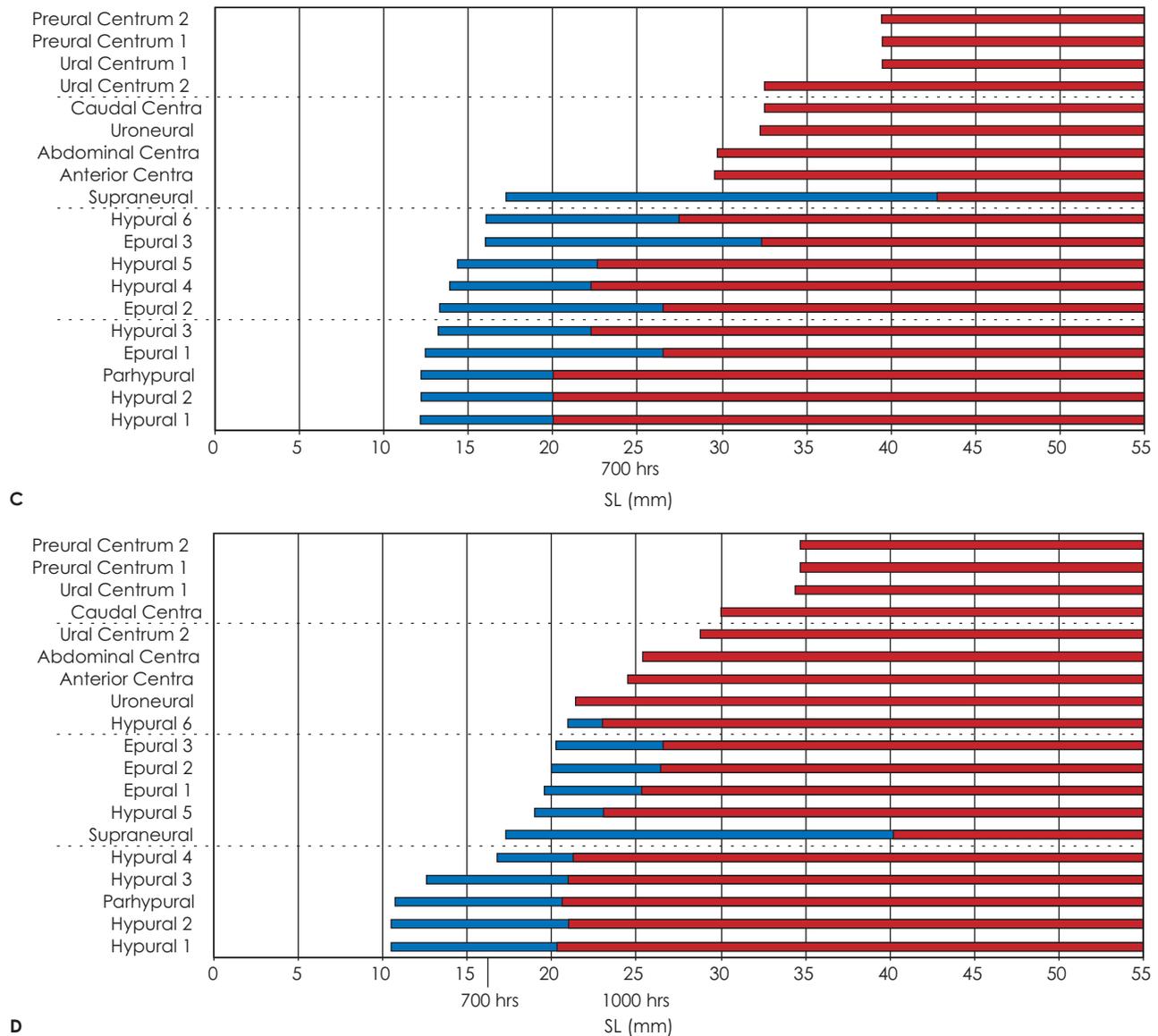


Figure 19.23. First appearance or mineralization of individual bones within the axial skeleton of (A) cranial and (C) post-cranial bone formation in Northern Pike, *Esox lucius*, and (B) cranial and (D) post-cranial bone formation in the Muskellunge, *Esox masquinongy*, relative to SL (mm) and development time (h). Note, for example, the greater number of mineralized cranial bones in Muskellunge relative to Northern Pike at similar lengths (e.g., at 20 mm SL 18 skull bones have begun to form in Muskellunge versus 11 in Northern Pike) and the faster early growth of Northern Pike versus Muskellunge (e.g., SL at 1,000 h). A similar pattern is apparent in post-cranial bone formation and mineralization. Cranial and post-cranial bones are divided by species and arranged in order from the last to form (top) to the earliest. Blue denotes cartilage, red mineralization. Specific ages in hours (h) are noted on the x-axis for comparisons (redrawn from Burdi & Grande 2010).

slower than in the Muskellunge (Figs. 19.23–19.25). At 25 mm SL, the axial skeleton of the Muskellunge is 55% mineralized but that of the Northern Pike is only 25% mineralized; this suggests early skeletal development in the Muskellunge is favored over increased size. This difference may reflect differences in early foraging strategy between the two species. Juveniles of the Muskellunge absorb their yolk sac earlier than those of the Northern Pike

and become active predators just a few days after hatching. A well-developed axial skeleton with fully mineralized teeth is likely necessary for early predacious behavior (Burdi & Grande 2010).

Adhesive organs, often seen in larvae, are described for a variety of teleosts (Braum et al. 1996; Grande & Young 1997; Echelle & Grande 2014; Kuhajda 2014). These structures enable the larvae to adhere to rocks or surfaces while

living in fast-moving waters. The adhesive organ of the yolk-sac larvae of the Northern Pike consists of two convex epidermal patches of folds and grooves located on the lateral aspect of the head (Fig. 19.26). The cells of the organs

are tall, prismatic-type granular cells with basal nuclei. Secretory activity of the organs begins shortly before hatching (Braum et al. 1996). After hatching, larvae begin to swim upward, stopping once they hit an object. Secretions from the adhesive organs then hold the larvae in place during the remainder of the yolk-sac stage (Kotlyarevskaya 1969). By adhering to objects higher in the water, column larvae can respire in areas of higher dissolved oxygen than is generally available near the substrate (Braum et al. 1996). Northern Pike and Muskellunge have active adhesive organs at hatching. Northern Pike young, however, may have a greater propensity to display adhesive behavior (Cooper et al. 2008). Adhesive organs also develop in *Kenoza* (Chain Pickerel, Underhill 1949; Grass Pickerel, Scott & Crossman 1973) and are used for larval attachment (Scott & Crossman 1973). Olympic Mudminnow larvae have two pores on the side of the head that extrude a sticky mucus allowing them to attach to vegetation (Meldrim 1968). Neither adhesive organs nor attaching behavior are documented in larvae of *Dallia* or *Umbr*a.

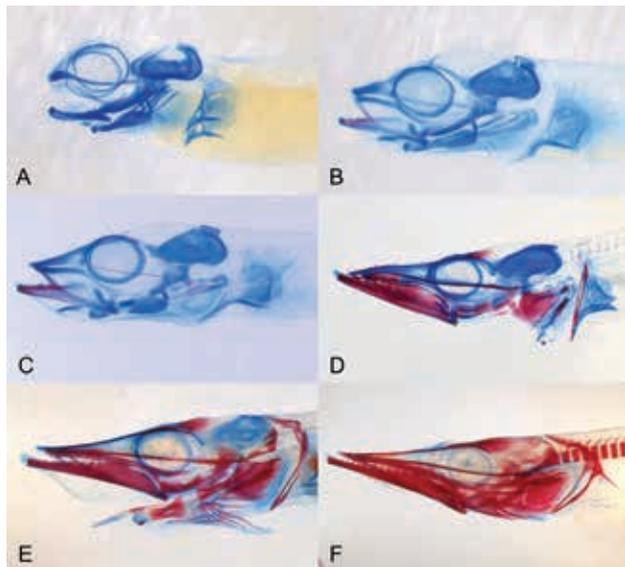


Figure 19.24. Skull development and mineralization in the Muskellunge, *Esox masquinongy*. (A) 10.6 mm NL (notochord length), LUD.F 241800; (B) 12.1 mm SL, LUD.F 241801; (C) 13.8 mm SL, LUD.F 241802; (D) 19.9 mm SL, LUD.F 241805; (E) 21.1 mm SL, LUD.F 241806; (F) 42.4 mm SL, LUD.F 241810. Cartilage is stained blue; bone is stained red (from Burdi & Grande 2010) (used with permission of TG).

Adaptations for Air Breathing in *Dallia* and *Umbr*a

Anatomical, physiological, and behavioral aspects of aerial respiration are described in *Umbr*a spp. and the Alaska Blackfish (Crawford 1974; Gee 1980, 1981; Krout & Dunson 1985; Currie et al. 2010; Nelson & Dehn 2010; Lefevre

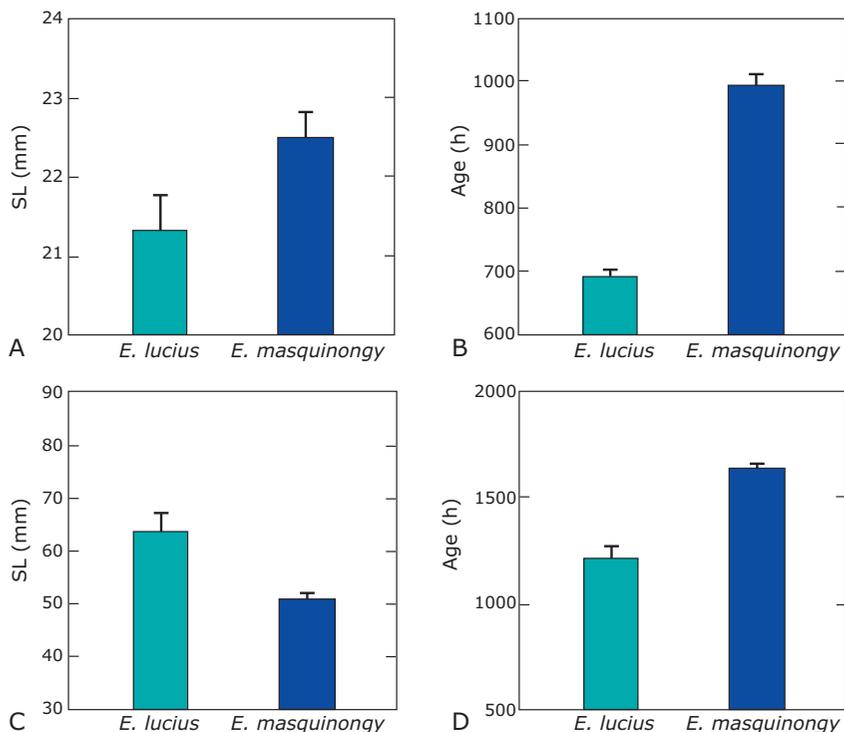


Figure 19.25. (A) Mean SL of the Northern Pike, *Esox lucius*, and Muskellunge, *E. masquinongy*, at the 3 cartilaginous hypural mark. (B) Mean ages (hours) of the Northern Pike and Muskellunge at the 3 hypural mark. (C) Mean SL of the Northern Pike and Muskellunge at the 20 vertebrae mark. (D) Mean ages of the Northern Pike and Muskellunge at the 20 vertebrae mark. Error bars denote 1 SE (redrawn from Burdi & Grande 2010).

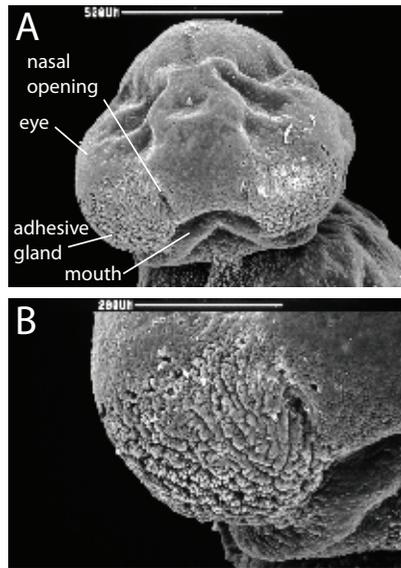


Figure 19.26. The adhesive gland of the Northern Pike, *Esox lucius*, from scanning electron micrographs. Lower micrograph (B) is an enlargement of the right adhesive gland shown in the upper micrograph (A). The specimen is about 10 days post-fertilization and <24 h post-hatching (9.16 mm TL, 9.04 mm NL, notochord length) (photomicrograph by CT).

et al. 2014; Nelson 2014). The morphology of these structures is described for Alaska Blackfish (esophageal wall; Crawford 1974) and European Mudminnows (swim bladder; Jasiński 1965). The swim bladder may have a similar function in the Central Mudminnow (Crawford 1974).

The epithelium on the internal esophageal wall of the Alaska Blackfish is profusely vascularized and densely populated by glandular cells. Posteriorly, the esophagus is separated from the stomach by a sphincter. Blood flows to the esophagus from the gastrointestinal artery, a branch of the celiac artery. Blood leaving the esophagus flows to the posterior cardinal vein. An air-breathing role for the

esophagus of *Dallia* was proposed based on these histological and anatomical characteristics (Crawford 1974), but functional studies of this respiratory organ are unavailable. The esophageal skeletal musculature may be involved in expelling gas from the esophagus (Crawford 1971). *Dallia* also possesses a highly vascularized swim bladder similar in gross anatomy to that of *Umbra*; however, capillaries do not penetrate the inner epithelial lining of the swim bladder and are separated from the epithelium by a layer of loose connective tissue and smooth muscle (Crawford 1974). The vascularization and its connection to the esophagus by a pneumatic duct makes it a good candidate for gas secretion (e.g., for buoyancy regulation) but a poor one for gas absorption.

The internal surface of the swim bladder of the European Mudminnow has the histological characteristics of respiratory epithelium (Rauther 1914). Blood reaches the swim bladder of the species via the dorsal aorta (Fig. 19.27). The aorta branches into smaller blood vessels, which give rise to a dense network of capillaries that surround the swim bladder and cover about 80% of its surface (Jasiński 1965). Blood from this capillary network flows to a vein that empties into the posterior vena cava. In contrast, blood leaving the swim bladder of fishes that do not use this organ to obtain oxygen typically flows to the hepatic portal vein as would be appropriate for a part of the digestive system. The vascularization and blood circulation of the swim bladder of the Central Mudminnow is comparable to that described in the European Mudminnow, and it presumably functions similarly (Black 1945). The Eastern Mudminnow also uses atmospheric air for respiration and probably also uses a modified swim bladder for oxygen absorption (Jasiński 1965).

Vascularization of the swim bladder of the Northern Pike does not suggest a significant role in oxygen absorption

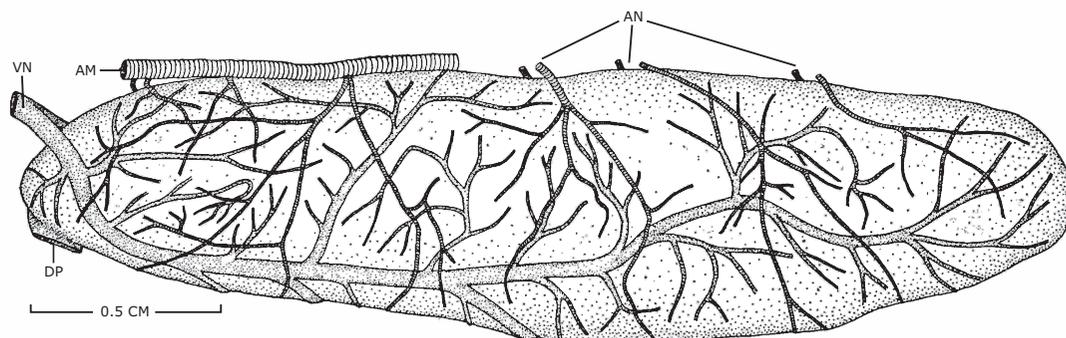


Figure 19.27. Vascularized swim bladder of the Eurasian Mudminnow, *Umbra krameri*, used for oxygen absorption. Key: AM = median dorsal aorta; AN = arterial vesicae natatoriae; DP = ductus pneumaticus; VN = venous vesicae natatoriae (redrawn from Jasiński 1965).

for respiration (Jasiński 1965). A small gas gland occurs in the anterior ventral aspect of the swim bladder of the Northern Pike. Elsewhere on the swim bladder surface, bundles of arteries from the median aorta and the connecting veins form a rete mirabile. Through comparison of swim-bladder circulation in different fishes, Jasiński (1965) concluded the vascularization of the swim bladder of the Northern Pike may indicate an accessory role in buoyancy control.

Body Form and Function

The body form of *Esox* is characteristic of an ambush predator. The body is elongate and slender, the snout, particularly anterior to the eye, is elongate resulting in elongated jaws, and the median fins are positioned posteriorly (Maxwell & Wilson 2013). In *Esox*, the elongation of the body, characteristic of transient-propulsion specialists, minimizes drag and maximizes thrust (Webb 1984). This elongated body-type is hypothesized to have evolved multiple times among Ray-finned Fishes (Actinopterygii) and in the case of *Esox*, is associated with an increase in numbers of abdominal vertebrae added at the boundary between the abdominal and caudal vertebral regions. This modularity of abdominal vertebrae and caudal vertebrae results from different Hox gene expression and developmental mechanisms in each region (Bird & Mabee 2003; Ward & Brainerd 2007).

Sensory Morphology and Biology

Within esociforms, the cephalic sensory canal system ranges in pattern from a complete set of canals as in the Northern Pike, Muskellunge, and Amur Pike to a reduction of sensory canals and an increase and elaboration of pitlines in *Kenoza*, *Novumbra*, *Dallia*, and *Umbra* (Figs. 19.28–19.32). The infraorbital canal in the Northern Pike (7–8 pores) and Muskellunge (7–9 pores) is closed and continuous. In the Redfin, Grass, and Chain Pickerel (8–9 pores), the canal is incomplete and interrupted, but the number of pores is not reduced (Fig. 19.28). In the other genera, however, the canal is greatly reduced and replaced by a pitline, and the number of pores is reduced (0–3) (Figs. 19.30 and 19.31). The mandibular canal, which runs the ventral length of the dentary, is continuous in *Esox*. Four (occasionally ≥ 5) pores occur in *Kenoza*, five in Northern Pike, and 8–9 in Muskellunge (Nelson 1972; Grande et al. 2004; Fig. 19.28). The canal is reduced in size (two pores) in the Olympic Mudminnow and European Mudminnow and lost

in the Central Mudminnow and Eastern Mudminnow (Nelson 1972; Figs. 19.30 and 19.31). The preopercular canal is present in all esociforms. Six pores are present in *Esox*, five in *Novumbra*, and four in *Dallia* and *Umbra*. Esociforms also have a complete supraorbital canal; six or seven pores are present in the esocids, and four pores occur in the umbrids. In all species of *Esox* plus *Novumbra*, three pores occur in the temporal canal, but *Dallia* and *Umbra* have two. Finally, a posttemporal canal occurs in all species of *Esox* but not in *Umbra* and *Novumbra* (Nelson 1972; Grande et al. 2004; Figs. 19.28 and 19.30).

Vision

As might be expected in shallow-water visual predators, the eyes of esociforms are moderately large and well developed (Fig. 19.15), possessing morphological adaptations for both acute vision in low light and the ability to distinguish color (Braekevelt 1975, 1980). Photoreceptor type and arrangement as well as photopigments in *Esox* are typical of crepuscular predators. Three photoreceptor types occur in the Northern Pike: rods, single cones, and twin cones (Braekevelt 1975). Rod photoreceptors predominate and perhaps reflect the crepuscular feeding behavior of the species. Single and twin cones are arranged in a well-defined, repeating mosaic pattern and possess a more elaborate and extensive synaptic region than that of the rods. The Northern Pike and Muskellunge color vision is most sensitive in the red-green spectrum between 500–600 nm wavelengths. Muskellunge also have a yellow cornea and lens that filters out short wavelengths (Bridges 1969). Vision in *Esox* spp. may be more attuned to detection and spatial orientation than to processing visual cues about size and shape attributes of prey. Acute vision of the Muskellunge is also used in the initial acquisition of the prey, and vision and the lateral-line system are important in determining the initiation of the fast start. Interestingly, suppression of the lateral line altered the approach of the Muskellunge to more distant prey, but bilaterally blinded fish did not stalk prey at all and only lunged at close prey (New et al. 2001). The pineal organ of the Northern Pike is photosensitive and as with the retina may play a role in circadian rhythm (Falcón & Meissl 1981; Falcón & Collin 1991). Although apparently little visual research is available on most non-*Esox* esociforms, early experimental evidence suggested that Central Mudminnows have acute color vision allowing them to discriminate between edible prey items and inedible material (Hineline 1927).

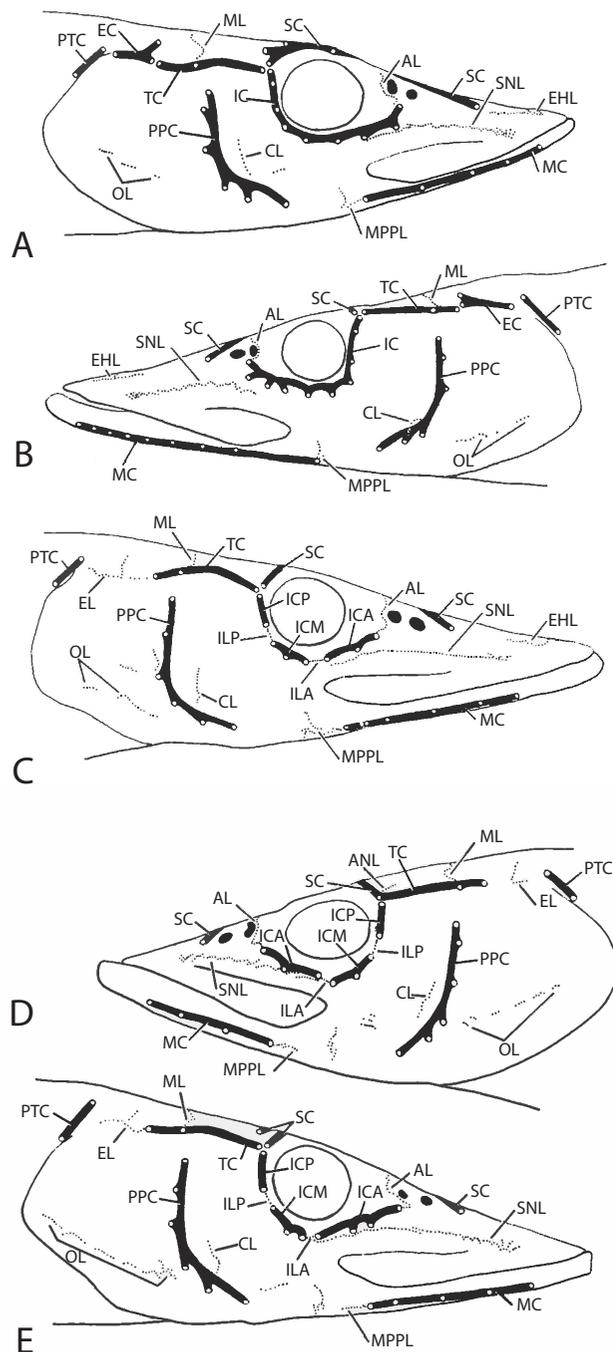


Figure 19.28. Head sensory canals, pores, and pitlines (lateral view) in the subgenus *Esox* (A) Northern Pike, *Esox lucius*; and (B) Muskellunge, *E. masquinongy* *Esox*; and subgenus *Kenoza* (C) Redfin Pickerel, *E. americanus vermiculatus*; (D) Grass Pickerel, *E. americanus americanus*; and (E) Chain Pickerel, *E. niger* (redrawn from Nelson 1972). (A) AMNH 20268, 40 mm SL; (B) AMNH, uncat., 88 mm SL; (C) AMNH, uncat., 56 mm SL; (D) ROM 25878, 126 mm SL; (E) AMNH 23714, 47 mm SL. Key: AL = antorbital pitline; ANL = anterior pitline; CL = cheek line; EC = extrascapular canal; EHL = ethmoidal pitline; EL = extrascapular pitline; IC = infraorbital canal; ICA = anterior infraorbital canal; ICM = middle infraorbital canal; ICP = posterior infraorbital canal; IL = infraorbital pitline; ILA = anterior infraorbital pitline; ILP = posterior infraorbital pitline; MC = mandibular canal; ML = middle pitline; MLI = mandibular pitline; MML = mentomandibular pitline; MPPL = mandibulopreopercular pitline; OL = opercular pitline; POL = postocular pitlines; PPC = preopercular canal; PC = posttemporal canal; SC = supraorbital canal; SL = supraorbital pitline; SNL = subnasal pitline; TC = temporal canal.

and Muskellunge rely primarily on vision and lateral sensory systems for stalking prey (New et al. 2001). Northern Pike are attracted by the release of alarm pheromone of Fathead Minnow, *Pimephales promelas* (Mathis et al. 1995; Chivers et al. 1996; Chivers & Smith 1998) and exhibit distinct foraging responses to hypoxanthin-3(N)-oxide, a component of fish alarm pheromones (Mathis et al. 1995). Olfaction may play a role in predator avoidance in esociforms, although the species examined (Northern Pike, Alaska Blackfish, and Central Mudminnow) apparently lack specialized epithelial cells that secrete alarm pheromones (Pfeiffer 1977; Wisenden et al. 2008). Northern Pike do not exhibit any alarm responses to conspecific skin extracts, but larvae decreased their feeding frequency on zooplankton and showed other anti-predator responses to chemical cues of Eurasian Perch, *Perca fluviatilis* (Lehtiniemi 2005; Lehtiniemi et al. 2005). In contrast, Central Mudminnows exhibit distinct alarm responses to conspecific skin extracts (Wisenden & Chivers 2006; Wisenden et al. 2008), which may reflect their small size and resulting vulnerability to predators.

Olfaction

Structurally, the olfactory system of the Northern Pike is similar to many fish species. Olfactory receptors are found on radially arranged lamellae in a bi-narial olfactory sac (Kasumyan 2004). Behavioral experiments conducted in captivity suggest a relatively minor role for olfaction in the sensory biology of esocids, at least in feeding behavior. Chemical cues from foraging Northern Pike elicit minor responses from conspecifics (Nilsson & Brönmark 1999),

GENETICS

Karyology

The chromosomal organization of the genomes of esociform fishes is a particularly well-studied aspect of their biology. The genome size, karyotype, and location of the nu-

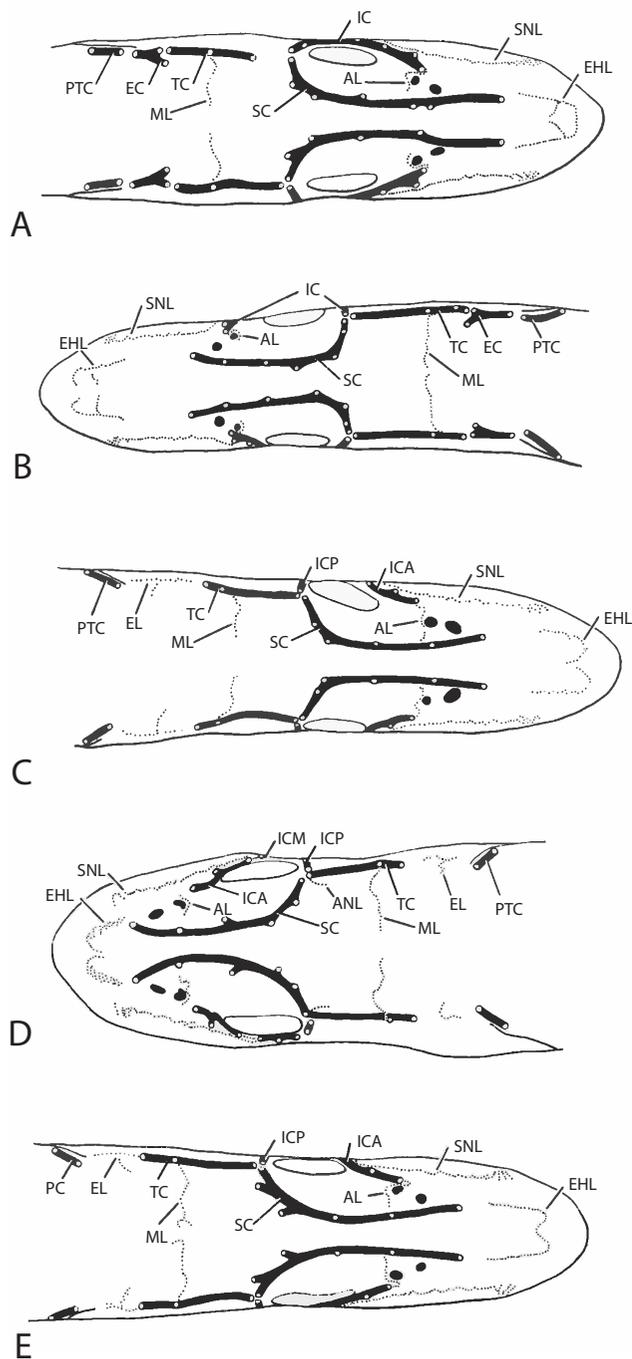


Figure 19.29. Head sensory canals, pores, and pitlines (dorsal view) in subgenus *Esox*, (A) Northern Pike, *Esox lucius*, and (B) Muskellunge, *E. masquinongy*, and subgenus *Kenoza*, (C) Redfin Pickerel, *E. americanus vermiculatus*, (D) Grass Pickerel, *E. a. americanus*, and (E) Chain Pickerel, *E. niger* (redrawn from Nelson 1972). Abbreviations as in Fig. 19.28.

cleolar organizing region (NOR) is known for most species (Beamish et al. 1971). In addition, various chromosome-banding techniques were applied to the karyotypes of most esociform species (e.g., Ráb & Mayr

1987; Ráb et al. 2002). Together, these measures of genome organization revealed that the relatively low species diversity of living esociforms belies a rich diversity of genomic arrangements. Each of the four esociform genera is characterized by a distinct genomic organization with diploid chromosome numbers ranging from 22 in the North American Mudminnows to 71–79 in *Dallia* spp. *Dallia* and *Umbra* exhibit intrageneric variation in chromosome number. Chromosomes may be exclusively acrocentric (centromere near one end) (*Esox* spp.), exclusively metacentric (centromere in the middle) (both North American species of *Umbra*), or complicated and distinct (*Novumbra* and *Dallia*) (Crossman & Ráb 2001). The extent of this variation fits well with the ancient origin of the esociform lineages inferred from fossil evidence. The information on karyological characteristics of the genomes of esociforms suggested karyotypic evolution proceeded along three distinct lineages represented today by *Esox*, *Dallia* + *Novumbra*, and *Umbra*, relationships compatible with those derived from genetic and other morphological evidence (Crossman & Ráb 1996; Ráb et al. 2002) (see phylogenetic relationships section).

Karyotypic Stability in *Esox*

Esox has a conserved genomic organization. The karyotypes of the five extant species consist of 25 pairs of acrocentric chromosomes ($2n = 50$) of gradually differing sizes (Beamish et al. 1971). The NORs in all North American species of *Esox* are located near the centromere of an intermediately sized chromosome pair (Ráb & Crossman 1994). Notably, the techniques used to determine NOR localization did not produce information regarding the homology of chromosomes from different species. Hence, the fact that NORs in the different species of *Esox* are located on similarly sized chromosomes does not rule out the possibility that these actually are non-homologous elements. The genome size of esocids range from 2.2 to 2.7 pg/cell (Beamish et al. 1971).

A remarkable aspect of the cytological observations is that if the fossil *E. kronneri* is assigned correctly to the subgenus *Kenoza*, then the gross genomic organization of this genus (i.e., $2n = 50$, all acrocentrics and pericentric NORs on chromosome pair 11 by size) has remained unchanged for >50 million years despite observed changes in morphology and genes among extant taxa (see phylogenetic relationships and morphology sections). This remarkable genomic stability may partly explain the viability of hybrid offspring from intra-subgeneric crosses of species

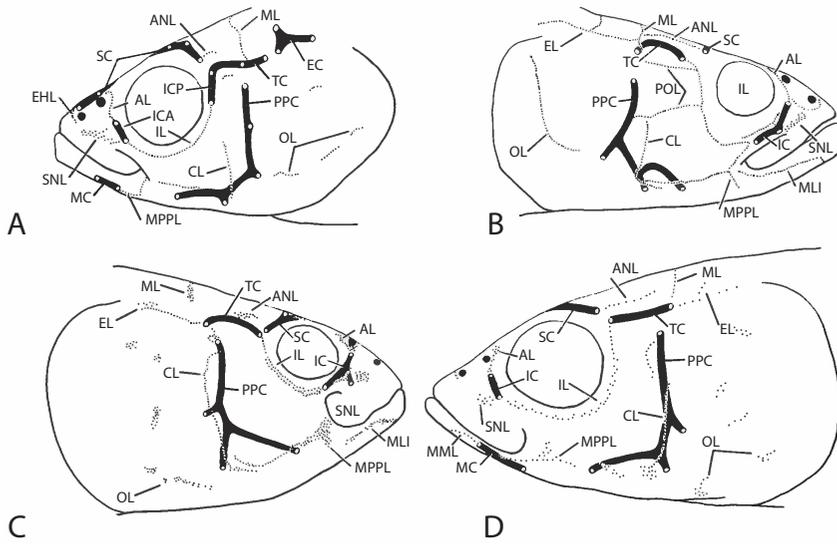


Figure 19.30. Head sensory canals, pores, and pitlines (lateral view) in the (A) Olympic Mudminnow, *Novumbra hubbsi*; (B) Alaska Blackfish, *Dallia pectoralis*; (C) Eastern Mudminnow, *Umbra pygmaea*; and (D) European Mudminnow, *U. krameri* (redrawn from Nelson 1972). Abbreviations as in Fig. 19.28. (A) UMMZ187427, 18 mm SL; (B) AMNH 1526, 34 mm SL; (C) AMNH 22745, 25 mm SL; (D) UMMZ 185076, 13 mm SL.

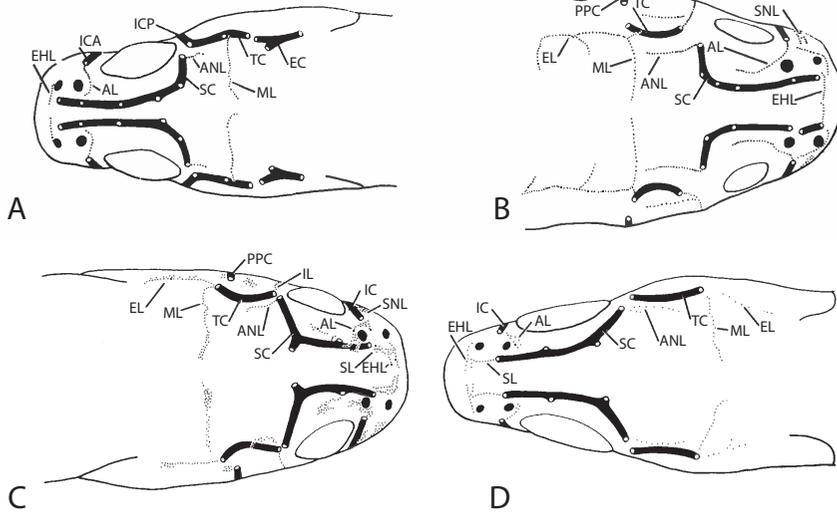


Figure 19.31. Head sensory canals, pores, and pitlines (dorsal view) in the (A) Olympic Mudminnow, *Novumbra hubbsi*; (B) Alaska Blackfish, *Dallia pectoralis*; (C) Eastern Mudminnow, *Umbra pygmaea*; and (D) European Mudminnow, *U. krameri* (redrawn from Nelson 1972). Abbreviations as in Fig. 19.28.

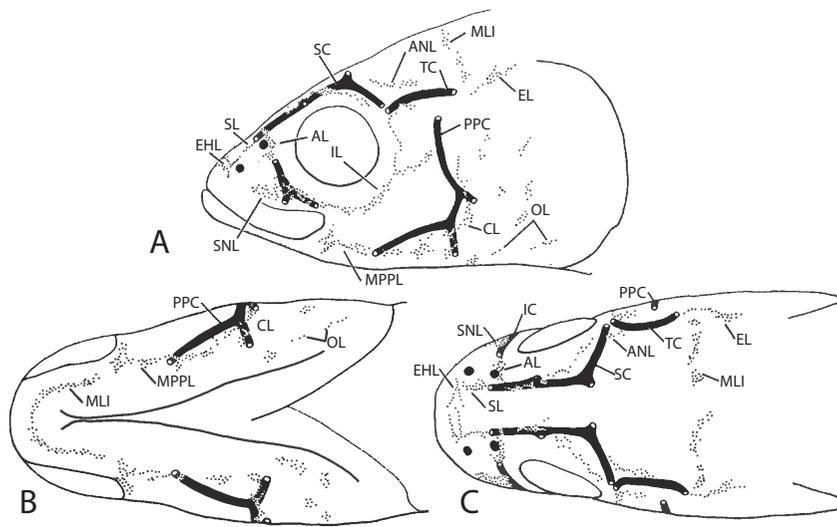


Figure 19.32. Head sensory canals, pores, and pitlines in the Central Mudminnow, *Umbra limi*. (A) Lateral view; (B) ventral view; (C) dorsal view (redrawn from Nelson 1972). Abbreviations as in Fig. 19.28.

of *Esox* and suggests interesting avenues of research into the evolution and maintenance of genomic synteny.

Sex Determination in *Esox lucius* and *E. masquinongy*

Eggs of the Northern Pike experimentally manipulated into developing without genetic input from sperm generate exclusively female offspring. This indicates females of this species are homogametic, and the species has an XX:XY sex-determination system (Luczynski et al. 1997). Similar experiments on the Muskellunge produced more ambiguous results, but females of this species apparently are heterogametic because a few gynogenetically (no genetic contribution by sperm, only initiates ovum development) derived males were observed, suggesting the action of a WZ:ZZ sex-determination system (Rinchard et al. 2002). Although no readily identifiable sex chromosomes are in the karyotypes of these *Esox*, incipient heterochromatic differentiation between homologues was correlated with sex in a European population of the Northern Pike in which only male karyotypes possess a chromosome with a distinct telomeric C-band.

Karyotype of *Novumbra*

The Olympic Mudminnow karyotype has 48 chromosomes (Beamish et al. 1971; Crossman & Ráb 1996) consisting of two pairs of metacentric, five pairs of submetacentric (centromere closer to the middle), seven pairs of subtelocentric (centromere closer to one end), and 10 pairs of acrocentric chromosomes. Crossman & Ráb (1996) consider the metacentric and submetacentric chromosomes as biarmed resulting in an FN = 62 (number of major chromosome arms). This suggests that the karyotype of the Olympic Mudminnow may represent a linkage between a hypothetical esocoid ancestor (with $2n = 48$, FN = 48) with the unusual karyotype of the Alaska Blackfish by pericentromeric inversions (chromosome inversion that includes the centromere) and amplifications of NOR sites (Crossman & Ráb 2001). The genome size in the Olympic Mudminnow is 2.08 pg/cell (Beamish et al. 1971).

Intraspecific Karyotypic Variation in *Dallia pectoralis*

Among species of *Dallia*, the karyotypic characteristics are described only for the Alaska Blackfish. The species has a mixture of metacentric, submetacentric, and ex-

tremely small acrocentric chromosomes with $2n = 78$ (Crossman & Ráb 1996; Beamish et al. 1971), but $2n$ varies within individuals and among populations. Interestingly, different modal diploid chromosome numbers characterize populations of Alaska Blackfish in the Yukon and Colville river drainages. Fish from the Yukon River system exhibited an unstable karyotype with a modal $2n$ number of 78 (range 71–79). In contrast, Colville River fish had an invariable, fixed karyotype of $2n = 74$ (Crossman & Ráb 1996). This difference may be grounds for taxonomic separation, but to date separation is not formally proposed.

Genome Size and Karyotype Changes in *Umbra*

Gross genomic organization in *Umbra* shows significant intraordinal and interspecific variation. The estimated DNA content of Central Mudminnow and Eastern Mudminnow cells is about two times that of all *Esox*, *Novumbra*, and *Dallia*, leading Beamish et al. (1971) to conclude that the tendency at that time to include *Umbra*, *Novumbra*, and *Dallia* in the same family might be ill advised. Although the North American species of *Umbra* have genomes >2.5 times larger than the European Mudminnow (Crossman & Ráb 1996), they possess half as many chromosomes ($2n = 22$, metacentric and submetacentric) as their European congener ($2n = 44$, acrocentric; Beamish et al. 1971; Ráb 1981). The genome size and chromosome number of European Mudminnows more closely resemble those of other esociforms and other basal fishes. As such the evolution of the genome of the North American species of *Umbra* must have involved significant amplification of DNA sequences accompanied by the pairwise fusion of all chromosome elements in the ancestral karyotype (Gornung 2013). Whether the two events are related is unknown, but the coinciding karyotypic and genome-size changes evident among species of *Umbra* are possibly the result of processes with genome-wide consequences, which may play an important role in molecular and organismal evolution (e.g., repetitive element amplification and repetitive sequence-mediated chromosomal rearrangements).

The relatively simple gross genomic organization in the North American species of *Umbra* (22 large, metacentric and submetacentric chromosomes) made this karyotype suitable for the study of factors that affect genomic stability, such as the mutagenic effects of radiation and environmental pollutants (Kligerman et al. 1975). At least two laboratory cell lines derived from fin epithelium of the Central Mudminnow were developed, and the effects of

radiation and mutagenic substances on their karyotypes investigated (Suyama & Etoh 1988; Park et al. 1989).

Hybridization and Introgression

Hybridization among species of *Esox* is common in nature and is documented experimentally (Crossman & Buss 1965; Crossman & Meade 1977; Reist & Crossman 1987). Fertile hybrids of the Chain and Grass Pickerel occur in the wild where their ranges overlap. Similarly, hybrids between the Northern Pike and Muskellunge (the tiger muskellunge) are observed frequently in the wild and some anglers favor them. Female tiger muskellunge are sometimes fertile, but males are always infertile. Infertile hybrids between the Northern Pike and members of *Kenoza* were produced in the lab and documented in the wild (Crossman & Buss 1965; Herke et al. 1990). In light of the fossil evidence suggesting that the two subgenera of *Esox* diverged >50 mya (see fossil record section), it is remarkable that hybrids between species of these two lineages are viable even if sterile.

To document the genetic basis of morphometric variables, artificial hybrids between the Redfin Pickerel and Grass Pickerel were produced and reared in a common laboratory environment (Reist & Crossman 1987). Ten morphometric variables were measured on the F_1 and F_2 hybrids (parentage known), parental samples across the range of each subspecies, and specimens from the intergrade zone (unknown but likely mixed parentage) (Figs. 19.33 and 19.34). Univariate and multivariate analyses statistically confirmed the distinctiveness of the two subspecies. The multivariate centroid for the F_1 and F_2 hybrids was intermediate between Redfin Pickerel and Grass Pickerel samples in discriminant space (Fig. 19.34). The intermediacy of the hybrids indicated at least a partial ge-

netic basis for the morphometric variables, but hybrid individuals tended to resemble the male parent. Interestingly, the intergrade individuals most closely resembled the Grass Pickerel, a result consistent with an earlier study (Crossman 1966), although they did show variability in multivariate discriminant space. The multivariate centroid for the intergrades was near the centroid of the Grass Pickerel (Fig. 19.34). The authors offered five explanations for the non-intermediacy of the intergrades. First, the variation is genetically based, and the fish examined were intergrades, but proximity to pure Grass Pickerel populations caused the skewed placement toward that subspecies. Second, the variation is genetic but distributed clinally to cause the gradation. Third, the specimens thought to be intergrades were actually Grass Pickerel, implying a narrower zone of intergradation than Crossman (1966) originally delineated. Fourth, the variation is nongenetic and caused by clinal responses to the environment. Finally, the specimens were indeed intergrades, but equal genetic contribution by the parental types is untrue for fish; that is, the overlap of F_1 hybrid crosses with the parental centroid indicated in some crosses the offspring resemble the male parent. They concluded the correct explanation is likely some combination of these. Despite the solid morphological evidence for differentiation in the two subspecies and the well-defined morphological intergrade zone based on two scale counts and one measurement (Crossman 1966; Reist & Crossman 1987), genetic investigations of the population structure or historical demographics across the range of these two wide-ranging and clearly differentiated forms or their intergrade zone have limited geographic sampling (Grande et al. 2004; see April et al. 2011, 2013; see phylogenetic relationships section). DNA barcoding provided strong support (2–2.8%)



Figure 19.33. Intergrade of the Redfin Pickerel \times Grass Pickerel, *Esox americanus americanus* \times *E. a. vermiculatus*, in McBride Slough Spring, Wakulla County, Florida, in October (courtesy of © Isaac Szabo / Engbretson Underwater Photography).

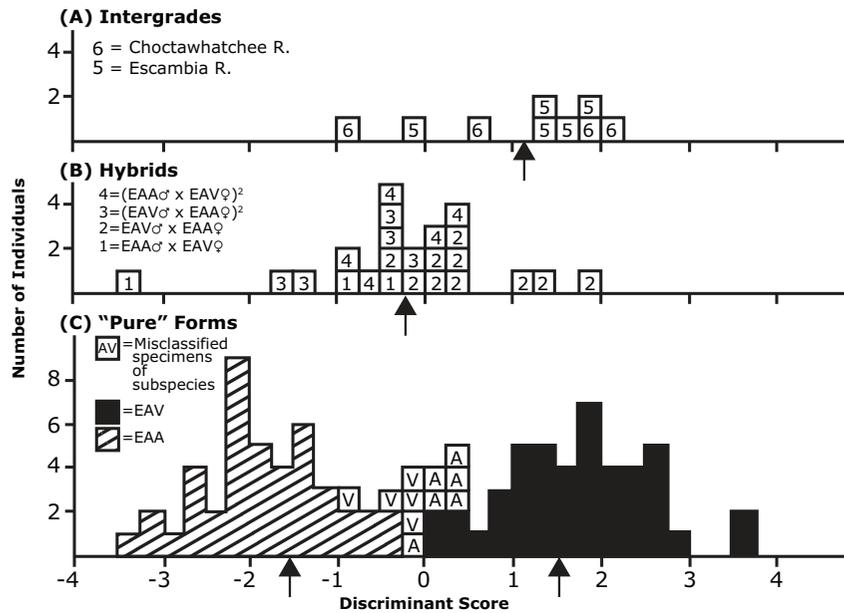


Figure 19.34. Histograms of discriminant function scores for the Grass Pickerel (*Esox americanus vermiculatus*), Redfin Pickerel (*Esox a. americanus*), their hybrids, and intergrades. Arrows indicate respective centroids; EAA or A, *E. a. americanus*; EAV or V, *E. a. vermiculatus*. (A) Scores of intergrades. (B) Scores of hybrids. Symbols 1 and 2 are F₁ hybrid crosses as indicated on the figure, 3 is the F₂ cross (EAV♂ × EAA♀) × (EAV♂ × EAA♀), and 4 is the F₂ cross (EAA♂ × EAV♀) × (EAA♂ × EAV♀). (C) Distribution of scores of reference parental samples. The open boxes indicate misclassified individuals (redrawn from Reist & Crossman 1987).

for divergence between Redfin Pickerel and Grass Pickerel (April et al. 2013) and provided evidence for large-scale hybridization between the Redfin Pickerel and Chain Pickerel (Grande et al. 2004; Hubert et al. 2008; April et al. 2011).

Interspecific Genetic Variability: *Esox*

Few reports on the population genetics of esociform species are available, and most focus on the economically important Northern Pike and Muskellunge (see genome size and karyotype changes in *Umbra* subsection, hybridization and introgression subsection, and gene expression levels and tissue specificity subsection, this section). Allozyme and microsatellite allele variation were used to examine the genetic diversity of and relationships between different populations of the two species with some interesting results, particularly concerning the genetic variability of the Northern Pike. In addition, sequencing of introns on the growth hormone across all *Esox* revealed unique minisatellites.

Studies of allozyme loci and microsatellite variation in populations of the Northern Pike indicated relatively low genetic diversity. Only a small percentage of the loci examined were polymorphic (e.g., 3–10%) (Seeb et al. 1987). The microsatellite genetic diversity of this species is reportedly lower than that of other animals with notoriously genetically homogeneous populations (e.g., cheetah, social wasps) (Senanan & Kapuscinski 2000). Even so, microsatellite-based studies revealed detectable and con-

sistent genetic differences among populations sampled from Europe, Asia, and North America. In addition, variability in mtDNA amplified fragment length polymorphism supported the distinctiveness of the Southern Pike (*Esox cisalpinus*) (Lucentini et al. 2011). Overall, genetic variability in extant populations of the Northern Pike is consistent with the idea this species survived the latest glacial maxima in a limited number of refugia and the sizes of the populations that survived in those refugia to eventually expand into its present range were effectively small.

Seventeen pairs of primers were developed and microsatellite markers amplified on 30 Northern Pike from the St. Lawrence River and tested on all five species of *Esox* (Ouellet-Cauchon et al. 2014). Average genetic variation was moderate but highly variable (mean number of alleles = 6.88, range = 2–23; mean expected heterozygosity = 0.49, range = 0.033–0.950; mean observed heterozygosity = 0.51, range = 0.033–0.967). All loci were successfully amplified in the Northern Pike from North America and Europe and Amur Pike. Among other species the number of successfully amplified loci varied from eight to 11 and the quality of amplification was lower than for Northern Pike and Amur Pike.

Microsatellite marker variation also was used to test natal site fidelity in the Northern Pike. Spawning individuals of the species may return to the same spawning grounds year after year (see reproduction section), but whether these individuals spawn in the same area where they hatched is unclear (see Engstedt et al. 2014). A small but significant amount of genetic differentiation as mea-

sured by microsatellite allele frequencies occurred between sympatric populations of the Northern Pike that spawn in different areas of the same lake (Miller et al. 2001). These results are consistent with natal site fidelity because in its absence, spawning site fidelity alone is not expected to give rise to genetic differences between populations spawning in close proximity. However, the low level of genetic variation observed in the study makes interpretation of the results problematic. Low genetic variation and the lack of structure among populations in the northcentral United States may have resulted from recolonization from a common glacial refugium, but stocking programs may also have obscured past structure (Miller & Senanan 2003).

Genetic analyses have helped determine the rapidity and extent of post-glacial dispersal from non-glaciated refugia. Ancient DNA was extracted from the remains of a Northern Pike (*E. cf. lucius*) in interior Alaska dated to 8,820 years before present. The DNA of the specimen was identical to modern Northern Pike and supports a biogeographic scenario involving rapid dispersal of this species from glacial refugia in the northern hemisphere after the last glaciation (Wooler et al. 2015). In another study, three well-defined mtDNA lineages of the Northern Pike indicated population expansion following isolation and dispersal from discrete glacial refugia. One lineage has a modern Holarctic distribution suggesting transcontinental dispersal from a single Eurasian or Beringian refugium (Skog et al. 2014).

The limited information available for populations of Muskellunge indicates that genetic variability, as measured with allozymes, mitochondrial DNA haplotypes, and randomly amplified polymorphic DNA (RAPDs), is considerably higher than that measured in populations of the Northern Pike (summarized by Senanan & Kapuscinski 2000; Kapuscinski et al. 2013). An early study of allozyme variation (57 loci, 9 populations) of the Muskellunge, including some hatchery fish, revealed polymorphism at 10 loci (Koppelman & Philipp 1986). Interestingly, the distribution of this variability among populations suggested some degree of genetic distinctiveness. Because information on the genetic structure was lacking, Muskellunge are typically managed as single stocks and have been stocked across drainage boundaries, even where evidence for stock structure exists (Crossman 1990; Farrell et al. 2007; Miller et al. 2009, 2012; Kapuscinski et al. 2013; Scribner et al. 2015). Microsatellite genotyping of the Muskellunge in Lake Huron and Georgian Bay indicated small, genetically discrete populations (Wilson et al. 2016), providing evidence for both high natal

site fidelity (Miller et al. 2001) and reproductive homing (Crossman 1990). Although Muskellunge can travel much greater distances (LaPan et al. 1996; Weeks & Hansen 2009), sites 20 km apart were genetically distinct, and divergence increased with distance between spawning sites (Wilson et al. 2016). Muskellunge in the North Channel and Georgian Bay showed significant spatial genetic structure despite the lack of habitat barriers to movement, and greater interpopulation genetic differences relative to other Great Lakes populations (Kapuscinski et al. 2013; Scribner et al. 2015) may result from a different native ancestry and a lack of introgression from stocking (Wilson et al. 2016). Clearly, further studies are needed to identify genetic structuring across the range of the species and to determine if the three geographical variants recognized in this species have a genetic basis (see genus *Esox* subsection, diversity and distribution section).

Seven polymorphic microsatellite loci with 2–11 alleles and heterozygosities between 0.190–0.917 were developed in Muskellunge and amplified across two other species of *Esox* (Reading et al. 2003). The seven microsatellite loci developed in Muskellunge amplified monomorphic products in Northern Pike and three of the seven amplified monomorphic products in Grass Pickerel. Northern Pike exhibited alleles at five and Grass Pickerel at one of the loci that was diagnostically different in size from the range of alleles found in Muskellunge. The amplification of products highly different in size, even though monomorphic, may prove useful as species diagnostic markers (e.g., identification of hybrids) (Reading et al. 2003).

Genetic studies to date in *Kenoza* used allozymes and DNA bar codes. A study of allozyme variation in populations of Grass Pickerel occupying different areas along a short stream reach in Pennsylvania revealed some genetic diversity. This variability, however, did not differentiate among spatially defined populations, and it remained stable over the time period of the study (1971–1973) (Eckroat 1975). Because the study included only one locus (Lactate Dehydrogenase-A), diversity measures could not be calculated. Redfin and Chain Pickerel in two regions in Canada had high levels of genetic divergence in the cytochrome oxidase *c* I gene (>3%) with *E. a. americanus* from the St. Lawrence River differentiated from *E. a. vermiculatus* from the Laurentian Great Lakes (Hubert et al. 2008). More genetic divergence was observed between the two subspecies than with *Esox niger*. Samples of Chain Pickerel from Quebec and New Brunswick were more closely aligned with Quebec samples of Redfin Pickerel than Redfin Pickerel was with Grass Pickerel.

The growth hormone gene was examined in five species of *Esox* by cloning the fourth intron of the gene (Barnett et al. 2007). A 33-nucleotide minisatellite in the fourth intron is present in copy numbers ranging from seven to 16 among the species with no observed intraspecific variation in copy number (7 repeats in Chain and Grass Pickerels; 12 in Northern Pike; 13 in Muskellunge; and 16 in Amur Pike) (Barnett et al. 2007). This apparently unique minisatellite is present as a single copy element in all salmonids, indicating a recent expansion in the species of *Esox* since their divergence from a common ancestor. Point mutations and deletions in the minisatellites suggest a model for the evolution of this genetic element and corroborate molecular phylogenies (e.g., López et al. 2004) for the five members of the genus. Alignment of introns among the five species based on repeat number and shared polymorphisms places them into their hypothesized phylogenetic relationships. The discovery of the novel structure of the growth hormone gene across *Esox* raises the question of whether it is present in other esociforms.

Phylogeography: *Novumbra*

Range-wide genetic analysis from 21 whole-genome microsatellites of the Olympic Mudminnow (DeHaan et al. 2014) supported an earlier hypothesis that its biogeography was structured by glacial refugia, which existed during the Pleistocene, with limited subsequent range expansions (Meldrim 1968). High population genetic structure among sampled populations ($F_{ST} = 0.273$) and a correspondingly high level of genetic isolation in populations along the Olympic Coast ($F_{ST} = 0.350$) indicate historically limited gene flow (DeHaan et al. 2014). Populations of the Olympic Mudminnow in eastern Puget Sound (Cherry Creek drainage, Snohomish River drainage, and Issaquah Creek, Lake Washington drainage) had an allelic structure more similar to populations on the southern coast of the Olympic Peninsula than the nearby Chehalis River drainage. The lack of unique mtDNA alleles (Pickens 2003), which would reflect glacial relicts if present, suggests Olympic Mudminnow populations in eastern Puget Sound drainages are the result of intentional introductions.

Phylogeography: *Dallia*

A phylogeographic study of the Alaska Blackfish revealed a significant level of interspecific variability largely corresponding to historical and contemporary barriers with little to no mixing of mitochondrial haplotypes among geo-

graphic areas. The study examined the cytochrome *c* oxidase I gene and the control region and included 188 individuals from 23 localities broadly representing the range of the species across mainland Alaska, St. Lawrence Island in the Bering Sea, and three sites in eastern Siberia (Chukotka Peninsula), Russia (Campbell & López 2014). Phylogenetic and molecular variance analyses supported delineation of four distinct phylogeographic units: Interior Alaska (sample locations 1–2, 4–6); Norton Sound coastal drainages (13–14); Arctic Coastal Plain (samples north of the Brooks Range) (16–20); and Bering Coast, including populations from areas on or surrounding the Bering land bridge (eastern Siberia, islands on the Bering Sea, and western Coastal Alaska) (3, 7–12, 15, 21–23) (Fig. 19.35). Interestingly and perhaps of taxonomic relevance, populations north and south of the Brooks Range shared no haplotypes, which is consistent with chromosome differences noted between populations to the north and south of the range (see karyotypic stability in *Esox* subsection, this section). This geographic barrier apparently promoted development of distinct gene pools of Alaska Blackfish. Notably, no evidence was indicated for a distinct mitochondrial lineage at the three localities sampled in eastern Asia. Subsequent work including two nuclear gene introns, however, indicated an eastern Asian cluster (the West Beringia population) (Fig. 19.35) related to but distinct from the Alaskan coastal population (Campbell et al. 2015). The mitochondrial and nuclear diversity and spatial distribution patterns are consistent with persistence of lineages in multiple refugia through the last glacial maximum (Campbell & Lopez 2014; Campbell et al. 2015). Genetic structure within Alaskan populations was greater than that across the Bering Sea (Campbell et al. 2015). Interestingly, estimated pairwise migration rates between the populations was highest (2.42 individuals/generation) from West Beringia to Coastal Alaska populations followed by migration from Interior Alaska to Coastal Alaska populations (1.57). Other migration estimates ranged from 0.15 to 0.52 immigrants/generation.

Intraspecific Genetics of *Umbra*

Only scant genetic information is available for the North American Mudminnows. Kopp et al. (1992, 1994) measured heterozygosity (allozyme alleles at 21 loci) in populations of Central Mudminnows to determine the effect of stressful environmental variables (e.g., low pH, high aluminum concentration) on the genetic variability of individuals and the population. Control populations exhibited heterozygosity values ranging from 0.130 to 0.142.

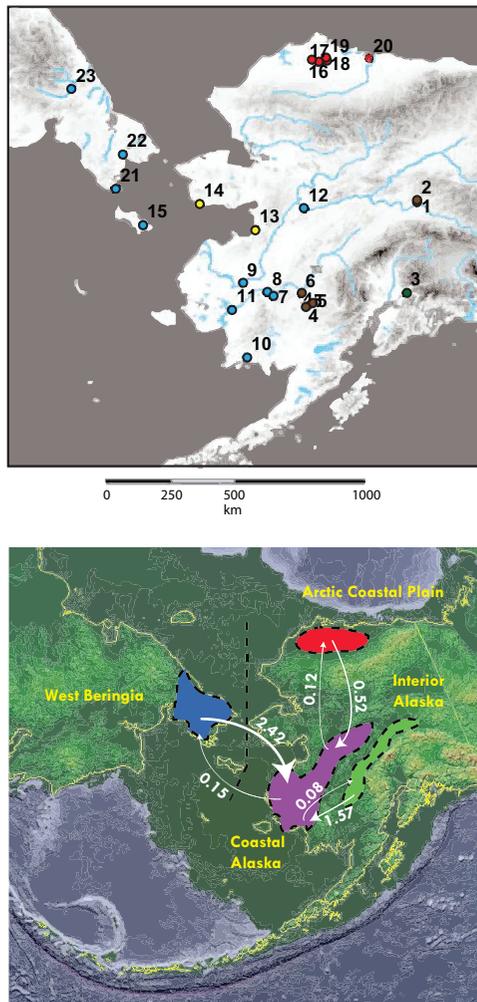


Figure 19.35. (upper) Map of the major phylogeographic regions revealed in a mtDNA analysis of 188 specimens of the Alaska Blackfish, *Dallia pectoralis*, sampled across the Alaska mainland and St. Lawrence Island (sample locations 1–20) and Chukotka, Russia (sample locations 21–23). (lower) Migration rates among Beringian *Dallia* populations. Migration rates in individuals/generation since the time of divergence (t) between populations of *Dallia* estimated by Isolation with Migration analyses. Approximate geographic distribution of populations defined by clustering algorithms are outlined with black dashed lines (Norton sound samples excluded). Arrows reflect the magnitude of migration rate. Current coastlines and international borders (yellow lines) are overlaid onto a map available from the U.S. National Geophysical Data Center of -110 m sea level (dark green layer) corresponding to the last glacial maximum (redrawn from Campbell & Lopéz 2014, upper, and Campbell et al. 2015, lower).

Heterozygosity values were significantly lower in stressed populations. In these experiments, the more genetically variable (i.e., heterozygous) individuals were significantly more tolerant of acutely toxic conditions (Kopp et al.

1994). Two Canadian populations of Central Mudminnows exhibited >2.7% genetic divergence of cytochrome c oxidase I (COI) (Hubert et al. 2008).

Gene Expression Levels and Tissue Specificity

Studies on gene expression illustrate another aspect of esociform genetics beyond karyotypes and intraspecific genetic variation. Genetic regulation of white muscle cytochrome c oxidase (COX) activity in the Northern Pike and Central Mudminnow indicated COX activity was significantly higher in winter in Central Mudminnows (3.5fold) but did not increase in the Northern Pike (Bremer & Moyes 2011). Laboratory acclimation to winter temperatures did not alter COX activity in Central Mudminnows, suggesting a role for nonthermal cues.

Exposure to mutagens affects tissue-specific gene expression, produces DNA adducts (DNA bound to a cancer-causing substance), and induces chromosomal and nuclear anomalies in Pikes and Mudminnows. Northern Pike exposure to perfluorinated compounds in municipal waste water resulted in tissue-specific expression of eight gene products in blood (metallothionein and vitellogenin), muscle and gill (metallothionein, glutathion-S-transferase, superoxide dismutase, catalase and cytochrome P450 1A1), and liver (vitellogenin, estrogen receptor beta-2, and cytochrome P450 3A27) tissues (Houde et al. 2013). Juvenile Northern Pike subjected to a single exposure (intra-peritoneal injection or food) of a mutagenic mixture of compounds exhibited rapid, dose- and time-dependent expression of DNA adducts in liver and intestine. Experimentally induced chromosomal mutations (sister chromatid exchanges) and nuclear anomalies (micronuclei) are described for *Umbra* spp. by several authors (Kligerman & Bloom 1976; Kligerman 1979; Metcalfe 1988; Alink et al. 2007). These abnormalities were induced by direct exposure to or injection of known mutagens, such as ethyl methanesulphonate and benzo(a)pyrene (Hooftman & Vink 1981; Hooftman & de Raat 1982).

Patterns of gene expression in *Novumbra*, *Dallia*, and *Umbra* revealed significant changes in the tissue specificity and the level of gene expression at 27 different loci (Kettler & Whitt 1986; Kettler et al. 1986). Two related, but different, measures of genetic distance from patterns of gene expression revealed a greater similarity between *Dallia* and *Novumbra* than between *Umbra* and *Dallia* or *Novumbra*, reflecting current phylogenetic relationships. Unfortunately, no comparable expression data are available for any of the species of *Esox*.

PHYSIOLOGY

Although factors affecting growth and reproduction of the large esocids are best known (see ecology and reproduction sections, respectively), esociforms exhibit several important, and extreme, physiological adaptations. Notable among these are cold tolerance in *Dallia* and *Umbra*, adaptations for air breathing in hypoxic conditions, and tolerance of low pH and brackish waters. Here we focus on aspects of esociform tolerances to temperature, hypoxia, pH and alkalinity, salinity, and swimming ability. Sensory adaptations are treated in the morphology section.

Temperature Tolerance

The temperature tolerances of esociform species cover a broad range. Latitudinal ranges and the mean annual temperatures characteristic of those latitudes differ among species (Newbrey et al. 2008). For example, *Esox lucius* inhabits latitudes from 37 to 71 degrees N latitude in areas with mean annual temperatures ranging from -7° to 15°C . Its southern extent appears to be temperature-limited; Northern Pike are absent from the Mississippi and Ohio Rivers south of the $31\text{--}32^{\circ}\text{C}$ isotherm and summer die-offs occur in midwestern lakes and reservoirs when surface temperatures reach 32°C . *Dallia* range from 58 to 71 degrees N latitude with mean annual temperatures of $0\text{--}3^{\circ}\text{C}$. At the other extreme, the ranges of *Esox niger* and *E. americanus* extend from 27 to about 46 degrees N latitude in regions with mean annual temperatures of $2\text{--}23^{\circ}\text{C}$. The species of *Umbra*, *Novumbra*, and both *Esox reichertii* and *E. masquinongy* inhabit regions with intermediate mean annual temperatures. The oldest esociforms likely inhabited much warmer climate zones between the Cretaceous and Early Eocene. Large body sizes in the subgenus *Esox* and to some extent, *Dallia*, may represent adaptations to climatic cooling during the latter part of the Cenozoic (Newbrey et al. 2008). Muskellunge occur throughout the Ohio River basin (including the Tennessee-Cumberland River systems) south of the 31°C isotherm. *Novumbra* individuals tolerate temperatures of $0\text{--}27^{\circ}\text{C}$ but preferred temperatures are $11\text{--}14^{\circ}\text{C}$ as inferred from a habitat occupancy study (Meldrim 1968).

Some information is also available for large *Esox* spp. on critical thermal maxima (CTM) and preferred temperature versus optimal temperature for growth. Northern Pike acclimated to temperatures of 25.0 , 27.5 , and 30.0°C ceased

feeding at temperatures of $32.0\text{--}35.3^{\circ}\text{C}$ and mortality appeared to result from starvation (Scott 1964). Muskellunge ranging in age from 1–51 days post-hatching had a CTM of $27\text{--}36^{\circ}\text{C}$ (acclimation temperature range, $7\text{--}22^{\circ}\text{C}$) (reviewed by Beiting et al. 2000). Northern Pike and Muskellunge showed comparable results based on experimental determinations of growth optima and preferred and lethal temperatures (reviewed by Jobling 1981). Optimum temperature for growth is slightly higher for young-of-the-year ($22\text{--}23^{\circ}\text{C}$), than for juveniles and subadults (Casselman 1996). Muskellunge larvae held at ambient temperatures of about 20°C had an average CTM of 32.8°C ; CTM increased from 29.9°C on day 4 (at the onset of swim-up) to 35.6°C on day 31 (Bonin & Spotila 1978). Laboratory experiments and predictions from bioenergetics models suggested that Northern Pike should grow faster than Muskellunge at cool temperatures, but slower than Muskellunge at warm temperatures ($>25^{\circ}\text{C}$), although no significant differences in metabolic rates were observed (Bevelhimer et al. 1985). Preferred temperatures of Chain Pickerel was 24°C and Grass Pickerel was 26°C ; Chain Pickerel avoided temperatures $>27^{\circ}\text{C}$ and $<20^{\circ}\text{C}$ (Ferguson 1958; Coutant 1977; Wismer & Christie 1987).

Temperatures affect abundance, growth, metabolic rate, and habitats occupied by esociforms. Canadian fisheries surveys report an increase in Northern Pike abundance in eastern Lake Ontario over seven decades, correlated with a significant increase in water temperature (Casselman & Dietrich 2003). Growth rate increases rapidly at $>10^{\circ}\text{C}$ and is highest between 19°C (for biomass) and 21°C (for length); upper lethal temperature is 29.4°C , and the species can tolerate temperatures $\geq 0.1^{\circ}\text{C}$ as lakes approached freeze-up (Casselman 1978). In laboratory studies, the final preferred temperature of the Northern Pike was slightly higher ($2\text{--}3^{\circ}\text{C}$) than the optimum for growth (McCauley & Casselman 1981). Use of temperature-sensitive radio transmitters on adult Northern Pike in two southern Ohio impoundments indicated that, when water temperature was $>20^{\circ}\text{C}$, fish sought a cooler average temperature, but they sought significantly cooler temperatures only when the surface was $>25^{\circ}\text{C}$. Once the surface temperature reached 25°C , fish sought the coolest available water with >3 mg/l dissolved oxygen. Northern Pike maintained body temperatures $\leq 25^{\circ}\text{C}$ when surface water temperatures were $>26^{\circ}\text{C}$. Adult fish lost weight during this period of habitat constriction (Headrick & Carline 1993).

The ability of many esociforms to survive extremely low temperatures is poorly understood despite long-standing

interest in this aspect of esociform physiology, which originated in anecdotal accounts from the earliest encounters of populations of Alaska Blackfish by western explorers. According to these accounts individual Alaska Blackfish can survive complete freezing of their tissues for prolonged periods of time. Barton Evermann (in a letter to the editors of *Forest and Stream*, 18 January 1913) recounted the enduring story (often repeated but largely undocumented) of native Alaskans capturing Alaska Blackfish in the autumn and retaining them frozen in baskets to be fed to their sled dogs during winter. The fish, allegedly thawed by the warmth of the dog's stomachs, revived sufficiently to cause the dogs to regurgitate them alive (Turner 1886:101; "This I have seen, but have heard some even more wonderful stories of this fish."). Scholander et al. (1953) investigated the claim and found that Alaska Blackfish can survive partial freezing, if only for a few days, but not being frozen solid. Extensive tissue damage eventually led to death. Over a temperature range of 0–15°C, Alaska Blackfish had the lowest metabolic rate of any Arctic fish examined.

Other anecdotes confer similar tolerance to the European and Central Mudminnows. For example, Berg (1948) related an account of individuals of the European Mudminnow surviving >2 days of winter temperatures without water. The fact that some populations of Alaska Blackfish and the Central Mudminnow occur in shallow water bodies that undergo extensive winter freezing nurtured the expectations raised by those early accounts (e.g., Gudkov 1998). So far, however, careful observation indicates that, although well suited to survive cold-water temperatures, these species cannot survive complete freezing and partial freezing usually results in necrosis of the affected tissue (e.g., Scholander et al. 1953). Whether physiological (e.g., seasonal production of freeze-resistant substances) or behavioral (e.g., local movement to suitable microhabitat) adaptations allow these species to inhabit areas with apparent complete winter freezing (e.g., shallow Siberian lakes) is unstudied. Regardless, most esociforms are clearly well adapted to low water temperatures and remain active during the winter even under ice cover (Scott & Crossman 1973). For example, 14 of 66 Central Mudminnows examined had fed (food in stomach or intestine) in Fish Lake, Ontario, under the ice at water temperatures of 4°C (Keast 1968).

Hypoxia Tolerance: *Esox* and *Novumbra*

Northern Pike tolerate depressed oxygen concentrations ≤ 0.3 mg/l in shallow lakes and reportedly survive levels ≤ 0.04 mg/l although survival may depend on lake trophic

condition. Northern Pike exhibited 100% mortality during 1 h exposures to oxygen concentrations of 0.5–2.0 mg/l in highly eutrophic lake water. As in most fishes, critical oxygen concentration depends on temperature (reviewed by Casselman 1978, 1996; Casselman & Lewis 1996). In Northern Pike acclimated at 15 and 19°C, dissolved oxygen concentrations of 4.5 and 5.0 mg/l had no effect on survival, larval development, and onset of feeding. At concentrations < 2.5 mg/l, hatching and survival were significantly impaired (Siefert et al. 1973). Under experimentally induced hypoxia (dissolved oxygen < 3 ppm), Northern Pike growth rate and food consumption were reduced (Adelman & Smith 1970). Greater relative survival of smaller individuals suggested that small Northern Pike were more resistant to hypoxia-related winterkill (Casselman & Harvey 1975).

Low dissolved oxygen responses affect feeding, vertical and horizontal distribution, and survival in Pikes and Mudminnows. Stress avoidance (seeking more oxygenated conditions) in the Northern Pike begins at concentrations < 4 mg/l and feeding ceases when oxygen concentration is < 2 mg/l. The vertical and horizontal fish distribution under ice was a function of low dissolved oxygen and high carbon dioxide (Magnuson et al. 1985). Northern Pike can avoid low dissolved oxygen in late winter by occupying deeper habitats (Casselman 1978), and juveniles are attracted to traps with an aerated discharge under the ice (Johnson & Moyle 1969). Eutrophic lakes experience winterkill, particularly when surface ice is cloudy or snow-covered. Resident Northern Pike and Grass Pickerel appeared to actively seek areas of higher dissolved oxygen in a stream inlet. In lakes where no inlet or outflow occurred, survival of Northern Pike was greater at dissolved oxygen concentrations > 0.5 mg/l with severe winterkill at 0.2–0.0 mg/l; Grass Pickerel survived at lower concentrations (dissolved oxygen between 0.1 and 0.3 mg/l) (Cooper & Washburn 1949). Sudden onset of near-anoxic conditions (0.01–2.0 mg/l) following Hurricanes Fran, Bonnie, and Floyd resulted in mortality of Chain Pickerel and other fishes (Mallin et al. 2002).

Although it lacks morphological adaptations for air breathing, individuals of *Novumbra* can tolerate oxygen levels < 0.2 mg/l (Meldrim 1968). Olympic Mudminnows occurred in wetland habitats as dissolved oxygen concentrations decreased from 10 to 0 mg/l (Henning et al. 2007) and occupied riverine habitats with dissolved oxygen concentrations of 1.1–11.5 mg/l (Kuehne & Olden 2016). Olympic Mudminnows may actively seek areas with low dissolved oxygen, low temperatures, and high

conductivity associated with groundwater contributions from springs (Meldrim 1968; Kuehne & Olden 2016).

Hypoxia and Air Breathing: *Dallia* and *Umbra*

The ability to breathe atmospheric oxygen is documented in *Dallia* and *Umbra*. In both, modified vascularization of areas of the gut or swim bladder surface serve in gas exchange (see morphology section). Facultative air breathing enables Alaska Blackfish to survive under hypoxic conditions that occur in warm shallow wetlands when summertime dissolved oxygen is <2.3 mg/l (Ostdiek & Nardone 1959; Crawford 1974; Morrow 1980) or by using trapped air bubbles in ice covered habitats during winter (Haynes et al. 2014). Individual Alaska Blackfish maintained normal metabolic rates at <2 mg/l dissolved oxygen by supplementing aquatic respiration with air breathing (Crawford 1971), which appears to be influenced by central carbon dioxide chemosensitivity (Hoffman et al. 2009). Alaska Blackfish could maintain standard oxygen uptake ($\dot{M}O_2$) in hypoxic conditions by increased aerial respiration (Fig. 19.36); when air was denied, standard $\dot{M}O_2$ was reduced by about 30–50%. Additional mechanisms must exist for Alaska Blackfish to survive hypoxic submergence during the winter, such as hypoxia-induced enhancement in the capacities for carrying and binding blood oxygen, behavioural avoidance of hypoxia, and suppression of metabolic rate (Lafevre et al. 2014).

Despite these adaptations, winter mortality in Alaska Blackfish may be significant (Campbell et al. 2014). Ob-

servations of winterkill may have resulted from methane discharge that is typical of the thermokarst lakes where Alaska Blackfish are frequently found on the Chukchi Peninsula (Gudkov 1998) and in Interior Alaska (Blackett 1962). Methane production in these lakes can be extremely rapid and average 73–88% by gas volume (Walter et al. 2008, 2010). When trapped under ice, methane can be oxidized aerobically (producing carbon dioxide) or anaerobically (producing hydrogen sulfide) in lethal concentrations (Scidmore 1957; Magnuson et al. 1985; Reiffenstein et al. 1992). If Alaska Blackfish exhibit the same behavior as described in Mudminnows, methane discharge trapped under ice would reduce the concentration of oxygen in trapped bubbles, leaving insufficient oxygen for survival. Methane bubbling, however, may be large enough to maintain open leads in the ice and contribute to the long-term survival of Alaska Blackfish. Subsistence fishermen frequently exploit the behavior as fish aggregate at the holes (Andersen et al. 2004) and refer to them as blackfish holes (Campbell et al. 2014).

The physiology of air breathing and some of its environmental and behavioral correlates were studied in the Central Mudminnow (Gee 1980), which is a facultative air breather that continuously breathes air when it is accessible. The fish appears to efficiently use both air and water-derived oxygen and to switch between the two modes of breathing depending on many variables, including water temperature, dissolved oxygen concentration, presence of conspecifics, availability of vegetation cover, and predator risk. Because fish swimming to the surface to gulp air

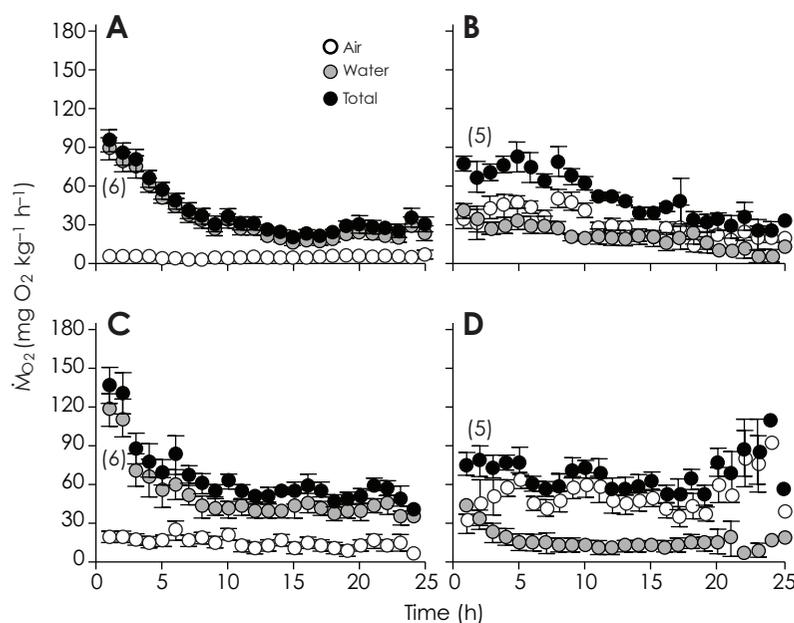


Figure 19.36. Bimodal oxygen uptake over 24 h in the Alaska Blackfish, *Dallia pectoralis*. Oxygen uptake ($\dot{M}O_2$) from air, water, and in total recorded over 24 h for 5°C (A, B) and 15°C (C, D) acclimated fish in normoxia (A, C: 19.8 kPa) and hypoxia (B, D: 2.5 kPa). Values are mean \pm SE. Different individuals were used in the four experimental treatment groups; sample sizes are given in parentheses (redrawn from Lafevre et al. 2014).

increases their predation risk, individuals of the Central Mudminnow switch from random to synchronized air breathing in the presence of simulated predators. An interesting aspect of the physiology of air breathing in the species is the relationship between buoyancy and the changes in swim bladder volume caused by air breathing and subsequent gas absorption. In the absence of simulated predators, buoyancy and air breathing are tightly coordinated to minimize the energy cost (increased swimming effort) incurred by changes in buoyancy caused by air breathing and gas absorption. When predator presence is simulated, this coordination is disrupted, which results in the fish spending more energy swimming against their changing or increasing buoyancy (Gee 1980).

Under ice-covered habitats, Central Mudminnows use bubbles composed of gas mixtures other than air for respiration (Klinger et al. 1982), likely an adaptation to the oxygen-depleted, carbon-dioxide rich water of northern winterkill lakes (Magnuson et al. 1983). Central Mudminnows held in field enclosures with air bubbles in a winterkill lake (dissolved oxygen near 0.0 mg/l) survived longer than fish in enclosures lacking air bubbles (Fig. 19.37). The oxygen content of the naturally occurring bubbles was 3% (range, 0–11%) at dissolved oxygen levels of 0.5 mg/l; the bubbles also contained 1–75% nitrogen and 23–98% methane (Klinger et al. 1982). In a series of labo-

ratory simulations of winterkill conditions (1.6–3.9°C water temperature, water surface covered), Central Mudminnows also frequently engulfed gaseous bubbles (Magnuson et al. 1983; Fig. 19.38). The use of bubbles was unrelated to methane or nitrogen content (0–80%) if all bubbles contained 20% oxygen. If oxygen content was varied (0–20%), fish visited bubbles randomly but remained longer and engulfed gas at lower frequencies at

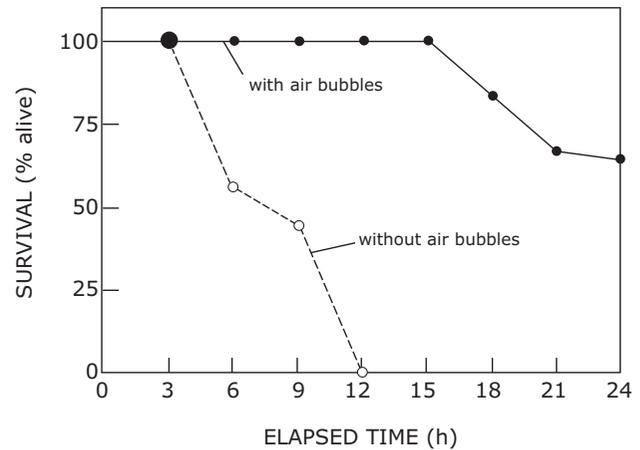


Figure 19.37. Survival of Central Mudminnows, *Umbra limi*, held in enclosures with air bubbles (closed circles) and without (open circles) during winter ice over in Mystery Lake, Wisconsin (redrawn from Klinger et al. 1982).

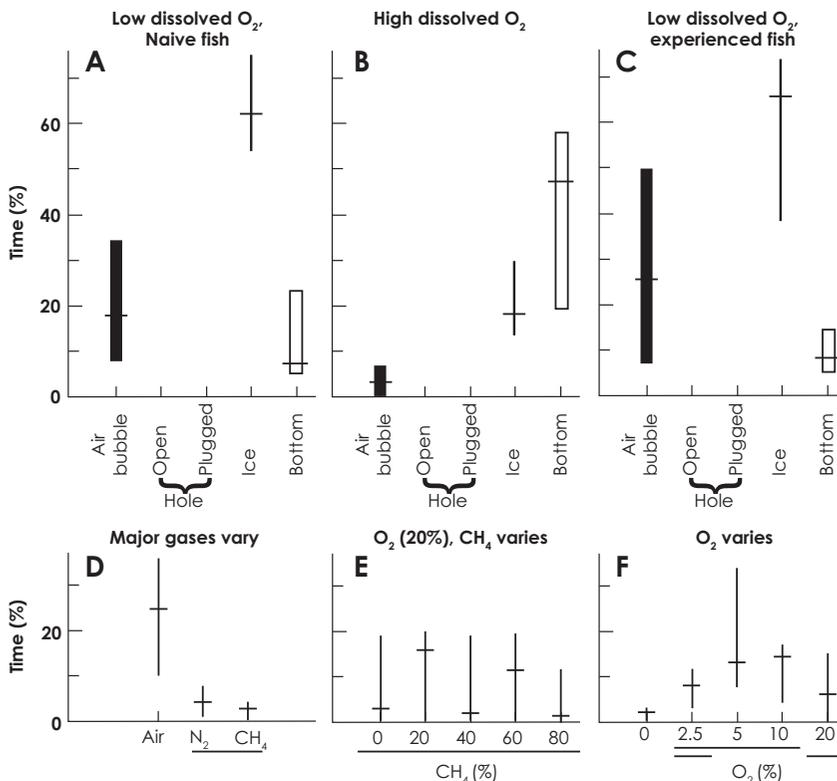


Figure 19.38. (upper) Time (mean \pm 95% CI) spent by Central Mudminnows at air bubbles, open holes, plugged holes, simulated ice at surface, and the bottom under three experimental conditions to simulate winterkill conditions in northern lakes: (A) low dissolved oxygen-high carbon dioxide (naïve fish); (B) high dissolved oxygen-low carbon dioxide; and (C) low dissolved oxygen-high carbon dioxide (experienced fish). At open holes fish could ventilate at the holes and pull in oxygenated water but could not breathe air. (lower) Time spent by Central Mudminnows at bubbles with various gas mixtures: (D) air, nitrogen, and methane bubbles; (E) bubbles varying in nitrogen and methane content; and (F) bubbles varying in oxygen content. Values that do not share a common underline are significantly different ($P < 0.05$) from each other. Water temperatures were 1.6–3.9°C in all experiments (redrawn from Magnuson et al. 1983).

bubbles with higher oxygen content. Although fish occasionally visited open holes in the surface (used to simulate cracks in the ice), they were not recorded there during observation periods, indicating that the Central Mudminnows preferred to use bubbles rather than to pump oxygenated water down through the holes. Whether the bubbles come from sediments, from gases extruded in water when it freezes, or from gases exhaled or escaping from the fur of aquatic mammals (e.g., muskrats, beavers), they are a critical winter resource for Central Mudminnows, allowing them to survive in environments that are lethal to other fishes (Magnuson et al. 1983). Central Mudminnows also actively seek areas of higher dissolved oxygen in a stream inlet in ice covered lakes.

The ability of Central Mudminnows to use their lung-like gas bladder to serve as an oxygen reservoir also has foraging implications in stratified lakes with hypoxic bottom waters. Using field observations and laboratory simulations, Central Mudminnows in a stratified northern Wisconsin lake were documented foraging during the day in hypoxic bottom sediments for phantom midge larvae. The Central Mudminnows ingested air bubbles at the surface to enhance the time they could forage on the bottom in the otherwise lethal hypoxic conditions of the hypolimnion (Rahel & Nutzman 1994).

Between 5–20°C the Central Mudminnow could compensate all of the systems involved in energy metabolism so that its metabolic rate and oxygen consumption were nearly constant (Hanson & Stanley 1969, 1970; Currie et al. 2010). This allows the fish to sustain a high degree of activity at both cold and warm temperatures.

Alkalinity and Acidity

Esociforms show varying levels of tolerance to low and high pH levels. Northern Pike tolerate a wide range of alkalinity. In Wisconsin lakes they occur at pH of 6.1–8.6 (Margenau et al. 1998). In highly alkaline Nebraska lakes, a population survived about 14 months at pH 9.5 until total alkalinity was >1200 mg/l and carbonate alkalinity was >600 mg/l. In another Nebraska lake a population survived and recruited, albeit sporadically, for decades at pH 9.3 (total alkalinity range, 460–950 mg/l; carbonate alkalinity mean = 130 mg/l) (McCarragher 1971). At the other extreme, a Northern Pike population in Saskatchewan reportedly sustained itself at pH 5.0 (Inskip 1982). Chain Pickerel had a probability of occurrence of >0.8 across a pH range of about 4.0–9.0 (median, about 7.0) in 85 New Jersey lakes. In contrast, the probability of occur-

rence of Redfin Pickerel increased gradually as pH increased from about 4.5 to 8.5 (median, about 7.2), although sample sizes of that species were somewhat low (Graham 1993). Habitats of the Olympic Mudminnow generally have pH levels of 5.9–8.2, although the fish tolerates pH \leq 3.8 (Washington Department of Ecology 2012; Kuehne & Olden 2014). Those for Alaska Blackfish range from pH 6.8–8.0 (Ostdiek & Nardone 1959).

As would be expected from their preferred habitats, *Umbra* spp. are highly acid tolerant occurring at a pH that would stress or even kill many fishes. The species may possess physiological and cellular adaptations, which allow it to compensate for sodium loss at low pH (Krout & Dunson 1985; Flik et al. 1987). Across 85 New Jersey lakes, Eastern Mudminnows were captured at pH of 4.0–8.2 (median, about 5.6); their probability of occurrence was near 0.8 at pH = 4, but decreased with increasing pH, and approached a probability of occurrence of 0.1 at pH = 8 (Graham 1993). In The Netherlands, Eastern Mudminnows occurred at pH of 3.5–4.0 (alkalinity <0.1 meq/l) (Dederen et al. 1986). In experimental settings, Eastern Mudminnows showed no mortality at a pH of 2.8 (den Hartog & Wendelaar Bonga 1990). Notably, growth rates in the Eastern Mudminnow acclimated to acid waters surpassed those held at a pH of 6.5–7.5 (Flik et al. 1987). In another laboratory trial (Rahel & Magnuson 1983), Central Mudminnows were ranked 10 out of 12 species tested for ability to tolerate low pH. Of individuals tested, 41% survived a pH of 3.05 for a median of 240 h. In 43 northern Wisconsin lakes, Central Mudminnows occurred at the lowest pH (4.0) of 31 species captured (Rahel & Magnuson 1983). They occurred most often in lakes with median pH of 5.1–5.3 (overall range, 4.3–6.9) and least often in lakes with median pH of 6.5 (range, 6.1–7.4) (Rahel 1984).

Salinity Tolerances

Tolerances of salinity are best documented in *Esox* spp., but research in that arena is confined primarily to the Northern Pike. Although most populations of Northern Pike are confined to fresh waters in lakes and rivers, the species can also tolerate brackish water. In a review of estuarine salt marsh fishes in eastern North America, the Northern Pike was categorized as a freshwater transient species (Nordlie 2003) based on its occurrence in the brackish waters of five estuaries in eastern James and Hudson Bays (Morin et al. 1980). Northern Pike are also occasionally caught in commercial coastal fisheries (Lee 1999; Southcentral Alaska Northern Pike Control Committee

2007). Such reports raise the possibility of the species seeding new freshwater habitat through coastal infiltration. Its importance as a commercial species in the Baltic Sea has prompted several studies of salinity tolerance (Mann 1996). Microsatellite analysis of Northern Pike populations in the southern Baltic Sea showed that stocking programs aimed at supplementing the Baltic Sea commercial harvest failed to increase recruitment when freshwater-reared fingerlings were used. This suggests that wild-spawned fish are adapted to the slightly saline water of the southern Baltic Sea (around 6 ppt) (Larsen et al. 2005). In a study of salinity tolerances of embryos and larvae of the Northern Pike, brackish-water populations exhibited greater salinity tolerance ($LC_{50} = 13.2$ ppt at 15°C) than those of freshwater origin ($LC_{50} = 12$ ppt at 14°C), although differences were relatively slight (Jacobsen et al. 2007; Jørgensen et al. 2010). Salinity tolerance of the Northern Pike varies during different life stages, and high salinity affects both fertilization and development (Raat 1988; Jacobsen et al. 2008). Growth was also reduced at high salinities, suggesting metabolic energy that otherwise might support growth is diverted to osmoregulation (Engström-Öst et al. 2005; Jacobsen et al. 2008). Temperature may be a factor affecting salinity tolerance. Larvae reared at 3, 14, and 18°C showed the least resistance to osmotic stress in a 90 min exposure in saline solution (2% sodium chloride in hatchery water) with optimum temperatures for fertilization, hatching rates, and quality of larvae of $6\text{--}10^{\circ}\text{C}$ (Bondarenko et al. 2015). Chain Pickerel are reported from brackish water (Scott & Crossman 1973; Jenkins & Burkhead 1994). The species occurred at 3 ppt salinity and Redfin Pickerel at 10 ppt (Keup & Bayless 1964).

Little is known definitively about salinity tolerances in other esociform genera. The Eastern Mudminnow occurs in brackish (salinity <5 ppt) habitats in Delaware (Wang & Kernehan 1979) and survived salinities of 10 ppt in laboratory experiments (Hoesle 1963). Olympic Mudminnows can tolerate salinities of 11.5 ppt but prefer salinities <0.5 ppt (Meldrim 1968). The apparent absence of any reports of capture in brackish waters or laboratory exposure to salinity suggests that Olympic Mudminnows, Alaska Blackfish, and Central Mudminnows are obligate freshwater species. An analysis of otolith Sr:Ca ratios in Alaska Blackfish supports that observation for the species (Brown & Severin 2009).

Aspects of Esociform Swimming Ability

Although esociforms excel at fast strikes, they are poorly suited for maneuvering and sustained swimming (Webb

1984). The sustained swimming effort of Northern Pike over a 10 min period was related to size but was among the lowest of 12 species tested (Jones et al. 1974). For example, 20 cm FL individuals were fatigued in 10 min at a water velocity of only 10 cm/s and 50 cm FL individuals fatigued at about 25 cm/s. In comparison, Walleye, *Sander vitreus*, at the same sizes fatigued at much higher flow rates of 45 and 80 cm/s. Swimming activity of the Northern Pike in the laboratory is highly correlated with temperature with an activity optimum at 19.5°C (Casselman 1978).

Similarly, swimming endurance studies comparing a continuous swimmer, the Creek Chub, *Semotilus atromaculatus*, a cyprinid (Carp and Minnow), with the esociform, the Central Mudminnow, revealed the esociform was best suited for short bursts of activity. The metabolism of the Central Mudminnow is adapted to meet the anaerobic energy demands associated with fast strikes (Goolish 1991). From these results and the common morphological and ecological features shared by all esociforms, all of the species can be presumed to fare poorly under sustained strong flow.

Other Aspects of Esociform Physiology

The Northern Pike was used as a model organism in the study of a number of disparate aspects of physiology, such as circadian rhythm (Gaildrat & Falcón 2000 and references therein), and cadmium tolerance (Norey et al. 1990). Considerable effort was directed at understanding factors related to the physiological variables affecting production in the Northern Pike, and to a lesser extent, the Muskellunge. These efforts were motivated in part by the need to improve management programs. Diana (1996) presented an in-depth review of the literature on the energy demands and budget of the Northern Pike with allusions to relevant information for the Muskellunge.

BEHAVIOR

Movement and Activity

A behavioral feature shared by all esociform species is the tendency to be sedentary. Esociforms may remain at the same location either resting on the bottom or hovering among aquatic vegetation for extended periods of time (e.g., Cook & Bergersen 1988; Jepsen et al. 2001). In *Dallia*, *Novumbra*, and *Umbra* foraging or air breathing periodically interrupts these sedentary periods. Local movement and holding in place are typically accomplished by

the sculling undulation of median or pectoral fins. An important determinant of behavioral changes in these and all other esociform species is the onset of the spawning season when relatively short migrations to the spawning grounds are undertaken and other behavioral changes associated with reproduction occur (e.g., territoriality in *No-vumbra* and *Umbra*) (see reproduction section). Short migrations not associated with reproduction are known in some species (e.g., Alaska Blackfish, Laske et al. 2016; Olympic Mudminnow, Henning et al. 2007; Kuehne & Olden 2014; Northern Pike, Cook & Bergersen 1988; Muskellunge, Weeks & Hansen 2009).

Radio tagging and mark-recapture studies aimed at understanding the daily and seasonal patterns of activity and movement of the Northern Pike and Muskellunge indicate many factors interact in complex ways to influence behavior of individuals in a given population. Noting that Northern Pike exhibited a much greater versatility in the range of habitats they used than was previously believed, most studies confirmed that the Northern Pike primarily occupied littoral areas with dense aquatic vegetation but display little site fidelity (Bregazzi & Kennedy 1980; Jepsen et al. 2001; Koed et al. 2006).

This complexity in activity and movement results in considerable behavioral variation among individuals in a population and between different populations. Some factors apparently influencing activity in these species are water turbidity and temperature, availability of prey and vegetation cover, current velocity, water-level changes, and weather conditions; even so aquatic vegetation is the key factor in habitat selection (Cook & Bergersen 1988; Chapman & Mackay 1984ab; Jepsen et al. 2001; Rosell & MacOscar 2002).

Adult Northern Pike and Muskellunge are often recaptured in the vicinity of the location of original capture. Thus, migration between populations is generally assumed to be rare. Further, natal site fidelity might help maintain genetically distinct co-occurring populations (Westin & Limburg 2002; Rohtla et al. 2012). Reproductively mature Northern Pike exhibit relatively high spawning site fidelity, returning from year to year or in alternating years (Roach 1998). Earlier telemetry-based studies failed to demonstrate that Northern Pike established well-defined home ranges or detect differences in the extent of movement or habitat selection between summer and winter (Diana et al. 1977). On a smaller scale, two types of movement are reported in the Northern Pike: localized, directionless roving parallel to shore along the edge of submerged vegetation, and medium range (100–2,000 m) directed swimming across open

water (Miller & Menzel 1986) with forays into open water being rare (Cook & Bergersen 1988). In Alaska, movement into and out of lakes occurs during the ice-out (May–June) then declines between June and July. Northern Pike may aggregate in groups shortly before movement to overwintering habitats.

Northern Pike home range and frequency and distance of movement are extensively studied but do not provide a clear picture of the characteristics that govern their behaviors. Habitat types (e.g., lakes, reservoirs, rivers; clear and turbid systems) affect behavior, habitat use, and the location and size of home ranges (Andersen et al. 2008; Kobler et al. 2008b, 2009). Populations and individuals within populations are described as highly mobile or resident (Mann 1980; Chapman & Mackay 1984ab; Minns 1995; Jepsen et al. 2001). Individual use and size of home range varies seasonally, and the effect of fish size on home range variability is contradictory (Minns 1995; Cook & Bergersen 1998; Knight et al. 2008; Kobler et al. 2008a, 2009). Fish with larger winter and spring home ranges may compete more successfully with conspecifics for access to larger areas, prey and access to spawning grounds and mates (Billard 1996). Large Northern Pike moved at a greater rate than small individuals and movement differed significantly between seasons (Vehanen et al. 2006).

Capture site fidelity for the Muskellunge can vary greatly (Miller & Menzel 1986). Tagged Muskellunge moved between lakes from year to year (Weeks & Hansen 2009) or showed strong homing and site affinities, returning to the same lake after spawning in multiple years or to their original capture locations after ≥ 1 year at large (Crossman 1956; Miles 1978; Diana et al. 2015). Transplanted Muskellunge returned to a specific locality and fish return to previous year's activity areas after extensive spawning movements. After spawning, males moved downstream and immediately established home range areas (Crossman 1977; Minor & Crossman 1978).

Following spawning, Muskellunge generally remain in spawning areas until water temperature approaches 16°C before moving to deeper water to establish summer home ranges (Miller & Menzel 1986). Some Wisconsin populations exhibited home range tendencies throughout the year (Dombeck 1979, 1986). The duration of the post-spawning occupancy of spawning areas before movement to summer home ranges varied considerably among the fish (Miller & Menzel 1986). Males establish home ranges earlier in summer than females (Minor & Crossman 1978).

Both the Northern Pike and Muskellunge become more active with the higher water temperatures of the summer

and early autumn (Younk et al. 1996). During this period feeding is most intensive. As water temperatures decline in the late autumn and winter, both species reduce swimming activity and tend to occupy deeper waters, but they continue feeding at a lower rate. Seasonal differences in site occupancy and movements of Northern Pike range from increased frequency of movement over shorter distances in winter and increased activity when winter water temperatures increased (Diana et al. 1977; Jepsen et al. 2001; Koed et al. 2006). Seasonal differences in site occupancy and movement are similarly masked by individual differences rather than a species, habitat, or sex-related characteristic.

Northern Pike behaviorally thermoregulate in response to changes in both internal and external conditions (Wahl & Stein 1991). Where habitats including thermal refugia are available, they may avoid temperatures above their optimum due to the high metabolic costs, allowing metabolic energy to be allocated for activity, somatic growth and maintenance, and gonad development (Wieser & Medgyesy 1991). Evidence for a strong seasonal effect of temperature on Northern Pike movement is mixed. Although extremes of low and high-water temperatures may inhibit activity and movements (Vehanen et al. 2006), many field studies found no difference in the level of movement with temperature (Diana et al. 1977; Rogers & Bergersen 1995; Jepsen et al. 2001).

Similarly, Muskellunge display seasonal changes in movement with the greatest movement in spring and decreasing in summer (Gillis et al. 2010; Wagner & Wahl 2011). Summer home ranges are generally large (mean = 612 ha) but can vary greatly (range 17–1,309 ha) (Younk et al. 1996; Diana et al. 2015). Muskellunge may undertake large movements over the course of a year, but focus on limited areas during spawning when they tend to move to shallow embayments and marginal river wetlands for spawning (Crossman 1977; Weeks & Hansen 2009). Movement by radio-tagged Muskellunge in the Mississippi River varied seasonally but was also influenced by habitat characteristics (free-flowing versus regulated river). Winter habitat use (defined by home range) was greater in the regulated section of the river than in the free-flowing section. Muskellunge established winter ranges that were distinct from and smaller than summer ranges (Younk et al. 1996).

Other factors may influence Muskellunge habitat selection and use, including water level and discharge rate in human altered lotic systems. In one canal, Muskellunge showed expected seasonal movements; increased water levels in the spring still corresponded with increased home ranges and increased movement, most likely tied to

spawning. When water levels were dropped for the winter, the Muskellunge moved to deeper areas to overwinter and displayed restricted movements (Gillis et al. 2010). Increased discharge rate, however, causes Muskellunge to move to shallower waters during the summer and winter and occupy slack-water habitats along riverbanks during the winter (Brenden et al. 2006). Potentially, these Muskellunge could be forced into habitats with higher energetic demands than the habitats that would have been selected otherwise, a consideration for the health of populations in canals or near dams.

Canals and water management are implicated in the range expansion of Chain and Redfin Pickerels into areas of southern Florida, including Big Cypress National Preserve and Everglades National Park, but the specific mechanism for their occupancy and dispersal is unidentified (Loftus & Kushlan 1987; Gandy et al. 2012; Kline et al. 2014; Zokan et al. 2015). Canals may break down dispersal barriers such as shallow-vegetated wetlands that experience seasonal dry-down or brackish coastal marshes.

Studies of diel activity in *Esox* have produced somewhat mixed results. The diel rhythm of the Northern Pike in a lake and reservoir in Denmark changed significantly over the course of a year, but no differences occurred in the degree of movement between different times of the day (e.g., Jepsen et al. 2001). Others found Northern Pike to be most active at lower light intensities at dawn and dusk when peak feeding seemed to occur and inactive during night (Dobler 1977; Diana 1980; Chapman & Mackay 1984a, 1990; Casselman 1996). Northern Pike were active about 37% of the time with crepuscular activity peaks during summer and a diurnal peak during winter. In a Colorado reservoir, Northern Pike were most active during April and May and least active during October (Cook & Bergersen 1988). Muskellunge, on the other hand, display an increase in movements during nocturnal periods in comparison to crepuscular periods but only during the summer (Crossman 1977; Wagner & Wahl 2011). Chain Pickerel move into shallow water at dusk and appear to show some site fidelity (Scott & Crossman 1973; Helfman 1981).

Activity levels and movement in the smaller esocids and umbrids typify the sedentary behavior of the esociforms. Olympic Mudminnows generally avoid swift currents and prefer sloughs, wetlands, oxbows, and other habitats with little or no flow (Meldrim 1968). In the mainstem habitats of the Chehalis River, Washington, Olympic Mudminnows occupy stream margins, backwater and off-channel habitats, frequently where groundwater reaches the surface (Kuehne & Olden 2014). They occur in large numbers in

both regulated and natural wetlands and may move into and out of those habitats when they are inundated (Henning et al. 2007; Kuehne & Olden 2014), but longer-range movements have not been reported. Dietary studies and behavioral observations in aquaria indicate that they are visual predators, responding strongly to prey movements (Meldrim 1968; Tabor et al. 2014), which would suggest that they are diurnal predators. The dispersal behavior of Alaska Blackfish has not been observed, although their absence from ephemerally connected waterbodies (Ostdiek & Nardone 1959; Haynes et al. 2014), divergent life histories among populations (Ostdiek & Nardone 1959; Blackett 1962; Aspinwall 1965), and limited gene flow (Campbell et al. 2015) suggest limited dispersal capabilities.

In aquarium studies, Central Mudminnows rested on the bottom in shelters or artificial vegetation during daylight hours, swimming slowly along the bottom along the edge of the tank or darting rapidly across the open bottom. Feeding attempts decreased in the presence of a predator (Tonn et al. 1986). Central Mudminnows exhibited more crepuscular and nocturnal activity and overall greater activity in autumn than summer (Spencer 1939). Diurnal rhythms changed with seasons as activity during the day increased in autumn. Perhaps to exploit the cover afforded by darkness, fish actively sought darkened areas in response to light. In situ enclosure experiments confirmed crepuscular peaks in Central Mudminnow activity (Tonn & Paszcowcki 1987). Central Mudminnows were more active offshore and during the day in winter but activity shifted beginning in the spring when fish were concentrated inshore near the bottom. Winter distributions appeared to be responses to abiotic conditions (ice cover and low oxygen availability); overall patterns during open-water periods appeared to be linked to prey emergence and availability.

Alarm Pheromones: *Esox*

Prey species significantly alter their behavior (activity) when Northern Pike are present (Ranåker et al. 2012). Minnows exhibited a fright response to a stimulus of Northern Pike feces if the Northern Pike had eaten minnows. Apparently, the minnow alarm pheromone is in the feces; the minnows exhibit the same reaction to alarm pheromone in water without feces. In what may indicate a behavioral adaptation to avoid detection, captive Northern Pike spent significantly more time in the area where they were fed but deposited feces in the opposite end of the tank. Such chemosensory cues would potentially reveal the presence of a predator in hiding, its activity level,

and its diet (Brown et al. 1995; see summary by Gidmark & Simons 2014).

Anti-predator Behavior: *Umbra*

Central Mudminnows exhibit several anti-predator behaviors. Anti-predator behavioral responses to chemical cues in conspecific skin extract were tested in field avoidance experiments (Wisenden et al. 2008). Treated field traps caught fewer individuals than controls, and in laboratory trials, activity was reduced, and fish were displaced to the bottom of the tank (Fig. 19.39); both components of an anti-predator response. In the wild, Central Mudminnows escape predators by concealing themselves in the mud, their brownish coloration helping to camouflage them (Peckham & Dineen 1957; Becker 1983; Tonn & Paszowski 1986). Central Mudminnows also exhibit shoaling behavior (fish grouped together), another anti-predator strategy, but show no preference for a large over a small shoal of conspecifics (Jenkins & Miller 2007).

REPRODUCTION

Esociforms share some common features in their reproductive biology, including timing of spawning, pre-spawning movements, preferred spawning habitats, and, except in Eastern Mudminnow, the absence of nesting behaviors. The literature presents conflicting reports about differential growth between males and females in the

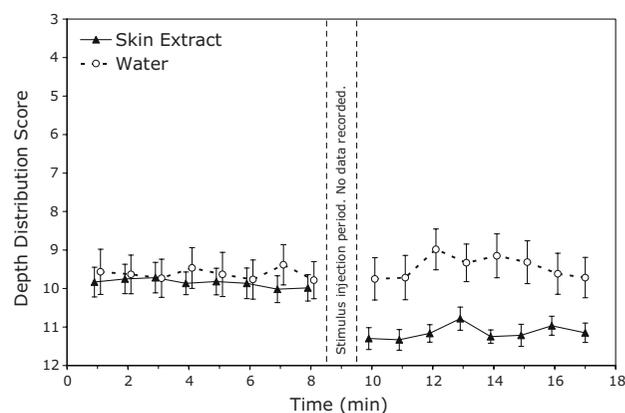


Figure 19.39. Mean (\pm SE) vertical distribution of Central Mudminnows, *Umbra limi*, in test tanks (15 trials, 3 fish/trial) before and after addition of water or conspecific skin extract. Minimum distribution score is 3 (at surface); maximum score is 12 (on bottom). Mann-Whitney U-test and $P < 0.001$ (redrawn from Wisenden et al. 2008).

Esociformes, and size at maturity appears to vary within and among species as a function of locality, spawning, and rearing conditions (Table 19.3). This appears to vary as much by locality and conditions as by species. Primary spawning is in the early spring, starting in February to as late as May (although *Dallia* spawns until August), and spawning preceded by movements (see behavior section) in some species. Where winter conditions result in freezing of surface waters, initial spawning movements coincide with ice off, which provides access to smaller tributary streams, ditches, off-channel marshes, and inundated shorelines. In most esociforms, the preferred spawning habitat is densely vegetated areas of moderate to shallow depths and mud or sand bottoms (Table 19.3). Many of the differences in spawning timing among esociform species result from variation in the prevailing environmental conditions important for reproduction that prevail in the areas they inhabit (e.g., seasonal fluctuation of water levels and temperature). The timing of spawning for any given population is directly correlated with the latitude where it is located because latitude dictates seasonal water temperature changes and the onset of optimal spawning temperatures. Day length does not appear to be a primary factor in the onset of spawning but is one of several non-temperature variables that stimulate spawning activity (Svardson 1949; Fabricius 1950; Fabricius & Gustafson 1958; Franklin & Smith 1963). Windy or cloudy days seem to reduce spawning activities and cool nights appear to delay spawning activities the following morning (Clark 1950a). In most esociform species, spring spawning usually takes place over a period of 2–4 weeks.

Spawning Time and Temperatures: *Esox*

Peak spawning in the spring is triggered by rising water temperatures, but for wide-ranging species, identifying spawning temperatures depends as much on local conditions as on latitude. Northern Pike typically spawn earlier and at cooler water temperatures (about 4.4–11°C) than Muskellunge (9.4–17.2°C). As a result, spawning for either species at the southern limits of their distribution may begin as early as late February or early March and be completed in April, but in the north spawning may not begin until May. Where the Northern Pike and Muskellunge co-occur, the spawning period of the two species may partially overlap at water temperatures of 13–18°C (Farrell et al. 1996). Spawning in species of *Kenoza* typically occurs in late winter through early spring at water temperatures from 2–22°C depending on latitude, peaking over a

period of 7–10 days at temperatures in the middle of that range (Armbruster 1959; Scott & Crossman 1973; Jenkins & Burkhead 1994). Late summer and autumn spawning also occurs (Lagler & Hubbs 1943; Underhill 1949; Armbruster 1959; Miller 1962; Kleinert & Mraz 1966; Scott & Crossman 1973), and in support of these observations, large fingerlings of Chain Pickerel sometimes are captured in the spring (Kleinert & Mraz 1966).

Spawning Time and Temperatures: *Dallia* and *Novumbra*

When water temperatures increase 5–10°C and ice off occurs, *Dallia* migrate to off-channel areas where spawning occurs from May to July in the interior of Alaska but apparently occurs only in late July in the Bristol Bay area (Blackett 1962; Aspinwall 1965). Most spawning in the Olympic Mudminnow occurs between March and mid-June with the greatest activity in April and May at water temperatures of 10–18°C (Meldrim 1968; Hagen et al. 1972). Some additional spawning takes place in late autumn, subsides in the winter, and resumes in spring (Mongillo & Hallock 1999).

Spawning Time and Temperatures: *Umbra*

In *Umbra* spp., spawning is most likely prompted by warming water temperatures and flooding in spring (Peckham & Dineen 1957; Becker 1983). Central Mudminnows spawn in early spring, usually in March or April. Preferred water temperature for spawning is 12.8°C but can occur at ≤15.3°C (Becker 1983). In the Eastern Mudminnow, courtship reportedly begins in March with peak spawning occurring in mid-April at temperatures of 9–12°C, and all females are spent by late April (13–15°C) (Panek & Weis 2013).

Reproductive Cycle in *Esox*

Reviews of reproductive biology in the Northern Pike (Billard 1996) and Muskellunge (Parsons 1959; Scott & Crossman 1973; Becker 1983; Hall 1986) provide a generalized depiction of reproduction in *Esox*. Even so, the Northern Pike differs from other esociforms in producing a single synchronous group of maturing oocytes / spawning season. In contrast, the oocytes of other esociforms mature in two distinct groups and presumably result in fractional spawning (Lebeau 1991).

In Northern Pike, gonad growth begins in July and proceeds at a similar rate between sexes through late summer. Testicular growth ceases in September, but ovarian

growth continues through autumn and winter until April (Medford & Mackay 1978; Lenhardt & Cakić 2002). Sperm maturation is completed over a short period between July and September preceding the spawning season in the Northern Pike. In females, oocyte maturation begins in the summer with the ovaries continuing to gain weight until spawning. The somatic body weight of females does not decline during the period of gamete development and gonad growth. Somatic body weight decreases in males and females during spawning (Medford & Mackay 1978; Diana & Mackay 1979).

Fecundity of the Northern Pike increases with size of the female; Inskip (1982) cites an average fecundity of 32,000 eggs/female, although much larger numbers are reported. Fecundity for several populations of the species in the British Isles varied between 10–24 eggs/g (Treasurer 1990). Further, the relationship between population fecundity and recruitment is weak (see ecology section). Although bigger females produce bigger eggs, the average size of the month-old larva is the same regardless of mature female size; genetic and environmental factors, primarily water level and temperature, appear to affect growth and survival more than egg and larval size (Craig 1996). Even though the estimates cited above serve as rough estimates of fecundity, fecundity of the Northern Pike is a difficult-to-measure, highly variable characteristic, which depends on many factors such as female health, available energy, temperature, and even population biomass (Billard 1996). As with the Northern Pike, fecundity in the Muskellunge increases with female size, ranging from about 6,000–265,000 eggs. Average fecundity is about 120,000 (Scott and Crossman 1973; Cook & Solomon 1987). Relative to the largest *Esox* spp., females of species of the subgenus *Kenoza* produce similar sized but fewer eggs/season (Table 19.3), both in absolute numbers and in proportion to body weight (e.g., from a few hundred in Redfin and Grass Pickerel to an average of 8,000 in Chain Pickerel) (Scott & Crossman 1973; Becker 1984; Jenkins & Burkhead 1994). Fecundity estimates in pickerel are complicated by the fact that ovaries may contain three different stages of eggs with mature, ready for spawning eggs usually the fewest in number. For example, Grass Pickerel may have 800 ripe eggs and 4,000 and 11,000 eggs in two developmental classes (Scott & Crossman 1973).

Northern Pike can reach reproductive maturity in a year (females at 30 cm TL and males at 19 cm TL), but age at maturation appears to be highly variable (Raaf 1988). In Scotland, the age at first spawning is variously reported as two years for males and three years for females. First spawning of more northerly populations may occur at a later age (Treasurer 1990); however, Diana (1983) found

no relationship between reproductive age and latitude. Age at maturation depends on temperature, food availability, growth rate, and stock exploitation (Billard 1996; Diana 1996). Heavy fishing pressure and associated mortality appears to induce earlier maturity and increase energy allocation to reproduction in some populations (Diana 1983). Muskellunge reportedly reach sexual maturity at age 3–5 with males maturing earlier than females (Scott & Crossman 1973; Cook & Solomon 1987). River populations grow and mature more rapidly than fish from lake populations (Harrison & Hadley 1979). Pickerels typically mature at 3–4 years but some populations reportedly were mature as early as year 1 (Underhill 1949).

Reproductive Cycle in *Novumbra*

Olympic Mudminnows are sexually mature at 41–65 mm TL (Mongillo & Hallock 1999). Water temperatures during the breeding season ranged from 10–18°C (Meldrim 1968). Eggs are adhesive and are usually deposited one or two at a time on vegetation or algal mats near the bottom where they are fertilized during courtship and left unattended. In aquaria, eggs hatched in nine days at 15–17°C. The sedentary larvae adhere strongly to vegetation.

Reproductive cycle in *Dallia*

Like the Muskellunge and pickerels, the Alaska Blackfish appears to be a fractional spawner with two distinct size groups of eggs in the ovaries during spawning (Blackett 1962; Aspinwall 1965; Morrow 1980). As in *Esox*, inter-population differences exist. By August only one rather uniform size class of eggs remains in the ovaries; those are assumed to be recruitment stock to be developed by the next spawning season (Blackett 1962). Females deposit about 40–300 eggs; the number increases with increased size of the female (Morrow 1980). Partially spawned females are captured during most of the spawning season, suggesting only a few eggs are extruded with each spawning act. Sexual maturity is reached at age 2+ or 3+ (about 80 mm TL, 5 g for females) so some females likely spawn in multiple seasons over their lifetime.

Reproductive Cycle in *Umbra*

Gonadal development in *Umbra* begins in autumn or winter (September–January) and peaks in the spring (Dederen et al. 1986). Average fecundity in *Umbra limi* is 425–450 eggs/female; fecundity increases with age to nearly 1,500

for age-5 individuals (81–94 mm TL) (Evermann & Clark 1920; Peckham & Dineen 1957; Martin-Bergmann & Gee 1985; Table 19.3). Within individual ovaries all eggs were the same size before spawning season and ripen at the same time, suggesting a single, short spawning season (Peckham & Dineen 1957). Age-specific fecundity estimates for *Umbra pygmaea* ranged from 250 eggs/female at age-1 to 2,168 at age-5 (Panek & Weis 2012). *Umbra*, particularly males, may reach sexual maturity at age-1, but maturity is usually delayed in females until age-2.

Reproductive Behavior

Esociforms undertake migrations of varying lengths to reach their preferred spawning areas. These may entail short migrations from streams into lakes (or vice versa) or moving inshore from deep water or onto spring-flooded areas. Many references note spring migration of esociforms upstream into flooded or marshy areas shortly after the ice disappears (e.g., *Umbra*, Abbott 1870a; *Dallia*, Blackett 1962; Morrow 1980; *Esox*, Clark 1950a; McNamara 1937; Becker 1983; Tomelleri & Eberle 2011). Northern Pike may migrate to distant localities during spring, despite suitable spawning areas near where they resided most of the year (Koed et al. 2006). Mark-recapture, genetic, and otolith microchemistry studies uncovered evidence of annual returns to preferred spawning areas and natal site fidelity in the Northern Pike and Muskellunge (Crossman 1990; LaPan et al. 1996; Miller et al. 2001; Engstedt et al. 2014).

Aside from this directed migration, spawning also is accompanied by a significant increase in swimming activity in the normally sedentary Northern Pike. Changes in activity levels associated with spawning are different for males and females. This disparity may be related to sex differences in spawning behavior, but information on this aspect of esocid biology is limited. At the spawning grounds, males outnumber females, which arrive later and persist longer. In most populations of esocids, females grow faster and live longer, thus the females are usually larger than the courting males. Spawning aggregations can be impressive; in the 1950s, a spawning run of 6,000 Northern Pike was tabulated in a creek in Saskatchewan (Scott & Crossman 1973 citing Schultz 1955).

Spawning Behavior in *Esox*

Spawning behavior is similar in the Northern Pike, Muskellunge, and pickerels. The large esocids exhibit no territoriality or nesting behavior (Ming 1968; Scott & Cross-

man 1973). One to three males may attend one female with many matings over a period of several days (Armbruster 1959; Clark 1950a; Ming 1968; Scott & Crossman 1973; Billard 1996). The behavioral cues causing the female to be receptive to a given male and triggering gamete release are unknown. After successful courtship, a spawning group swims slowly side-by-side with their vents aligned, paused frequently to complete the spawning act, then continue swimming until spawning is complete. Eggs (<100) and milt are broadcast over the vegetation. On gamete release, the spawning fish direct a strong, quick body undulation against each other, helping scatter the fertilized eggs, which sink and stick to vegetation or the bottom, hatching about two weeks later without parental care (Billard 1996). Hatching success, at least in the Northern Pike in one study, was higher in eggs deposited on sand or silt compared with those laid on aquatic plants (Wright & Shoemith 1988).

Muskellunge in inland lakes commonly spawn in shallow bays (<1 m deep) with detritus, vegetation, submerged logs, and gravel, sand, silt, or muck substrates (Dombeck et al. 1984; Zorn et al. 1998; Rust et al. 2002; Nohner & Diana 2015). In larger systems (e.g., Great Lakes), Muskellunge spawn at sites with greater depths (1–3 m) and with vegetation coverage of 0–100% and substrates of gravel, sand, and silt (Haas 1978; Farrell 2001; Crane et al. 2014).

Spawning Behavior in *Novumbra*

Among esociforms, the Olympic Mudminnow is unique because the males exhibit spawning site territoriality and aggressively repel rival males and intruders of other species (Hagen et al. 1972). During the spawning period, males acquire their distinct breeding coloration, which consists of a dark chocolate brown to almost black body with a series of about 15 thin iridescent-green, white, or blue vertical bars along the entire length of the fish. The dorsal and anal fins, used in display, are conspicuously banded on their edges with a sky-blue coloration (sometimes appearing white or yellow). In contrast, females are a dull olive-brown becoming lighter ventrally with a few faint vertical bars along the sides. The outer margin of the branchiostegal membrane of males also develops a wide black band along the edges of the membranes during the spawning season. These can be greatly expanded in a striking display that greatly enlarges the apparent size of the head. Gular flaring is more common in aggressive interactions between resident males with abutting territories when they meet at their territorial boundaries. The

gular-flaring posture may be held ≤ 10 s and may be followed by circular fighting in which the two males circle one another closely and attempt to strike one another with the tail (Hagen et al. 1972).

Male *Novumbra* select a suitable patch of vegetation and establish a territory, which they patrol and defend against intruders. Territories are large (about 1.0×0.5 m) relative to the size of the male and are maintained for the entire length of the spawning season (>7 weeks; Hagen et al. 1972). Residents patrol the margin of their territory with a stylized swimming movement in which the tail is slowly swept from side to side in a wide arc. The male abruptly halts, hovering for a few seconds, and then patrols again for a short distance. If intruding fishes (whether conspecifics or not) approach a territory, the resident male rapidly turns to face the intruder and hovers. Holding the body rigid, the male fully expands the colorful dorsal, anal fins, and pelvic fins and rapidly vibrates them. Persistent intruders may be attacked with a forceful blow with the head or the side of the body with an impact sufficient to turn the opponent upside down. In the wild, strikes against conspecific intruders were rare and were more commonly directed against intruders of other species (Hagen et al. 1972). Coloration of breeding males and patrolling behavior intensifies once eggs are deposited on their territory. Colors are also more conspicuous during courtship or fighting. Submissive males or those defeated in territorial fighting become a light brown and lose the colored bands on the fins.

The most elaborate display during Olympic Mudminnow courtship is the wigwag dance of the male. The body is strongly oscillated from side to side in a wide arc along the direction of swimming with the dorsal and anal fins maximally expanded. During each dance, males move only about 7 cm with bouts of dancing alternating with freezing and fins displayed. Display is usually parallel to the female, and males then sweep in an arc round her head while dancing.

If the display is successful, the receptive female enters the male's territory, where the male repeatedly swims along the female and tries to make contact. After an interval of courtship lasting 5–20 min, the female swims into the vegetation and allows the male to swim along her side and make body contact. The female apparently selects the exact site for depositing eggs and moves into the vegetation, and rather than moving away, responds to the male by mutually pushing against his side while vibrating. The pair maintains contact while their bodies vibrate until they finally push off each other with a sudden thrust at which point eggs and milt are released into the vegetation. The pair may spawn repeatedly for >1 h.

Spawning Behavior in *Dallia*

Nothing so elaborate as observed for the Olympic Mudminnow is described in the spawning behaviors of the Alaska Blackfish, but little is published on the species. During the spawning season, males develop a reddish fringe along borders of the medial fins (Blackett 1962; Morrow 1980). No direct observations of spawning exist but massive upstream movement to shallower waters occurs following ice break up when temperatures warm $6\text{--}8^\circ\text{C}$ and flows decrease (Blackett 1962). The eggs are probably deposited in vegetation at the bottom of shallow ponds and quiet streams (Nelson 1884; Morrow 1980). The capture of partially spawned females through the season suggests that spawning proceeds over a period of several days with only a few eggs being extruded at each spawning act.

Spawning Behavior in *Umbra*

Detailed accounts of reproductive behavior in North American *Umbra* spp. are lacking. As with other esociforms, Central Mudminnows move toward margins of streams or lakes following ice off before moving into channels connected to marshes or inundated shorelines during periods of spring flooding and heavy rains (Peckham & Dineen 1957; Jones 1973). Adams & Hankinson (1926) noted marked migratory movements to streams for breeding; females preceded males. Sexual dimorphism occurs in the Central Mudminnow in the form of an elongation of the anal fin and an intensification of bluish-green coloration of the anal and pelvic fins in males during the breeding season. In Eastern Mudminnows, adults during the breeding season can have ragged fins suggestive of aggressive behavior during courtship. Males flare their pectoral fins and approach gravid females and nudge them to induce egg release. Females affix eggs individually directly to vegetation (Peckham & Dineen 1957), but nesting and attaching eggs to the underside of loose rocks is also described (Breder & Rosen 1966).

The only detailed accounts of reproductive behavior of any species in *Umbra* are from laboratory observations in the European Mudminnow (Bohlen 1995; Kováč 1997). Preceding spawning, a period of courting lasts 1–4 days. During courting, males pursue females and attempt to nudge the vent of the female with their mouths. Eventually, females become receptive and pick a suitable spawning site. Females reportedly often excavate shallow nests in the substrate before spawning (Kováč 1997); however, Bohlen (1995) never observed this behavior. The preferred

spawning substrate is dense, soft vegetation, but spawning can proceed even in the absence of the preferred substrate (Bohlen 1995). Receptive females swim into the spawning site followed by one to five males. One male pairs with the female and swims up to her side. Their bodies vibrate, and the gametes are released and fertilized. The pair leaves the site until the female is ready for another spawning bout. As spawning proceeds the female becomes progressively more aggressive toward the males until all males are repelled from the nest area. Similar aggressive display behavior, although seemingly unrelated to spawning, was observed in female Olympic Mudminnows and in male and female Central Mudminnows and Eastern Mudminnows kept in aquaria (Peckham & Dineen 1957).

Parental Care in *Esox*, *Novumbra*, and *Dallia*

Parental care is lacking completely or minimal across all esocids. Evidence of parental care to the embryos or larvae is lacking in any species of *Esox* or in Alaska Blackfish. Males of the Olympic Mudminnow may still defend their territories for a period of about seven weeks but do not tend to the developing eggs or larvae (Meldrim 1968; Hagen et al. 1972). When spawning is completed the adults leave the spawning grounds; the fertilized eggs develop unattended. In the laboratory, larvae dispersed from the egg deposition site after seven days (Hagen et al. 1972).

Parental Care in *Umbra*

In *Umbra* spp., females exhibit some egg-guarding behavior and weak fanning of the embryos, but other parental behaviors are unknown (Peckham & Dineen 1957; Becker 1983). Females reportedly consume undeveloped eggs. The literature differs regarding the quality and extent of parental care in European Mudminnows. In one aquarium-based study, females fanned the nest over a period of two weeks, although the females seemed unaware of the developing embryos and occasionally ate them (Bohlen 1995). In contrast, Kovác (1997) reported that aquarium-held females guarded the nest after hatching and could discriminate offspring from food. Further, one female carried fertilized eggs in her mouth from their place of deposition to a presumably better site (i.e., more secluded).

Spawning Sites and Dissolved Oxygen

Spawning habitats eventually provide shelter to the larvae (see review of the role of vegetation in the life cycle of the

Northern Pike by Bry 1996). The substrate at spawning sites is typically covered by abundant loose organic matter or vegetation. Water velocity is low or negligible. Under these conditions, dissolved oxygen levels may vary widely because of microbial respiration in the substrate and lack of mixing currents. Because an adequate oxygen supply is critical for embryo development and oxygen levels may be temporarily low in the spawning habitat, embryo asphyxiation from hypoxia can cause catastrophic mortality in the Muskellunge (Zorn et al. 1998). The tendency of larvae to attach to standing vegetation via adhesive glands located on the head may help avoid anoxic or toxic conditions directly above the substrate.

Eggs and Larvae

Mature esociform eggs are adhesive and demersal, pale yellow to orange in color and range in diameter from 1.83 to 3.29 mm in Northern Pike (Raaf 1988) and 1.6 to about 2.0 mm in *Dallia*, *Novumbra*, and *Umbra*. The time required for embryos to hatch is temperature dependent, but hatching usually occurs in six days to two weeks at 10–13°C (Underhill 1949; Aspinwall 1965; Hokanson et al. 1973; Morrow 1980; Kendall & Mearns 1996; Panek & Weis 2012). In *Novumbra*, embryos hatch in about nine days at 15–17°C (Meldrim 1968).

Development of *Esox*

Embryos of *Esox* spp. develop on the substrate or attached to debris and vegetation where they are subject to predation, fungal infestation, and other environmental conditions contributing to high mortality during the first summer of life (Farrell 2001). Yolk-sac larvae are 6.5–10.0 mm TL at hatching (Franklin & Smith 1963; Kotlyarevskaya 1969; Fuiman 1982) and can swim soon after hatching (Fig. 19.40). Muskellunge yolk-sac larvae are 7.9–9.2 mm TL at hatching. Embryo and larval development in *Kenoza* species is generally similar to that of the large esocids except that yolk-sac larvae are slightly smaller at hatching (4–8 mm TL) (Jones et al. 1978; Fuiman 1982). Typically, newly hatched larvae of *Esox* spp. swim upward facilitated by the heterocercal shape of the tail and attach vertically to available substrates by means of a nasal adhesive gland (Bry 1996). They remain relatively inactive if undisturbed until the yolk sac is absorbed, at which point they begin to swim and feed. Depending on water temperature, yolk absorption occurs during the next 5 days at 19°C and 16 days at 10°C (Underhill 1949; Raaf 1988). Oxygen exchange is

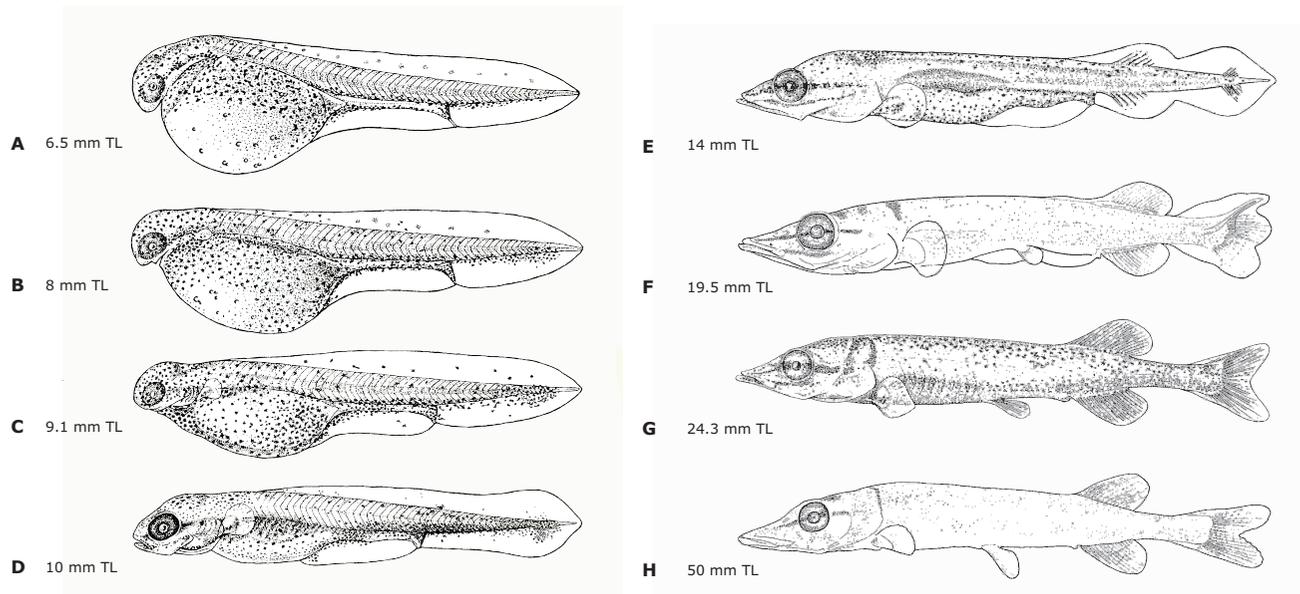


Figure 19.40. Larvae and juveniles of the Chain Pickerel, *Esox niger*. (A–D) Yolk-sac larvae; (E–H) Post yolk-sac larvae and juveniles (redrawn from Yeager 1990).

through the body surface until gills develop (at 10.5–12.0 mm TL in Northern Pike; Franklin & Smith 1963), so some water movement is necessary (Braum et al. 1996). Lin et al. (1997) gave a detailed description of the post-hatching (14–250 mm TL) development of the gonads and sex differences in young of the Muskellunge.

Development of *Novumbra*

Newly hatched larvae of the Olympic Mudminnow (5 mm TL) remain attached to surrounding vegetation by adhesive glands located on the head (Meldrim 1968) until yolk-sac absorption is completed and they become mobile (7 mm TL under laboratory conditions; Hagen et al. 1972). Kendall & Mearns (1996) detailed embryo and larval development of Olympic Mudminnows (Fig. 19.41).

Development of *Dallia*

Newly hatched larvae of the Alaska Blackfish are about 6 mm TL at hatching and have a large yolk sac (Fig. 19.42). They transition from yolk-sac to post yolk-sac larvae at about day 10 post hatching at 12–13°C in the laboratory. By day 22 the fish are about 12 mm TL and are beginning to resemble adults. By day 44 at about 20–21 mm TL, the transition to juvenile is complete (Aspinwall 1965; Morrow 1980). Alaska Blackfish growth is rapid in the first year; annual incremental growth declines thereafter (Blackett 1962; Aspinwall 1965), but growth is continuous. Blackfish in Bristol Bay, Alaska, are slower growing

and live longer than populations in Interior Alaska (Morrow 1980).

Development of *Umbra*

In *Umbra*, embryos hatch in about six days (Ryder 1866), hatching time being dependent on water temperature. The transparent larvae hatch at about 5 mm TL becoming pigmented and dark on their sixteenth day after hatching (Peckham & Dineen 1957; Fig. 19.43). In Eastern Mudminnows, the yolk sac is absorbed in ≤ 2 weeks. Until young reach 25 mm TL they have a notochord lobe above the developing caudal fin (Breder 1933; Becker 1983). Young Central Mudminnows migrated from breeding areas to the main stream at about 30 mm TL (Peckham & Dineen 1957; Wallus 1990). The young grow rapidly and may reach 55 mm by October (Becker 1983).

The yolk sac of developing Eastern Mudminnow larvae is covered by a circulatory rete formed by a sub-intestinal vitelline vein, which extends over the posterior two-thirds of its surface. This rete may function as adaptation to the unpredictable dissolved oxygen concentrations associated with esociform spawning habitat as is hypothesized for European Mudminnows (Kováč 1995).

Embryo, Larval, and Juvenile Survival

Artificial fertilization in hatchery conditions affords much higher embryo survival than under natural condi-

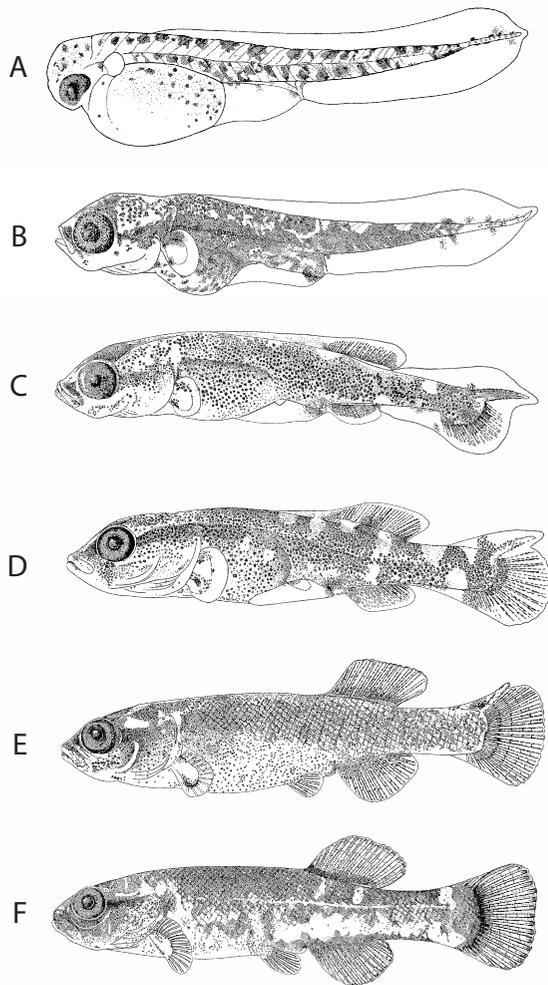


Figure 19.41. Larvae and juvenile of the Olympic Mudminnow, *Novumbra hubbsi*. (A) Yolk-sac larva, 5.2 mm SL; (B) pre-flexion larva, 7.7 mm SL; (C) early flexion larva, 12.2 mm SL; (D) late flexion larva, 14.5 mm SL; (E) post-flexion larva, 15.7 mm SL; (F) juvenile, 22.0 mm SL (redrawn from Kendall & Mearns 1966).

tions. Billard (1996) reviewed the literature on incubation and hatching of Northern Pike embryos under controlled conditions, providing many useful insights into the tolerance of developing embryos to temperature, oxygen concentration, and physical shock. Embryo mortality is generally high and determined by many variables (e.g., oxygen levels, water temperature fluctuations, nursery habitat conditions) (Casselman & Lewis 1996; Zorn et al. 1998; Farrell 2001). Two important factors determining year-class strength and mortality rates in juvenile Northern Pike are temperature and water level (Kipling 1983; le Cren 1987; Casselman 2002). Temperature dictates how quickly the juveniles reach a size rendering them less vulnerable to cannibalism, and water level affects the extent of habitat with

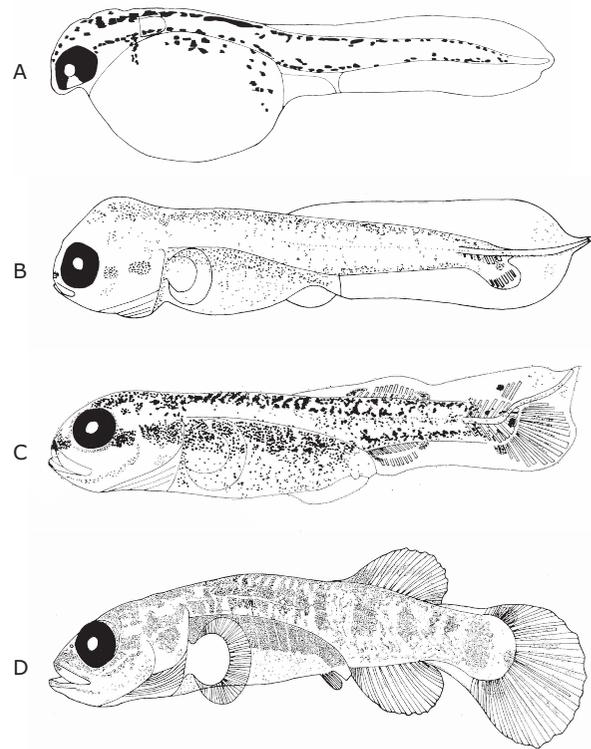


Figure 19.42. Larvae (A–C) and juvenile (D) Alaska Blackfish, *Dallia pectoralis*, reared in the laboratory (mean water temperature 12–12.5°C). Parental stock was obtained in Lake Aleknagik, Bristol Bay, Alaska (redrawn from Aspinwall 1965). (A) 5.7 mm TL, hatchling, x35; (B) 9.0 mm TL, 10.5 days post-hatch, x22; (C) 12 mm TL, 21.75 days post-hatch, x16.7; and (D) 19.5 mm TL, 44 days post hatch, x10.1.

submerged vegetation, which serves as shelter and supports food for juveniles (Kipling 1983; Werner & Gilliam 1984; le Cren 1987). Maintaining ecological flows in regulated rivers can benefit Northern Pike reproduction and recruitment by maintaining access to littoral habitats for spawning and rearing (Mingelbier et al. 2008). Variation in Northern Pike population dynamics among spawning and nursery habitats and between years highlights the role of temperature in influencing the timing of spawning and subsequent growth (Craig & Kipling 1983; Casselman & Lewis 1996; Minns et al. 1996; Farrell et al. 2006). High, stable water levels through larval development produce larger year classes (Johnson 1957) as do higher summer temperatures (Craig 1996). Access to shallow nearshore areas with abundant aquatic vegetation for cover, abundance of prey species inhabiting nearshore areas, and low shoreline development contribute to increased recruitment success in young-of-the-year Muskellunge (Murry & Farrell 2007).

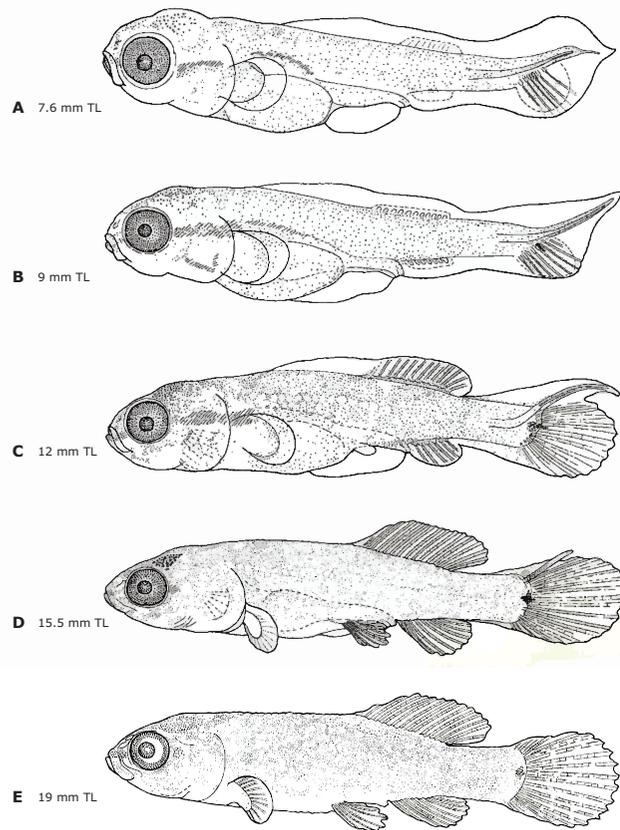


Figure 19.43. Development of young Central Mudminnows, *Umbra limi*. (A) Late yolk-sac larvae; (B–D) post yolk-sac larvae; (E) early juvenile. A–C, drawings of wild-caught specimens from Big Sandy River floodplain, Tennessee; D–E wild-caught from same locality and reared in the laboratory (redrawn from Wallus 1990).

ECOLOGY

From an ecological perspective the esociforms are broadly divisible into two groups. Ecologically, the traditional taxonomic grouping of *Dallia*, *Novumbra*, and *Umbra* is easy to understand. These generally diminutive fish have similar habitat requirements, tolerate similar conditions, and have similar diets in the majority of their life histories. Likewise, the habits and habitats of their larger *Esox* relatives overlap markedly. The main difference in diet between young and old *Esox* and among the large esocids and small esociforms is in the sizes of their prey. Like many other fishes, diets shift from microcrustaceans and smaller invertebrates to larger food items as fish size increases.

Habitat of *Esox*

Species of *Esox* generally inhabit slow moving, vegetated waters in lakes, swamps, and large rivers (Scott & Cross-

man 1973; Becker 1983; Rohde et al. 1994; Page & Burr 2011; Figs. 19.18, 19.33, and 19.44). Aquatic vegetation is an important factor for esocid reproduction and recruitment, and vegetated habitats provide cover for hunting as well as refuge from other predators (Grimm 1983, 1989; summarized in Raat 1988). Within lotic systems, Grass Pickerel avoid riffle habitats and prefer to be associated with submerged vegetation or underwater woody debris (Cain et al. 2008). This environment is ideal for waiting and ambushing prey, a tactic shared by all members of *Esox*. Habitat use, however, may not remain static. For example, seasonal changes in habitat use by Muskellunge in West Okoboji Lake, Iowa, was related to spawning and foraging (Miller & Menzel 1986). In regulated rivers, Muskellunge occurred in deep water habitats but moved into shallower areas closer to shore when discharge increased (Brenden et al. 2004), and Muskellunge also showed seasonal movements in the Mississippi River (Younk et al. 1996). Seasonal changes in temperature may also alter the habitat selection of esocids (Chapman & Mackay 1984a). For example, Chain Pickerel inhabit deep, cool waters during mid-summer, but move into the shallow weedy areas in the autumn when the water cools (Raney 1942; Armbruster 1959). Habitat partitioning between juvenile and adult esocids is not apparent; they appear to equally exploit all habitats frequented.

Habitat of Other Esociforms

Among the other esociforms, little differentiates the types of habitats most occupied, other than perhaps the extremely harsh winter conditions imposed on the habitat of the Alaska Blackfish. Tolerant of a wide range of environmental conditions, Alaska Blackfish and Olympic, Central, and Eastern Mudminnows are sedentary inhabitants of heavily vegetated lowland marshes, swamps, ponds, and sloughs and occasionally exploit medium to large rivers with slack flows at channel margins, braided and backwater habitats, and lakes with abundant aquatic macrophytes (Peckham & Dineen 1957; Scott & Crossman 1973; Harris 1974; Smith 1985; Mongillo & Hallock 1999; Currie et al. 2010; Page & Burr 2011; Tabor et al. 2014; Haynes et al. 2014). Most species occur in habitats with thick layers of organic material at the bottom in which they occasionally bury themselves.

Olympic Mudminnows usually occur in heavily vegetated lowland swamps and ponds (Fig. 19.45), but also persist in disturbed areas such as sloughs and roadside ditches, tolerating low dissolved oxygen levels and high water temperatures that might otherwise be stressful for



Figure 19.44. A solitary Northern Pike, *Esox lucius*, cruising along the edge of vegetation, its usual habitat, in Baker Creek, a tributary to Great Slave Lake, Northwest Territories, in June (courtesy of © Paul Vecsei / Engbretson Underwater Photography).

other native fishes of western Washington (Mongillo & Halleck 1999; summary by Wydoski & Whitney 2003).

The Alaska Blackfish is most abundant in tundra regions but does occur in forested areas (Fig. 19.46). They are tolerant of harsh conditions and exploit late successional beaver ponds over other habitat types presumably because these habitats afford greater respite from stream flow and provide off-channel refugia from predators (Malison et al. 2014). Occupancy models showed that Alaska Blackfish are more likely to occur in lakes with more deep-water refugia, probably because they overwinter in these lakes (Haynes et al. 2014). The species does not appear to exploit ephemeral connections between waterbodies for dispersal (Laske et al. 2016).

During periods of high flows, *Umbra* species move from their normal habitats and venture into the flooded areas along the banks to avoid strong water currents. They can breathe air and thus can survive for short periods of time under extreme hypoxic conditions (Peckham & Dineen 1957; Klinger et al. 1982; Becker 1983; Chilton et al. 1984; Rahel & Nutzman 1994; Schilling et al. 2006). Central Mudminnows form shoals of several individuals, perhaps to avoid predators or find food (Jenkins & Miller 2007). When threatened, they flee into soft sediment and ooze (Applegate 1943; Peckham & Dineen 1957).

Feeding

Esociforms feed almost exclusively on animals, although small amounts of algae, plant material, and detritus are often found in the stomachs of *Dallia* and *Umbra* (Ostdiek &



Figure 19.45. Habitat of the Olympic Mudminnow, *Novumbra hubbsi*, in Conner Creek, Washington (courtesy of RT).



Figure 19.46. Habitat of the Alaska Blackfish, *Dallia pectoralis*, in Big Eldorado Creek, Tanana River drainage, Alaska (photography by AL).

Nardone 1959; Martin-Bergmann & Gee 1985; Panek & Weis 2013). They are primarily diurnal or crepuscular foragers as befits visual predators with well-developed eyes (except for *Dallia*).

The mainly piscivorous esocids strike at potential prey with a powerful lunge once they have visually identified the target. In *Esox*, feeding strikes are usually launched from ambush at the edge of submerged vegetation after a slow stalking propelled by sculling the pectoral and caudal fins (Diana et al. 1977; Webb & Skadsen 1980). The posterior placement of the dorsal fin characteristic of all esociforms and a well-developed anal fin facilitate the fast, powerful strikes used by larger esociforms to capture prey (Higham 2007). In the species studied (i.e., *Esox*), vision is the most important sensory input in the earliest phases of prey capture, then, as the distance to the target is reduced, the cephalic and lateral-line sensor systems provide all the information necessary for successful prey capture (New & Kang 2000; New et al. 2001; New 2002). Large esocids may switch from strict ambush to pursuit as water clarity declines. The increased encounter rate may functionally offset the added metabolic costs (Turesson & Brönmark 2007; Carey & Wahl 2010; Pintor et al. 2014).

Esox exhibits fast-start swimming behaviors in feeding strikes (Webb & Skadsen 1980; Frith & Blake 1995; Domenici & Blake 1997; Hale 2002; Schriefer & Hale 2004). Muskellunge feeding behavior consists of a slow stalk of its prey (Fig. 19.47) followed by a C- or S-start lunge from a stationary position (Domenici & Blake 1997; New et al. 2001). Fast-start performance (mean maximum acceleration) for the Northern Pike is estimated at $119.2 \pm 19.0 \text{ m/s}^2$ with mean velocities approaching 4 m/s^2 (Harper & Blake 1990). S-start strikes usually occur over shorter distances and have higher success rates than C-start strikes (95 versus 58%).

Feeding behavior among *Novumbra* and *Umbra* is similar and shows some parallels to *Esox*. Observations of Olympic

Mudminnows in aquaria suggest they respond strongly to prey movements (Meldrim 1968; McPhail 1969). Typically, they remain motionless and then stalk and finally strike at passing prey (Meldrim 1968). They use their large pectoral fins to paddle slowly about the vegetation in search of food. Once a prey organism is spotted, they capture it with a quick dart, much like *Esox*. Olympic Mudminnows are diurnal foragers (Tabor et al. 2014).

Species of *Umbra* appear to use their vision to detect and target prey. In laboratory observations, these fishes hover in the water using slow, continuous undulations of their fins or slowly stalk a prey item to within striking distance and then strike with a quick lunge similar to *Esox* spp. (Keast & Webb 1966). In laboratory experiments, the Eastern Mudminnow exhibited no preference for prey location and captured items with equal success from the substrate, mid-water, surface, or on submerged plants (Paszkowski 1984, 1985). Aquarium observations of escape behavior of Central Mudminnows when startled revealed the fish froze and assumed a posture similar to the C- or S-start pose described in esocids (Jones 1973). Apparently, information on feeding behavior of Alaska Blackfish has not been published.

Prey Selection in *Esox*

Laboratory and field experiments indicated the Northern Pike, Muskellunge, and tiger muskellunge practiced prey selection, grew more slowly in pond systems where Sunfish (Centrarchidae) prey were present, and strongly preferred Gizzard Shad (*Dorosoma cepedianum*) over Bluegills (*Lepomis macrochirus*) when both species were available (Wahl & Stein 1988). Gape limits on prey size are linearly related to Northern Pike body length; a similar relationship is seen in the Muskellunge (Fig. 19.48). Northern Pike occasionally select prey smaller than would be predicted; the increased handling time for larger prey makes



Figure 19.47. Muskellunge, *Esox masquinongy*, in search of prey in Spread Eagle Chain of Lakes, Florence County, Wisconsin, in May (courtesy of © Eric Engbretson / Engbretson Underwater Photography).

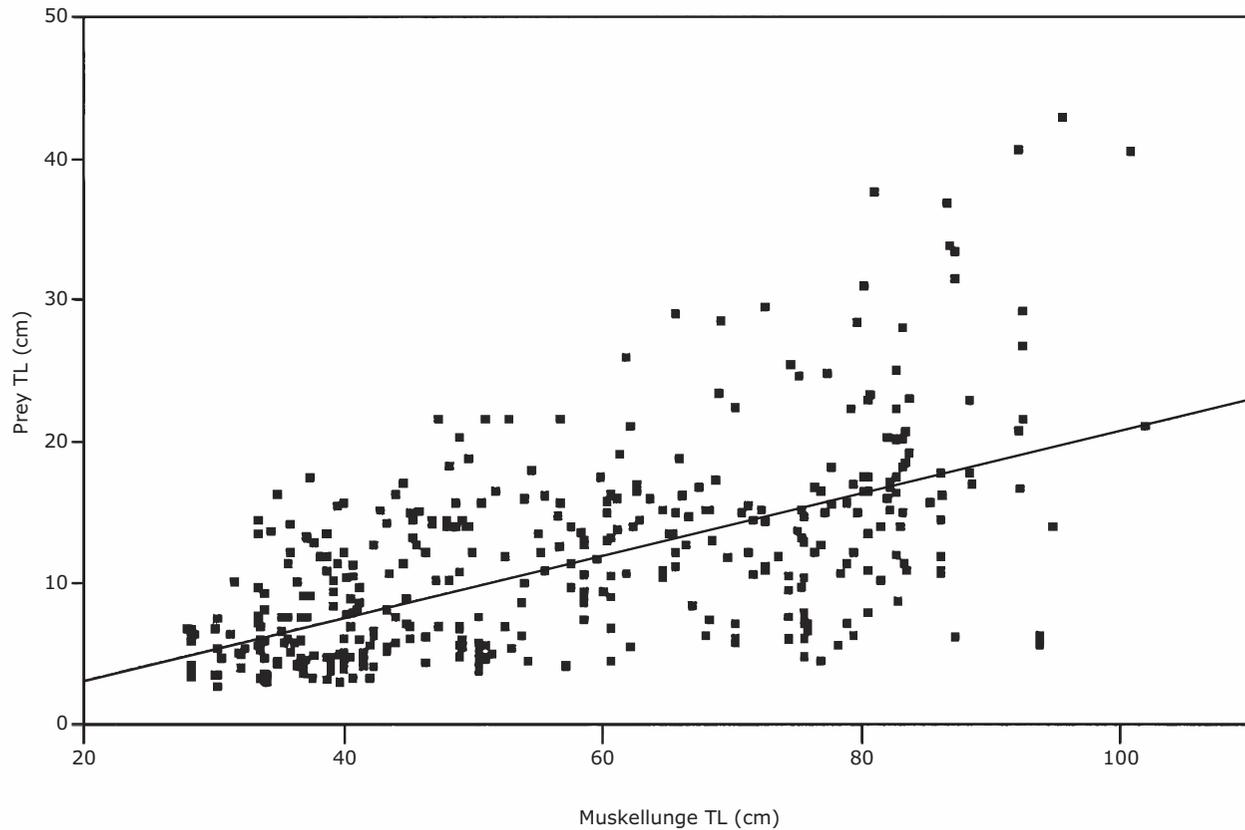


Figure 19.48. Relationship between TL of 427 prey fishes and TL of Muskellunge, *Esox masquinongy* ($R^2 = 0.340$, $p < 0.001$). Muskellunge ate prey fishes that ranged from 6 to 47% of their own TL. Muskellunge were captured from 34 Wisconsin water bodies from spring through autumn. Unidentifiable fish and non-fish prey items were excluded (redrawn from Bozek et al. 1999).

them more susceptible to predation by conspecifics and kleptoparasitism (i.e., one fish taking food from another fish) (Nilsson & Brönmark 1999). Northern Pike diets varied considerably with season and habitats and included higher than expected frequencies of invertebrate prey, especially in small (<600 mm TL) individuals, despite the role of the Northern Pike as a top piscivore in most environments (Lawler 1965; Mann 1976; Chapman et al. 1989). Fishes are an important food throughout the year, and Northern Pike exploit small cyprinids throughout the year, however, they shift to large-bodied prey when available (Frost 1954; Lawler 1965; Diana 1979). Small fishes serve as a primary component in the diets of small Northern Pike (200–500 mm TL) but decline in importance in the diets of the largest individuals (>600 mm TL) (Frost 1954; Lawler 1965; Bregazzi & Kennedy 1980; Mann 1982; Sammons et al. 1994). Similarly, small Grass Pickerel (≤ 95 mm TL) have a diet dominated by fishes compared to one dominated by crayfishes in large Grass Pickerel (>150 mm TL) (Weinman & Lauer 2007). Soft-bodied fishes without hard spines require less manipulation by

the predator and may be acquired at less metabolic cost (Eklöv & Hamrin 1989). In *Esox*, large fusiform prey may be important for fast growth (Beyerle & Williams 1968; Diana 1979; Gillen et al. 1981; Jacobson 1992).

Seasonality of Feeding

Northern Pike, and probably most *Esox* spp., feed throughout the year even though rates of feeding may change. Feeding appears to decline significantly in August, although it is not clear if the decrease is related to water temperature (Chapman & Mackay 1990). Winter predation by the Northern Pike is well documented (Casselmann 1978; Diana & Mackay 1979); Northern Pike gained energy reserves from winter feeding and this may serve to prepare fish for spring spawning.

Alaska Blackfish feed actively in winter and exhibit significant differences among seasons. Prey shifted from gastropods (summer) to gastropods and ostracods (autumn). In winter, ostracods and dipterans were the primary prey item but fish were the dominant food item by biomass (Eidam

et al. 2016). Prey selection also differed among stream, lake, and wetland habitats. Olympic Mudminnows also feed regularly in winter. The winter diet can show high overlap with the diet in spring and summer, although this can vary with size, class, and habitat (Tabor et al. 2014).

Umbra spp. feed actively during winter and digest food relatively rapidly at cold temperatures (Chilton et al. 1984). Of six Great Lakes fish species examined, Central Mudminnows exhibited the greatest tendency for winter feeding (4°C water temperature) with 50–65% of individuals age 0–2 containing food in their gut (Keast 1968); >85% of Central Mudminnows (40–94 mm TL) in a small Indiana stream contained food in their stomach in winter (Peckham & Dineen 1957). In small streams in southern Manitoba in winter, the percentage of full or distended stomachs of the species was as high as early summer; fish were primarily consuming small fishes and

mayflies in the ≤4°C sub-ice waters (Martin-Bergmann & Gee 1985). Two populations of Eastern Mudminnows fed continuously through the winter and showed no significant difference in diet (Panek & Weis 2013).

Diet of *Esox*

Post yolk-sac larval *Esox* feed on planktonic organisms, then as their size increases they switch to macroinvertebrates and soon become primarily piscivores, and depending on gape size they occasionally eat crayfishes, amphibians, water fowl, and small mammals (Figs. 19.49 and 19.50). The timing of their diet shifts varies among species but shifts to piscivory among *Esox* occurs as young-of-the-year (Mittelbach & Persson 1998). Muskellunge shift to a mainly piscivorous diet in ≤5 days after exogenous feeding has begun or at 3 cm SL, but Northern Pike begin feeding

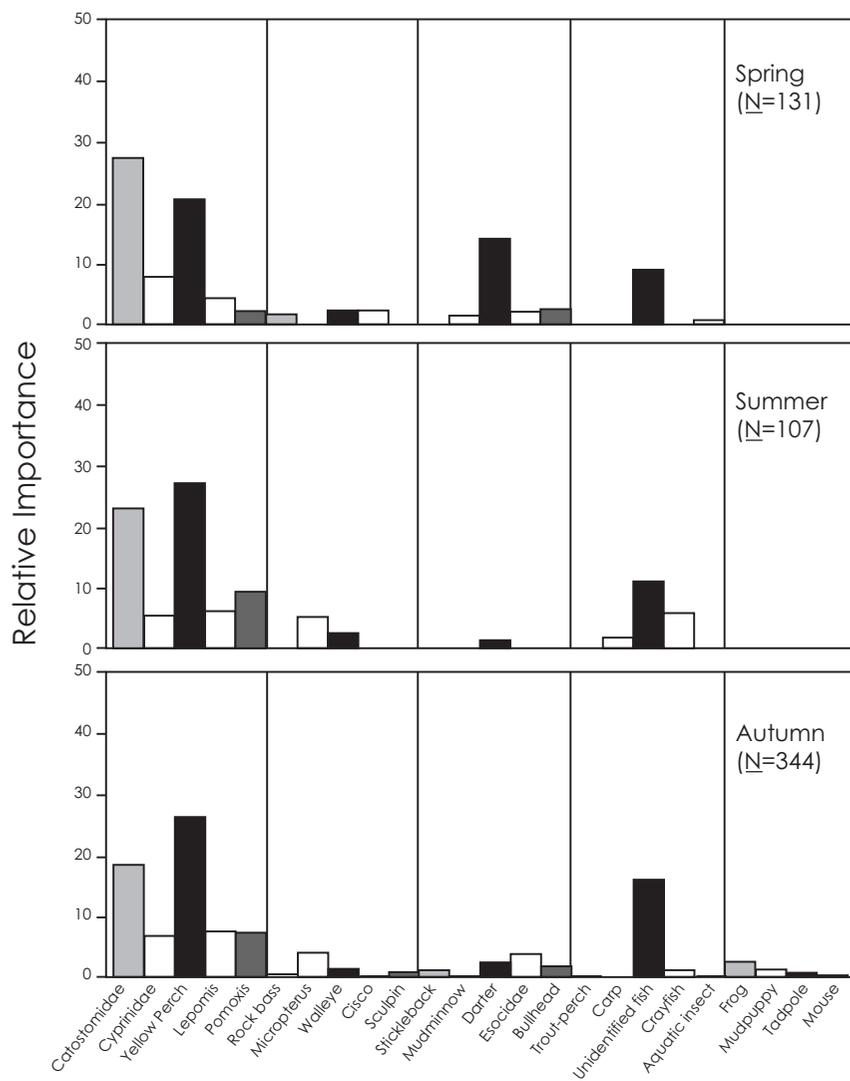


Figure 19.49. Relative importance of prey consumed by Muskellunge, *Esox masquinongy*, captured from 34 Wisconsin water bodies during spring through autumn. Of the 1,092 Muskellunge (22.6–118.0 cm TL) examined, 375 contained food items; N is the number of items identified (total N = 582) (redrawn from Bozek et al. 1999).

on fishes at a later point in development at ≥ 5 cm SL (see morphology section) (Scott & Crossman 1973; Becker 1983). In communities with low prey fish abundance, Northern Pike may rely heavily on macroinvertebrates (Beaudoin et al. 1999). The preferred prey species of Northern Pike varies by location, but in North America prey generally includes Yellow Perch (*Perca flavescens*), Suckers, *Coregonus* spp. (ciscoes and whitefishes), and cyprinids (Lawler 1965). Similarly, Yellow Perch and Suckers are typically the most important components of the diet of the Muskellunge, but the species consumes a diverse array of prey (Fig. 19.49). Whether this diet reflects a selective preference on the part of the predator or simply the relative abundance of those prey species and their habitat overlap with the predator is unclear. Fishes with deep bodies and spiny fins are rarely eaten by either species, but other environmental factors may change this preference. In short, esocids can be considered opportunistic predators, which will take any suitable prey. The Northern Pike and Muskellunge are considered voracious predators and as such are thought to be important competitors of other piscivores and to potentially affect biomass of prey species and indirectly all lower trophic levels (Søndergaard et al. 1997).

Post-yolk sac pickerel larvae begin feeding almost immediately on copepods and other micro-crustaceans (Raney 1942). Larvae switch to increasingly larger prey after feeding on invertebrates at <140 mm TL; yearlings and adults are piscivorous but opportunistically exploit aquatic insects, crayfish, and other invertebrates (Fig. 19.50). Fishes and crayfishes are about equally important food for pickerels (Raney 1942; Becker 1983; Weinman & Lauer 2007). Cyprinids and centrarchids are usually numerically dominant prey items, but catostomids predominate by volume (McIlwain 1970; Lewis 1974). Chain Pickerel diets differed between populations from freshwater and brackish water habitats; fishes and crustaceans dominated the diet in brackish environments, and the use of aquatic insects decreased (Meyers & Muncy 1962).

Diets of *Novumbra*, *Dallia*, and *Umbra*

The diets of *Novumbra*, *Dallia*, and *Umbra* are similar (Figs. 19.51 and 19.52; Table 19.4). These species are carnivorous, generalist predators whose diet varies among sites, seasons, and individual fish sizes. They consume a wide variety of benthic aquatic invertebrates but also occasionally fishes and terrestrial invertebrates (Peckham & Dineen 1957; Ostdiek & Nardone 1959; Keast 1978; Martin-Bergmann & Gee 1985; Gudkov 1998; Panek & Weis 2013; Tabor et al. 2014; Eidam et al. 2016). Dietary shifts with size do not appear to

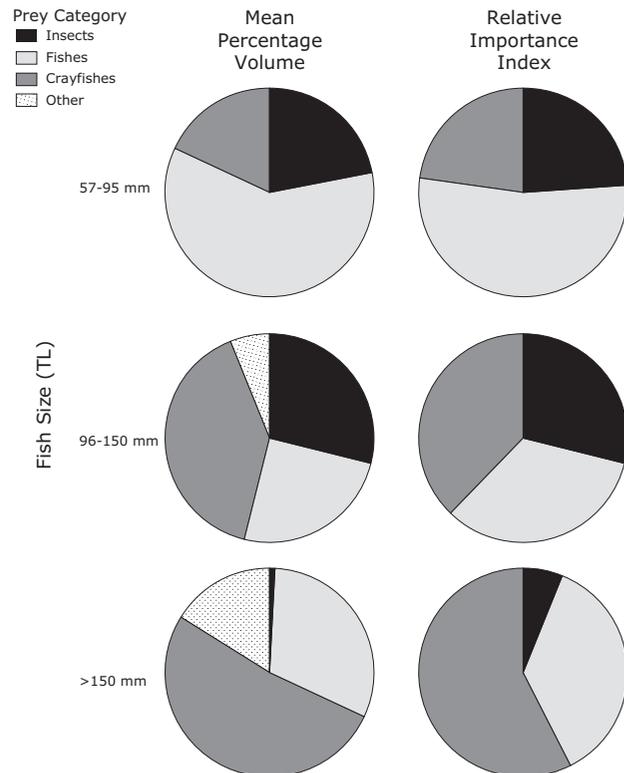


Figure 19.50. Stomach analyses for Grass Pickerel, *Esox americanus*, in three size classes and four prey categories (insects, fishes, crayfishes, and other) showing mean percentage volume and relative importance index value for individuals captured in northern and east central Indiana. Relative importance was not calculated for the other category, which included annelids, isopods, frogs, and unidentified (data from Weinman & Lauer 2007).

be consistent and may be masked by local conditions. Stomach samples from Olympic Mudminnows ≥ 40 mm TL revealed their diet comprised primarily aquatic invertebrates (oligochaetes, chironomid larvae, and copepods) (Fig. 19.51). Though larger fish displayed more dietary specialization, no consistent pattern of ontogenetic shifts in diet occurred. Similarly, Alaska Blackfish diets in summer showed a high occurrence of aquatic insect larvae, especially dipteran larvae, as well as microcrustacea (Fig. 19.52). Small fishes are also eaten by Alaska Blackfish (Ostdiek & Nardone 1959; Chlupach 1975).

Terrestrial insects occur in the diet of *Umbra* as do juvenile conspecifics, but stomach contents of both Central and Eastern Mudminnows suggest they are primarily benthic feeders (i.e., high volumes of detritus and benthic organisms) (Peckham & Dineen 1957; Panek & Weis 2013; Table 19.4). Juvenile winter diet of *Umbra* spp. during their first year included small crustaceans and crustacean

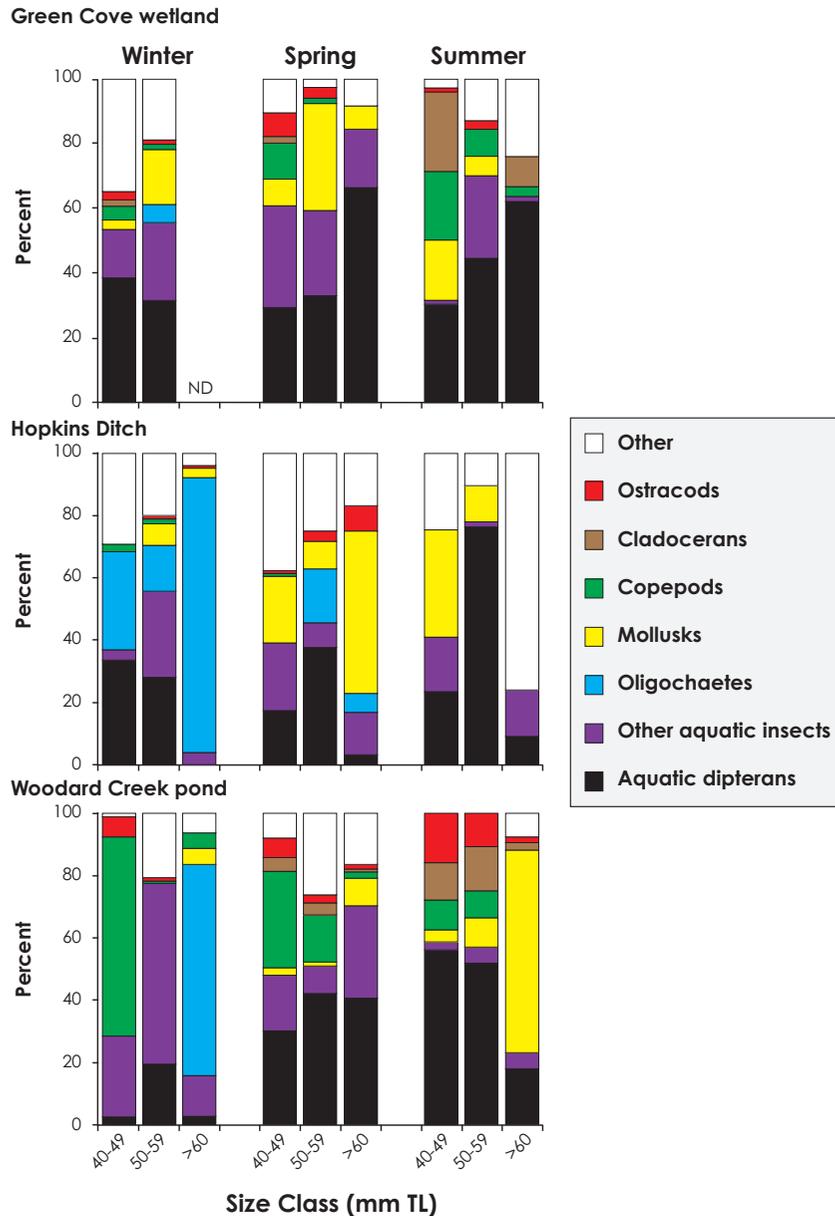


Figure 19.51. Diet composition (percentage by weight) of the Olympic Mudminnow, *Novumbra hubbsi*, at three sites in Thurston County, Washington, February to August. Size class of fish sampled given below bottom bars. ND = no data. The other category includes plant material, detritus, amphipods, water mites, and terrestrial invertebrates (redrawn from Tabor et al. 2014).

and insect larvae (Peckham & Dineen 1957; Becker 1983; Chilton et al. 1984; Rahel & Nutzman 1994). In addition to aquatic invertebrates, females of the Central Mudminnow will feed on small fishes (e.g., cyprinids), especially in the winter at the time of egg development when energy demands are expected to be particularly high. Only adult female Central Mudminnows were piscivorous during winter, and age 2+ females were nearly entirely piscivorous during this season (Chilton et al. 1984).

Age and Growth of Esociformes

Growth of Northern Pike and Muskellunge is rapid, reaching 150–250 mm TL by the end of the first summer

and ≤546 mm TL by the end of the first year depending on latitude (Scott & Crossman 1973; Becker 1983).

Growth rate remains high for several years before slowing once adults reach maturity. Females in the larger esocids are generally both larger and heavier than males of similar age. Northern populations of Northern Pike grow more slowly but live longer than southern populations (Scott & Crossman 1973). As with the larger esocids, growth of young-of-the-year pickerels is rapid, reaching >120 mm FL for Redfin and Grass Pickerel and >170 mm FL for Chain Pickerel (Scott & Crossman 1973; Trautman 1981; Becker 1983). Growth in Canadian populations of Chain, Grass, and Redfin Pickerel appears to be continuous and females grow more rapidly than males, achieving larger size (Scott

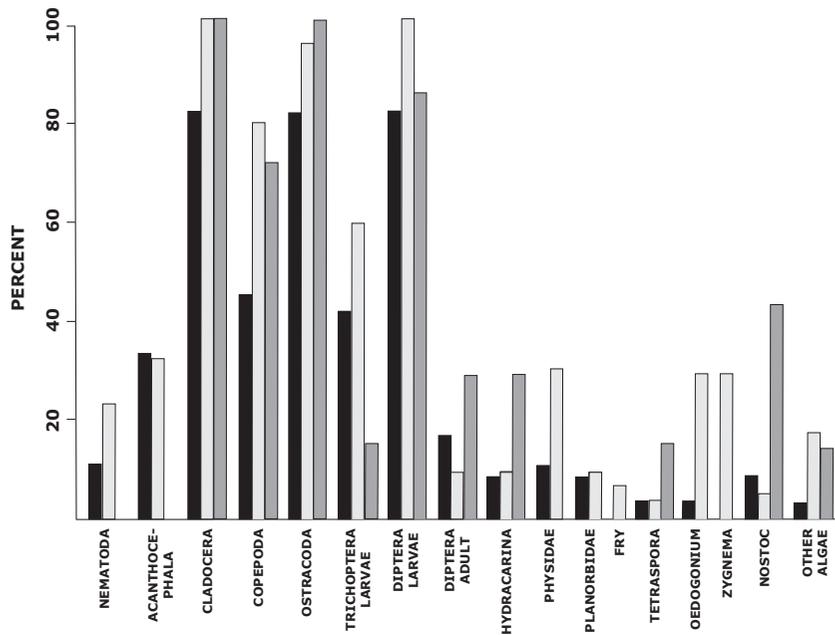


Figure 19.52. Percentage of occurrence of classes of organisms in the stomachs of Alaska Blackfish, *Dallia pectoralis*, sampled in July (4 stations; $n = 36$) and August (same 4 stations plus an additional station; $n = 41$) in a shallow tundra lake and adjacent tundra marshes, near Point Barrow, Alaska. The dark bars represent July samples (4 stations), the cross-hatched bars (same 4 stations) August samples, and the dotted bars August samples from the additional station (redrawn from Ostdiek & Nardone 1959).

& Crossman 1973). Alaska Blackfish growth is rapid in the first year; annual incremental growth declines thereafter (Blackett 1962; Aspinwall 1965), but growth is continuous. Bristol Bay Alaska Blackfish are slower growing and live longer than Interior Alaska populations (Morrow 1980). Information on growth of young-of-the-year Olympic Mudminnows is lacking. Growth of young-of-the-year umbrids is difficult to determine because scale annuli do not accurately reflect age. Central Mudminnows reach 37.5 mm SL by the end of the first summer and 90 mm SL at year 1 (Scott & Crossman 1973; Trautman 1981; Becker 1983).

Predators

In general, esociforms are subject to predation by a wide variety of piscivorous wildlife, including wading and diving birds, mammals, and reptiles (Peckham & Dineen 1957; McEwan & Hirth 1980; Becker 1983) and large predatory fish, such as the Largemouth Bass, *Micropterus salmoides*, and large esociforms, including conspecifics (Wahl & Stein 1989; Craig 2008). Larval and juvenile esociforms are preyed upon by aquatic invertebrates (e.g., diving beetles) and fishes (Lewis 1974; Bry 1996; Le Louarn & Cloarec 1997; Panek & Weis 2013; Eidam et al. 2016). Predation by Silver Lamprey (*Ichthyomyzon unicuspis*) on Muskellunge was documented in the lower Ottawa River, Ontario and Quebec. Sites of attachment, shallowness of the wounds, and evidence of buccal gland secretions suggested blood preda-

tion rather than flesh feeding (Renaud 2002). Large Muskellunge (>122 cm TL) were preferred over small individuals.

Cannibalism and Interspecific Predation

A leading cause for mortality in larval Northern Pike was identified as cannibalism between the larvae near Houghton Lake, Michigan (Hunt & Carbine 1951) and Pleasant Lake Marsh, Wisconsin (Fago 1977). Cannibalism also plays a role in older pike as well with some variation in the rate of cannibalism across the seasons. Cannibalism by the Northern Pike also increases with seasonal changes in availability of prey species (e.g., *Coregonus* spp.) associated with spawning behavior and habitat preferences of preferred prey (Lawler 1965). The frequency of cannibalism in the Northern Pike varies depending on the size differences between individuals and on prey abundance (Nursall 1973; Eklöv & VanKooten 2001). Because populations of Muskellunge spawn after those of co-occurring Northern Pike, predation of Muskellunge larvae by slightly older, larger juveniles of Northern Pike might contribute to early mortality and the apparent competitive disadvantage of the Muskellunge relative to sympatric Northern Pike (Scott & Crossman 1973).

Laboratory experiments with Northern Pike larvae showed that cannibalism appears as early as four weeks of age and accounted for 54–96% of daily mortality in the experimental tanks (Giles et al. 1986). The onset of cannibalism altered larval behavior; larvae established even

Table 19.4. Percentage composition by number (volume) of major food groups in the diet of the Eastern Mudminnow, *Umbra pygmaea* (22–89 mm TL), from the Great Swamp National Wildlife Refuge (GS), New Jersey, and Croatan National Forest (CNF), North Carolina (data from Panek & Weiss 2013).

| Food Group | Winter January-March | | Spring April-June | | Summer July-September | | Autumn October-December | |
|---------------------------|-------------------------|----------|----------------------|----------|--------------------------|----------|----------------------------|----------|
| | GS | CNF | GS | CNF | GS | CNF | GS | CNF |
| | (n = 68) | (n = 38) | (n = 32) | (n = 85) | (n = 30) | (n = 50) | (n = 17) | (n = 17) |
| Detritus | — | — | — | — | — | — | — | — |
| | (24.2) | (25.8) | (33.4) | (47.2) | (38.3) | (35.0) | (36.9) | (37.8) |
| Amphipoda | 0.1 | 0.9 | 0.1 | 2.1 | 0.1 | 3.0 | 1.4 | 4.7 |
| | (4.2) | (10.4) | (3.1) | (4.2) | (3.0) | (5.7) | (2.6) | (16.8) |
| Cladocera | — | 79.6 | 4.8 | 26.4 | — | 20.7 | 1.8 | 0.9 |
| | (6.2) | (9.3) | (1.1) | (4.2) | — | (0.5) | (0.1) | (0.4) |
| Copepoda | 0.9 | 0.7 | 34.2 | 4.6 | — | 6.1 | 21.2 | 14.2 |
| | (1.0) | (1.8) | (3.8) | (2.2) | — | (1.1) | (1.6) | (2.4) |
| Ostracoda | 24.7 | 0.5 | 50.4 | 3.4 | 97.4 | 9.7 | 53.8 | 4.7 |
| | (22.0) | (0.6) | (28.2) | (0.3) | (50.6) | (4.0) | (19.5) | (2.5) |
| Diptera | 73.9 | 15.3 | 5.5 | 44.1 | — | 37.1 | 10.1 | 62.0 |
| | (31.2) | (23.5) | (9.0) | (13.2) | — | (9.1) | (4.5) | (10.0) |
| Coleoptera | 0.1 | 0.8 | 0.8 | 5.9 | 0.1 | 6.7 | 5.3 | 5.7 |
| | (10.6) | (15.7) | (6.4) | (17.8) | (3.0) | (15.8) | (17.9) | (20.0) |
| Odonata | 0.1 | — | 0.4 | 0.4 | — | 3.0 | 1.6 | — |
| | (2.3) | — | (5.3) | (0.9) | — | (6.2) | (3.5) | — |
| Trichoptera | — | — | 3.2 | 3.8 | — | — | — | 0.9 |
| | (9.4) | — | (3.4) | (2.9) | — | — | — | (5.7) |
| Lepidoptera | — | — | — | 0.8 | — | — | — | — |
| | — | — | — | (0.6) | — | — | — | — |
| Ephemeroptera | — | — | — | — | — | 3.0 | — | — |
| | — | — | — | — | — | (6.2) | — | — |
| Collembola | — | 0.1 | — | — | — | 0.7 | — | — |
| | — | (0.1) | — | — | — | (1.0) | — | — |
| Heteroptera | — | 1.0 | — | 3.4 | — | 1.5 | — | — |
| | — | (7.1) | — | (4.8) | — | (2.3) | — | — |
| Hydrachnidae | — | 0.2 | — | 0.4 | — | — | — | 4.7 |
| | — | (1.0) | — | (0.1) | — | — | — | (1.2) |
| Formicidae | — | — | — | 0.8 | — | 2.3 | — | — |
| | — | — | — | (0.3) | — | (1.3) | — | — |
| Nematoda | — | — | — | — | — | 1.5 | — | — |
| | — | — | — | — | — | (0.2) | — | — |
| Oligochaeta | — | 0.8 | 0.4 | 1.7 | 0.1 | 0.8 | — | — |
| | (3.1) | (3.8) | (3.5) | (0.4) | (1.7) | (0.1) | — | — |
| Pelecypoda | 0.1 | — | 0.1 | — | — | 0.8 | 2.4 | — |
| | (0.9) | — | (1.3) | — | — | (1.8) | (6.3) | — |
| Gastropoda | 0.1 | — | 0.1 | — | — | 1.5 | 2.4 | — |
| | (2.2) | — | (2.5) | — | — | (5.9) | (6.3) | — |
| <i>U. pygmaea</i> | — | — | — | — | 0.8 | 0.8 | — | — |
| | — | — | — | — | (3.2) | (3.2) | — | — |
| Duckweed | — | — | — | — | — | — | — | — |
| | (1.2) | — | — | — | — | — | (1.0) | — |
| Filamentous algae | — | — | — | — | — | — | — | — |
| | (0.2) | — | — | — | — | — | (0.6) | — |
| Unidentified | — | 0.1 | — | 0.3 | — | — | — | 2.2 |
| | — | (0.9) | — | (1.5) | — | — | — | (3.3) |
| Percentage empty stomachs | 30.9 | 10.5 | 40.7 | 26.5 | 37.5 | 38.0 | 28.3 | 17.6 |

spacing in the tanks and remained still for long periods, particularly following the onset of cannibalism. Cannibals were attracted by larval movements which often resulted in attacks. Non-cannibals reduced feeding rates, and while stationary, oriented to cannibals.

Abundance, Population Dynamics, and Ecological Role of *Esox*

An extensive literature exists on population dynamics and ecological role of the Northern Pike (reviewed Craig 1996, 2008). In addition, Hall (1986) edited a compilation of studies on the Muskellunge propagation, ecology, and population biology. Mittelbach & Persson (1998) compared the ontogeny of piscivory among several families. Pike and pickerel generally tend to spawn at lower temperatures, have larger egg diameters, and hatch at larger sizes than other piscivorous genera except for some salmonids.

Estimates of population density and biomass of the Northern Pike vary extensively among populations and between years within a population. Densities of 2.5–80.0 individuals/ha and biomass of 1.5–31.3 kg/ha are known (Bregazzi & Kennedy 1980). Part of this variability is caused by wide fluctuations in recruitment success from year to year. A suitable prey base and the water temperature regime also impact population density. The size of the parental cohort and the size of the resulting offspring cohort are not correlated, pointing to the importance of mortality rates of eggs, larvae, and juveniles in determining recruitment success. Broad climatological patterns like the strength and direction of the North Atlantic Oscillation displacement (corresponding to different climatic conditions in autumn and winter) may be important explanatory variables for recruitment and year-class success (Paxton et al. 2009). Female recruitment was also influenced by young-of-the-year winter temperature.

Management strategies aimed at improving the quality of recreational fisheries of Northern Pike and Muskellunge generally include use of length and creel limits, critical habitat protection (i.e., spawning, rearing, and feeding), and stocking programs to supplement natural reproduction. The results of these programs are mixed as the effects of limits may be masked by recruitment failures and mortality in the population (Margenau & AveLallement 2000; Margenau et al. 2008). Stunting (poor growth) in the Northern Pike may be associated with a variety of biotic and abiotic factors, including high population abundance, competition for food, overstocking, and factors associated with lake size (Snow 1974; Goeman et al. 1993; Margenau et al. 1998).

Stunting is more common in small lakes where availability of littoral habitat, water temperature, dissolved oxygen, water visibility and productivity, and amount and type of food resources are limiting (Margenau et al. 1998). Stunting is less common in larger waters where Northern Pike density is lower and a greater diversity of prey exists (Margenau et al. 1998).

The importance of the functional role of the Northern Pike in ecosystems is the subject of debate. Because members of this species are voracious predators and because they can consume relatively large prey, they may be a significant factor in shaping fish communities, which in turn may influence entire ecosystems. In Denmark, Northern Pike are stocked in eutrophic lakes with the goal of reducing zooplanktivorous fishes and in turn increasing zooplankton levels so that water turbidity is decreased (Søndergaard et al. 1997). The results of this program are mixed. Whether the ambiguous results are caused by high mortality in the stocking process or the inability of Northern Pike to have a significant effect on prey populations is unclear. In the United States, a similar biomanipulation program was deemed successful (Lathrop et al. 2002); however, this program involved the introduction of the Northern Pike and Walleye so the specific contribution of the Northern Pike to the success of the experiment is unclear. Evidence from modeling suggested certain characteristics of the predatory behavior of the Northern Pike, such as cannibalism and kleptoparasitism, may make their effect on prey abundance and community structure short lived and relatively minor when compared with the effect other predators may have (Nilsson 2001).

In contrast, some populations of Northern Pike can indeed consume enough prey biomass to cause significant changes in prey abundance and potentially shape the structure of the community (Grimm 1983; Paukert et al. 2003). Craig (1996) reviewed the role of the Northern Pike in shaping the distribution of prey species, their growth rate, and their species composition. In the presence of the Northern Pike, species with deeper bodies and spiny fins, which are less vulnerable to predation by Northern Pike, increased in abundance, but this effect was somewhat dependent on habitat type (Eklöv & Hamrin 1989). Where vegetation is scarce, the Northern Pike preferentially takes the soft-rayed cyprinid *Scardinius erythrophthalmus* (Rudd), but in abundant submerged vegetation the preferred prey is the spiny Yellow Perch. This suggests Northern Pike are opportunistic, and the prevalence of Yellow Perch in their diet is the result of habitat overlap rather than prey selection. Seasonal change is an-

other source of variation in the composition of the diet of the Northern Pike (Sammons et al. 1994; Paukert et al. 2003). Brenden et al. (2006) estimated Muskellunge predation on other species in the New River, West Virginia, where they prey primarily on cyprinids and catostomids (0.31 kg ha/year and 0.63 kg/ha/year, respectively for 100 age-1 Muskellunge).

An interesting effect of the Northern Pike on prey species was a documented increase in body depth of resident Crucian Carp, *Carassius carassius*, after the introduction of the Northern Pike (Brönmark & Miner 1992). This effect is mediated by chemical cues detected by Crucian Carp in the odor of Northern Pike (Brönmark & Pettersson 1994). In another prey-related effect, larger gapes were observed in populations of Northern Pike living in conditions of low prey abundance (Magnhagen & Heibo 2001). The effect was attributed to either phenotypic plasticity or genetic differences driven by selection for those individuals likely to capitalize on the infrequent encounters with prey under conditions of low resource abundance. The emergence of a novel ecotype of Chain Pickerel (deeper body, more slender head, and shorter upper jaw) was documented in impounded coastal lakes with landlocked populations of Alewife (*Alosa pseudoharengus*). Morphological changes corresponded with differences in stable isotopes, dietary observations, and elevated lipid content and suggested that pelagic foraging by Chain Pickerel conferred a fitness advantage (Brodersen et al. 2015).

Due to the potential effect of Northern Pike introductions on native species, special attention is given to the relationship between introduced Northern Pike and salmonids, which are economically valuable in commercial and recreational fisheries. In this respect, the illegal introduction of Northern Pike to Pacific Coast drainages in Alaska has generated some alarm (Dalton 2002). Declines in fisheries stocks of Northern Pike around the Baltic Sea are attributed to eutrophication, climate change, and overfishing and have produced a trophic cascade resulting in a shift from a predator-dominated to a prey-dominated food web (Lehtonen et al. 2009; Ljunggren et al. 2010).

Abundance and Occurrence of *Novumbra*, *Dallia*, and *Umbra*

Olympic Mudminnows occur in greatest abundance in shallow, emergent wetlands with muddy substrate, dense vegetation, and little or no current, regardless of whether non-native species are present (Henning et al. 2007). They occur in large numbers in both regulated and natu-

ral wetlands with a peak in abundance in April and May when young-of-the-year emerge and access is increased due to inundation of off-channel wetland and oxbow habitats (Henning 2004). Electrofishing at 16 sites historically supporting the species produced 0–144 individuals (CPUE 0–1.9 individuals/s) (Mongillo & Hallock 1999). The occurrence of Olympic Mudminnows in wetland sites may be related more to habitat preference (Henning et al. 2007) than competitive exclusion or predation by non-native species (Beecher & Fernau 1983). An intensive survey of habitats in the Chehalis River system showed strong affinities for lower water temperatures, suggesting that Olympic Mudminnows persistence in marginal habitats may depend on cool-water refugia associated with groundwater springs (Kuehne & Olden 2016). Ordination and modeling of quadrat-scale environmental variables showed that detection and abundance of Olympic Mudminnows were strongly related to lower temperatures followed by shallow depths (associated with shorelines), low dissolved oxygen, and greater extent of macrophyte cover.

Although quantitative data are lacking, the Alaska Blackfish often occurs in vast numbers in tiny, weed-choked pools and shallow lakes in the tundra (Nelson 1884; Turner 1886; Aspinwall 1965; Haynes et al. 2014). In a multimethod survey in summer of 86 lakes across the interior of the Arctic Coastal Plain in Alaska, detection probabilities for Alaska Blackfish were highest in minnow traps set in the deepest portions of the shallow lakes relative to minnow traps set along the shorelines, pelagic and benthic gill nets, and fyke nets (Haynes et al. 2013). The probability of occupancy of Alaska Blackfish decreased as lakes became less densely distributed at the regional level, suggesting connectivity is an important life-history factor. Occupancy also increased as a greater percentage of the lake remained unfrozen during winter, probably because they overwinter in lakes with deep, unfrozen waters (Haynes et al. 2014). Alaska Blackfish had an observed occupancy of 0.74 and an estimated occupancy 0.76 (Haynes et al. 2014).

In suitable habits *Umbra* spp. can be quite common, although quantitative estimates of population sizes are few. For example, in a multimethod survey of fishes in the Great Swamp National Wildlife Refuge, New Jersey, the Eastern Mudminnow accounted for 73.8% (248 individuals) of the seven fishes captured over multiple months (17–68 individuals/season) (Panek & Weiss 2012). Similarly, in central Wisconsin, >3,000 Central Mudminnows were captured from undercut banks along a 200 m reach of an old ditch downstream of a marsh (Becker 1983).

Other Ecological Aspects of Non-*Esox* Esociforms

Little else is known about the ecological role played by other esociform species, most notably for *Novumbra* and *Dallia*. Generally, these species form part of fish communities that include only a few species (<4), and they appear to compete poorly with other fishes. The Olympic Mudminnow can be locally abundant and may be the only fish species present (Meldrim 1968; Tabor et al. 2014). As such, they may have important effects on the aquatic community, but their particular role in regulating aquatic communities is uncertain. Catch/unit effort of Olympic Mudminnows declines as fish species richness increases, suggesting they fare poorly when in competition with or potentially preyed on by other species (Mongillo & Hallock 1999).

Populations of Alaska Blackfish most often coexist with *Gasterosteus aculeatus* (Threespine Stickleback), *Cottus* spp. (freshwater Sculpins), and juveniles of various species of Pacific Salmon (*Oncorhynchus* spp.), but they occur at greatest densities in the absence of these or any other species (Reynolds 1997). Similarly, individuals of Alaska Blackfish in Siberia exhibit faster growth and attain larger sizes in the absence of other fish species (Gudkov 1998).

Although species of *Umbra* frequently form part of more diverse fish communities, they too appear to be poor competitors and to be more abundant in the absence of other species (Tonn & Paszkowski 1987). This may be attributed to the tolerance of these species to extreme environmental conditions that are stressful or lethal to other fishes. The Central Mudminnow was described as a resource generalist based on the breadth and variability of their diet and as a specialist based on their specific habitat requirements (Martin-Bergmann & Gee 1985).

In acidic systems, Central Mudminnows and Eastern Mudminnows may be important predators (Rahel & Magnusson 1983; Dederen et al. 1986). At high densities, Central Mudminnows may affect the structure of littoral macroinvertebrate communities (Brown & DeVries 1985), however their effect on littoral fish communities is unknown. Central Mudminnows may also serve as important prey items in some systems (Tonn 1985; Ward et al. 2008) but not in others (Weidel et al. 2000, 2007). As female Central Mudminnows apparently shift to piscivory during winter (Chilton et al. 1984), the size and age structure of a large adult female population could strongly influence the ability of other competing fish species to become established or maintain populations under some conditions.

Eastern Mudminnows often represent a significant component of the fish community in flooded marshes on

the U.S. Atlantic Coastal Plain (Bunnell 2006; Panek & Weis 2012). This suggests the species is ecologically important to the functioning of these systems. Like the Central Mudminnow, the Eastern Mudminnow is hardy and often lives in marginal habitats and withstands extreme environmental temperatures, periods of hypoxia, and low pH. Evidence suggests abundance of *Umbra* spp. is inversely related to the presence of predatory species (Dederen et al. 1986) and to the number of fish species present (Panek 1981).

Dallia, *Novumbra*, and *Umbra* all have some characteristics (small fish, inhabit shallow waters, locally abundant, associated with dense aquatic macrophytes, tolerant of a wide range of environmental conditions) of fishes that are used to control nuisance insects such as mosquitoes (Ahmed et al. 1988; Walton 2007; Pyke 2008). Because *Dallia*, *Novumbra*, and *Umbra* occupy marginal habitats and may be the only species present, they may be a useful control agent for reducing mosquito populations, either directly through predation or indirectly by affecting adult insect choice in oviposition sites (Lombardi 2009; Walton et al. 2009; Tabor et al. 2014).

Parasites

Common parasites in esociforms include myxozoans, ciliates, trematodes, cestodes, helminths, and acanthocephalans (Amin 1980; Amin & Myer 1982; Muzzall & Buckner 1982; Muzzall 1984; Hoffman 1999; Basson & Van As 2006). The diversity of parasites that occur in any one species can be quite high. The Northern Pike, one of the best studied species, for example, is documented as harboring parasitic fungi (2 taxa), protozoans (about 24), monogeneans (7), trematodes (about 50), cestodes (about 20), nematodes (about 27), acanthocephalans (about 21), hirudineans (6), molluscs (probably several), and crustaceans (about 13) (review by Hoffman 1999). Although most parasites of esociforms occur in a variety of fishes, some parasites apparently occur only in a particular esociform, such as the spiny headed worm, *Neoechinorhynchus limi*, in the Central Mudminnow (Muzzall 1984), the cestode, *Diphyllobothrium dalliae*, in the Alaska Blackfish (Rausch 1956), the monogeneans, *Gyrodactylus lucii*, in the Northern Pike (Cone & Dechtiar 1986), *G. fryi*, in the Muskellunge (Cone & Dechtiar 1984), and *G. neili*, in the Chain Pickerel (LeBlanc et al. 2006).

Parasitic infestations can be heavy in some species and predominate in larval and small fishes. For example, *D. dalliae* occurs free in the body cavity of Alaska Blackfish

throughout its range in Alaska (Hilliard 1959); infections transferred to dogs and humans may cause pernicious anemia (loss of stomach cells cause anemia) (Rausch et al. 1967). In an Indiana population, 10% of Central Mudminnows contained heavy infections of yellow grub (Trematoda: *Clinostomum* sp.) that hindered swimming movements and appeared to afflict small fish the greatest (Peckham & Dineen 1957). *Gyrodactylus limi* was common on the skin and gills of larvae (10–15 mm TL) and appeared to pass readily from one fish to another. A common parasite of the urinary bladder was a trematode *Phyllostomum brevicecum*. In Central Mudminnows, seasonal patterns of infection of two intestinal acanthocephalan parasites could be related to movements of the species, changes in water temperature, and possibly to dietary changes (Muzzall 1984). Eutrophication of aquatic systems linked to watershed disturbance in the acidic streams of the New Jersey Pine Barrens is correlated with high susceptibility and infection rates by helminth parasites in the Eastern Mudminnow (Acanthocephala, 2 taxa; Digenea, 2 taxa; Nematoda, 3 taxa; 8–75% prevalence) and Chain Pickerel (Acanthocephala, 2 taxa; Digenea, 2 taxa; Nematoda, 3 taxa; Cestoda, 1 taxon; 14–100% prevalence) (Hernandez et al. 2007). Schaufler et al. (2014) highlighted an unintended consequence of stocking programs of Northern Pike, reporting a subsequent epizootic outbreak of cestodes in resident char.

Unlike many other North American fishes, the esociforms apparently do not serve as specialized hosts for any North American freshwater mussel taxa (Haag 2012). Glochidia of the Creeper, *Strophitus undulatus*, a species that uses an array of fishes as host, transformed on the Central Mudminnow in laboratory trials. Laboratory infection of Chain Pickerel with glochidia of Fatmucket (*Lampsilis siliquoidea*) apparently caused the death of the host fish (Keller & Ruessler 1997). Some fishes in the wild, like the Redfin Pickerel, can be infected with glochidia (larvae) of generalist mussel species, like the Paper Pondshell, *Utterbackia imbecilis*, but transformation is unconfirmed. The occurrence of Yellow Lampmussel (*Lampsilis cariosa*) glochidia in a juvenile Chain Pickerel may indicate it is a potential host (Kneeland & Rhymer 2008). Likewise, Northern Pike in the wild carry glochidia of the Three-ridge, *Amblyma plicata*, another generalist species, but transformation is unconfirmed (Parmalee & Bogan 1998; Williams et al. 2008, 2014). Glochidia of European unionid mussels (*Unio* sp.) and Freshwater Pearl Mussel (*Margaritifera margaritifera*) occur naturally in the Northern Pike (Blažek & Gelnar 2006; Geist et al. 2006), but

transformation is unconfirmed; salmonids are the primary host fishes for Freshwater Pearl Mussels (Haag 2012).

CONSERVATION

Among esociform species, members of *Esox* and *Dallia* are considered of least conservation concern by the International Union for Conservation of Nature and Natural Resources (IUCN 2016; NatureServe 2018). These species are generally wide-ranging and abundant. As important sport fish, the Northern Pike and Muskellunge are also widely stocked to support recreational and commercial fisheries. Stocking of Muskellunge may be obscuring the taxonomic status of the color variants, and management strategies to conserve genetic diversity in Muskellunge populations are proposed (Casselman et al. 1986; Jennings et al. 2010).

Owing to its rarity and limited distribution, the Olympic Mudminnow is categorized as Vulnerable by the American Fisheries Society (Jelks et al. 2008), and as a Sensitive protected species in Washington because of its restricted range and highly vulnerable habitat (Mongillo & Hallock 1999; WDFW 2012). It was considered for protection under the U.S. Endangered Species Act until the rule change governing the status of candidate species. The current IUCN assessment lists it as Least Concern (IUCN 2016). Fishing for or collecting this species is prohibited even though it is not commonly fished or used for bait, and the main threat to its survival remains the destruction of suitable wetland habitat (Mongillo & Hallock 1999). A proposed impoundment on the upper Chehalis River would inundate significant sections of habitat of fluvial populations (Scott et al. 2013; Kuehne & Olden 2016).

Other umbrids are at risk in portions of their home ranges, but no range-wide threats are currently identified (Jelks et al. 2008; NatureServe 2018). In states where Central and Eastern Mudminnows are species of conservation concern, the species have limited distributions or occur at the periphery of their range (Page & Burr 2011). The European Mudminnow is classified as Vulnerable (IUCN 2016).

Climate Change Effects on Distribution

Climate change associated effects in freshwater ecosystems (including rising stream temperatures and sea levels) pose potential threats to esociform species (Ficke et al. 2007). Under the Canadian Climate Center general circulation model, Eaton & Scheller (1996) predicted a <50% loss of

the Northern Pike from gaged stations in the conterminous United States. Similar declines are predicted for the Northern Pike and Central Mudminnow in Wisconsin under multiple climate scenarios (Lyons et al. 2010). Though the successful invasion of subarctic lake ecosystems by the Northern Pike could not be directly associated with increased temperatures, the dramatic changes observed in abundance of prey species and trophic relationships in the lakes typified the possible effects of future Northern Pike invasions that could be enhanced by climate change (Minns & Moore 1992; Byström et al. 2007).

Climate change may affect food availability and productivity in freshwater systems (Linnansaari & Cunjak 2012) and in turn affect *Esox* spp. as well as other esociforms. Although reduced prey would suppress Northern Pike populations, increased nutrient budgets could increase Northern Pike production in systems with low productivity (Reist et al. 2006). A shifting thermal regime, however, may affect condition indices as metabolic demands on resident fishes increase (Spotila et al. 1979; Clapp & Wahl 1996). Rising temperatures may disrupt growth, reproduction, and recruitment as well as the phenology of prey availability to larvae and juveniles. For example, increases in summer and early winter water temperatures impaired year-class strength for Northern Pike (Casselman 2002). Rising temperatures can also trigger a cascade of effects, including increased susceptibility to epizootic diseases, magnification of pollutants, oxygen depletion, and degraded water quality (Jeppesen et al. 2010). As a geographically restricted, stenothermic cold-water fish, the Alaska Blackfish is among the most vulnerable species to climate change (Lehtonen 1996; Reist et al. 2006). Thawing permafrost may increase methane emissions; methane trapped under ice is linked with winterkill in Alaska Blackfish (Campbell et al. 2014).

Climate change can also impose habitat constraints because changes in timing of spring floods may affect availability and access to spawning habitats. Lower water levels from drought could also impose an added energy burden as fish seek to avoid temperatures >25°C. Northern Pike lose weight when their habitats are restricted as when thermoclines separating warm surface waters from cooler water approach hypoxic depths (Reist et al. 2006).

Rising sea levels present possible threats to populations of Olympic Mudminnows, Alaska Blackfish, and Eastern Mudminnows in coastal sloughs and marshes. Intrusion of saltwater into freshwater and brackish marshes could raise salinities above the maximum tolerance thresholds for those species. The high degree of genetic structuring of

the Alaska Blackfish (see genetics section) is maintained by the strictly freshwater nature and low dispersal ability of this genus. These ecological characteristics make the diverse populations vulnerable to rising temperatures and rising sea levels associated with climate change.

Habitat Alteration

Other than Olympic Mudminnows, all esociform species have relatively wide distributions that presently include many healthy, self-sustaining populations. Therefore, as species they are not considered at risk. However, because all esociforms require slow moving, heavily vegetated, shallow waters, their suitable habitat is usually adversely affected by land development practices that require water-level alteration and drainage of shallow wetlands. In fact, habitat alteration, not harvesting, likely is responsible for declines or extirpation of some populations of esociforms from their historical range (e.g., *Umbra*, *Kenoza*, Trautman & Gartman 1974; *Esox* spp., Axon & Kornman 1986; Cook & Solomon 1987; Minns et al. 1996; Rust et al. 2002; Cooper et al. 2008; *Novumbra*, Mongillo & Hallock 1999; Glasgow & Hallock 2009). Management programs are in place to prevent further losses of populations and decreases in population size of Northern Pike and Muskellunge, both of which are highly regarded targets for recreational anglers (see commercial importance section).

Pollution

As top piscivores, *Esox* spp. have the potential to accumulate contaminants in their tissues in environments exposed to human pollution, including mercury (Gariboldi et al. 1998; Stafford & Haines 2001; Jewett et al. 2003; Tang et al. 2013), other heavy metals (Harrison & Klaverkamp 1990), and organic pollutants (Lazorchak et al. 2003; Burreau et al. 2004; Sharma et al. 2009). Tissue concentrations of these pollutants tend to be strongly and positively correlated with size and age (Jewett et al. 2003; Kamman et al. 2005; Jewett & Duffy 2007) and with the length and complexity of lake food webs (Stemberger & Chen 1998) and catchment area (Peterson et al. 2007). In regional-scale assessments of mercury contamination, the highest mean mercury concentrations occurred in the Muskellunge (0.98 ng/g, fillets) and Northern Pike (0.64 ng/g, fillets; 0.56 ng/g, whole-body) (Kamman et al. 2005). Chain Pickerel had tissue mercury concentrations between 0.58–1.22 ng/g body weight (mean = 0.88 ng/g), the highest of nine species sampled

(Stafford & Haines 1997). Nearly 2,300 fish consumption advisories for mercury in the Northern Pike have been issued by state departments of health in the United States (USEPA 2013). Evaluations of the subsistence fishery of the Yup'ik people of western and southwestern Alaska found mercury contamination in the Northern Pike (443.8 ng/g) that far exceeded the USEPA's critical value for consumption advisory of 200 ng/g (USGS 2001). Alaska Blackfish (155.2 ng/g) and salmon species (mean concentrations 64.9 ± 11.1 SD– 119.7 ± 71.7 SD ng/g) had lower concentrations of mercury than the Northern Pike, presumably because of the position of the Northern Pike as a top piscivore. Even wider ranges of concentrations are documented in Alaskan subsistence fishes (Jewett & Duffy 2007); the highest concentrations exceeded consumption advisories fivefold. In one of the few studies of mercury tissue contamination in umbrids, Central Mudminnows had whole body mercury concentrations ranging from fairly low values (23 ng/g) to levels >200 ng/g wet weight, an estimated tissue threshold associated with sublethal and reproductive effects in fish (Rolfhus et al. 2015), and exceeding wildlife exposure values for piscivorous mammals (e.g., river otter, *Lutra canadensis* and mink, *Mustela vison*) and birds (e.g., belted kingfisher, *Ceryle alcyon*) (Lazorchak et al. 2003).

Environmental contaminants may also affect recruitment and year class success. Larval deformities characteristic of selenium exposure (i.e., skeletal curvatures, craniofacial deformities, fin deformities, and edema) were 20% more frequent than background levels in eggs obtained from female Northern Pike exposed to metal mining effluent (Muscatello et al. 2006). Pulp mill effluent induced severe skeletal deformities in the jaw and skull (Lindesjö & Thulin 1992).

Esociforms may be negatively affected by other sources of pollution. For example, degraded water clarity associated with increased turbidity and eutrophication can decrease visual range and reaction distance in visual predators like esocids resulting in lower predation success (Turesson & Brönmark 2004, 2007; Nilsson et al. 2009; Ranåker et al. 2012). Increasing eutrophication depressed larval condition of the Northern Pike in some parts of the Baltic Sea and has reduced population size (Salonen et al. 2009). Similarly in a small esociform, Central Mudminnows exhibited a threshold response of increased growth as agricultural and urban land use increased (Filgueira et al. 2016). Central Mudminnow populations from Adirondack Mountain sites exposed to acid deposition had lower genetic heterozygosity than at control sites (Kopp

et al. 1992). Laboratory toxicity tests revealed the most tolerant fish had greater genetic variation, suggesting genetic diversity conferred differential survival to individuals under acute physiological stress. Because of their occurrence in sloughs, small ponds, ditches, and backwater habitats, small esocids and umbrids may be disproportionately affected by exposure to pesticides used in mosquito control (Bender & Westman 1976).

Diseases of Esociforms

Diseases associated with pathogens and parasites vary across the native and introduced range of esociforms (Dick & Choudhury 1996; Harshbarger & Clark 1990; Roberts 2012). Owing to their commercial and recreational importance and their propagation in aquaculture, more attention has been devoted to the characterization of diseases in the Northern Pike and Muskellunge than in other esociforms. Northern Pike, particularly the larvae, in aquaculture are susceptible to a variety of diseases that have high infection rates and mortality (Bootsma 1971; Bootsma & van Vorstenbosch 1973; Graham et al. 2004; reviewed by Coffee et al. 2013).

Viruses can cause significant pathology in esocids. Viral haemorrhagic septicaemia virus (VHSV) occurs in the Muskellunge causing damage to internal organs and thickening and formation of fluid-filled vesicles on the inner wall of the swim bladder (Elsayed et al. 2006). An outbreak in the Upper St. Lawrence River caused size- and age-specific mortality of about 50%; the culling effect resulted in a growth-rate change (Casselman 2011). Red Disease (or Pike Fry Rhabdovirus Disease), which produces hemorrhagic areas in the trunk in the Northern Pike, is caused by a rhabdovirus and can be transmitted through water (De Kinkelin et al. 1973; Bootsma et al. 1975; Jørgensen et al. 1993).

Blue Spot Disease (caused by Esocid Herpesvirus-1, EsHV-1) occurs in the Northern Pike and Muskellunge and is associated with small, pale bluish-white, granular skin lesions that occur mostly over the dorsal skin and fins (Yamamoto et al. 1984; Margenau et al. 1995). Its prevalence in Wisconsin differed among lakes, years, and seasons, and was generally higher for female Northern Pike. Infection rates averaged 11% (<1–34%) for the Northern Pike and 20% (10–29%) for the Muskellunge from 23 northern Wisconsin lakes (Margenau et al. 1995) with the greatest prevalence in younger fish during the spring spawning season at water temperatures of 2–13°C. In general, larger and older Northern Pike were less likely to

have observable lesions. The pathogenesis of Blue Spot Disease is unknown. Clinical signs dissipated when water temperatures reach 14°C. The infection rates found by Margenau et al. (1995) were generally higher on average than those reported by Yamamoto et al. (1984) (<1% to 7%) in Canada.

Esocid lymphosarcoma, a malignancy caused by a Type C retrovirus that produces sores and tumors on the skin, muscles, and internal organs of fishes, occurs widely in the Northern Pike and Muskellunge adults in North America and Europe (Papas et al. 1976; Quackenbush et al. 2010). The tumor has a low prevalence in the summer, but its occurrence increases in the autumn, winter, and spring. The frequency in Northern Pike (19.9%) is the highest frequency of a malignant neoplasm in any known free-living vertebrate (Papas et al. 1976). Pike epidermal proliferation, another Type C retroviral disease, causes smooth, either transparent or translucent, plaque-like lesions with occasional hemorrhaging (Bowser & Casey 1993).

In experimental water-borne challenges, Northern Pike larvae showed significant infection rates and mortality from several Ranavirus isolates. Mortality rates following infection were higher at warmer temperatures (22 versus 12°C) (Jensen et al. 2009). Horizontal transmission of esocid lymphosarcoma may occur by contact during spawning (Coffee et al. 2013). Viral diseases can be transmitted to the Northern Pike from prey fishes (Ahne 1985).

COMMERCIAL IMPORTANCE

Subsistence and commercial fishing are of modest scale for some esociform species where regulations allow it. In the past, these fisheries had a significantly greater commercial monetary value. The Great Lakes historically supported a Northern Pike commercial harvest of 1.6 million kg in the early 1900s that declined to <0.05 million kg by the 1960s (Casselman & Lewis 1996). The decline coincided with the timing and extent of European settlement and shoreline development. The state of New York reported a commercial harvest of 40,370 kg of Muskellunge in 1894 and 46,779 kg in 1895, for a combined value at that time of \$29,270 (about \$857,000 in 2016). In the United States, however, the commercial fishing for Muskellunge was largely limited to the 19th century and was prohibited at the turn of the century (Crossman 1986). Other esociforms are unimportant in commercial harvest and recreational angling, but Alaska Blackfish historically represented an important, almost essential, subsistence

resource to the indigenous peoples of Alaska (Brown et al. 2005; Jewett & Duffy 2007; Fig. 19.53), although the importance of that subsistence fishery is much less today than in the past.

The Northern Pike and Muskellunge, both of which are important sportfish, are the only esociforms that have a significant economic impact. A substantial recreational fishery targeting these two species thrives in the United States and Canada (Fig. 19.54). The commercial value of



Figure 19.53. Into the mid-20th century, native peoples often used wooden, funnel-shaped fish traps known as taluyat (Yup'ik language) to catch Alaska Blackfish, *Dallia pectoralis*. These traps varied in size and shape and were set in holes in the ice or placed to block narrow, shallow stream channels. The funnel-shaped top (on the ground to the right) was inverted over the mouth of the trap. The narrow end of the funnel had a small orifice through which Alaska Blackfish entered. Many traps were made from split spruce, which was bound with spruce root. The tendency of the fish to congregate at holes in the ice to gulp air (Fig. 19.36) and then sink back to the bottom made them particularly vulnerable to these traps. The Alaska Blackfish was an extremely important staple in the diet of Alaskan natives, providing food for the people as well as their sled dogs at times of the year when other food was scarce. One native name for the fish roughly translates as the ones you survive on (Andersen et al. 2004). In the 1880s, $\geq 140,600$ kg (or perhaps double that amount) of the fish were being harvested by Alaskan natives each year (Nelson 1884; Turner 1886; Morrow 1980). The photograph of the fisher about to reset his trap was taken in February 1940 near Nunapitchuk, Alaska, by G. Dale and E. Butler. (photograph P306-0581 Alaska State Library Butler / Dale Photo Collection, used with permission).



Figure 19.54. An angler displays a large female Muskellunge, *Esox masquinongy* (1.4 m TL), caught as it leaped out of the water to engulf a lure being retrieved into the boat. The fish was caught (and released) in the St. Lawrence River, Montreal, in July. The species is a highly sought after gamefish in a specialized sport fishery. Finding, hooking, and catching fish of this size can take an enormous amount of effort (100s of hours) (courtesy of Marc Thorpe / Marc Thorpe Guiding Service).

this recreational fishery extends well beyond the transactions immediately associated with fishing, such as sales of permits and fishing supplies. In 2011, freshwater anglers spent about \$2.1 billion on tackle, trips, and other recreational items fishing for the Northern Pike, Muskellunge, and other esocids (USFWS 2014). In the Great Lakes region, the allure of landing a trophy Northern Pike or better yet, a Muskellunge, helps fuel a strong recreational fishing industry with the associated benefits to tourism and related operations. Great Lakes fishing alone had trip and equipment expenditures in 2011 that totaled \$1.9 billion, and 200,000 of the 1.7 million anglers who fished the Great Lakes reported fishing specifically for the Northern Pike and other esocids (USFWS 2014). Early in this century, an estimated 360,000 anglers targeted Muskellunge (Simonson 2003).

Another consideration when gauging the economic value of these species is the level of investment by governmental institutions through management programs. These programs often involve substantial stocking operations to supplement natural reproduction in declining populations or to maintain introduced populations to support active recreational fishing. Fishing for either species is under strict local government regulations with minimum size and bag limits in most areas. Some states apply trophy regulations (e.g., large minimum size limits, low bag limits) in the Muskellunge fishery with the goal of increasing the abundance of large fish (Kerr 2011). Further, thanks to angler-led catch and release initiatives, even regulation-sized Muskellunge are released at a high rate (Isermann et al. 2011).

LITERATURE GUIDE

The first written description of reproductive behavior in the Northern Pike was probably that of Walton (1653), who noted the basic pattern of external fertilization in shallow waters into which the fish migrated to spawn. The Northern Pike has the distinction of being studied by Frost and Kipling (Frost & Kipling 1967; Kipling & Frost 1969, 1970; Kipling 1983). Their work, and that of their collaborators, is significant for the long-term studies of Northern Pike biology in Lake Windemere.

As autecological studies have fallen from favor, many of the best sources for information on the diet, ecology, and habitats of species that lack importance as commercial or fisheries or are at conservation risk are older studies from the middle of the 20th century. The digitization of myriad older publications has restored the availability of this work. Information about the sporting species of interest to anglers is now widely available in agency literature because much of it is available on the Internet. Indeed, the literature is rife with population and even single lake studies of growth, reproduction, recruitment, and population dynamics of the Muskellunge and Northern Pike, but few broad-scale syntheses of these diverse findings exist. Crossman & Goodchild (1978) compiled an extensive bibliography on Muskellunge biology (Fig. 19.55), and Hall (1986) edited a treatise on their biology and propagation. Craig (2008) summarized advances in Northern Pike ecology in the decade since the volume he edited was published (authors cited herein). Harvey (2009) summarized the biology of the Northern Pike. Particularly succinct,



Figure 19.55. Edwin J. Crossman (1929–2003), long an employee of the Royal Ontario Museum, was a world-renowned expert on Pikes (Esocidae). His major works on the esocids are cited in this chapter, including his classic study on geographic variation in the Grass Pickerel, *Esox americanus*. In the massive volume on *Freshwater Fishes of Canada* (Scott & Crossman 1973) much of the earlier literature on esocids and umbrids (Mudminnows) was reviewed (courtesy of ichthyologist photograph collection of Brooks M. Burr).

but complete accounts summarizing the biology and ecology of the Central Mudminnow and *Esox* spp. are available in Scott & Crossman (1973) and Becker (1983). Wydoski & Whitney (2003) provide a thorough account of

the life history of the Olympic Mudminnow, and Scott & Crossman (1973) and Morrow (1980) synthesized nearly all that was known at the time on the biology of the Alaska Blackfish. Unfortunately little has been added since. Wanzenböck (1995) summarized the knowledge up to that time of the European Mudminnow; some references therein are relevant to the study of North American Umbridae and esociforms in general.

An abundant literature is available on management strategies for improving recruitment of the Northern Pike and Muskellunge (e.g., Hanson et al. 1986; Farrell et al. 2006, 2007, 2014), but many are focused on specific reaches of individual waterbodies. Management of large esocids may be improved if stream–lake (and wetland) network characteristics are incorporated into management plans (Weeks & Hansen 2009; Diana et al. 2015). Such networks support greater habitat and biological diversity (and productivity) than systems that lack lentic habitats. These considerations could improve Muskellunge management in regulated rivers like the Ohio and Tennessee Rivers.

Acknowledgments

We thank Gayle Henderson for painstakingly redrawing numerous figures. Mickey Bland patiently worked with library services to locate masses of often obscure literature. Ken Sterling and Gordon McWhirter were essential in formatting a large literature cited and proofing text, tables, and figures. Carolyn McCormick assisted with proofing the chapter and the literature cited.