

Ecology and Conservation of Mudminnow Species Worldwide

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ABSTRACT: *We review and summarize the ecology and conservation status of the group of fishes commonly known as “mudminnows” (formerly known as the family Umbridae but recently reclassified as Esocidae), consisting of only five species distributed on three continents. These small-bodied fish—residing in freshwater habitats and exhibiting limited mobility—often occur in isolated populations across landscapes and are subject to conservation threats common to highly endemic species in close contact with anthropogenic impacts, such as pollution, habitat alteration, and nonnative species introductions. Herein we summarize current knowledge of the distributions, phylogenetic relationships, ecology, and conservation status of each species of mudminnow, including nonnative occurrence and distribution. We also outline the primary conservation threats to particular species and make recommendations for future research to promote much needed knowledge and conservation attention.*

INTRODUCTION

Worldwide, biodiversity of freshwater fish species is increasingly threatened by anthropogenic pressures such as land use, pollution, water management, and species invasions (Dudgeon et al. 2006). In the 20th century, North American freshwater fishes had the highest extinction rate worldwide among vertebrates (Burkhead 2012), and predicted future rates of extinction are up to five times higher than for terrestrial organisms (Ricciardi and Rasmussen 1999). This includes many small-bodied species that are at global risk for extinction (Olden et al. 2007). With many competing interests in freshwater resources to balance, research on status, potential declines, and conservation threats inevitably focus on species of economic or particular ecological importance (e.g., large-bodied fish, game fish, or “keystone” species; Stone 2007). This can leave very large research gaps, however, in assessing the existing research knowledge and conservation status of nongame freshwater species that may serve important ecological roles or represent important components of biodiversity but are simply understudied and underappreciated (Monroe et al. 2009).

We believe this is the case (and seek to address a knowledge gap) with the group of fishes commonly known as “mudminnows,” composed of only five species worldwide that inhabit low elevation regions in Europe, the eastern and northwestern

Ecología y conservación a nivel mundial de los lucios

RESUMEN: *en este trabajo, se revisa y resume la ecología y estado de conservación del grupo de peces comúnmente conocido como “lucios” (anteriormente conocidos como la familia Umbridae, pero recientemente reclasificados en la Esocidae) los cuales se constituyen de sólo cinco especies distribuidas en tres continentes. Estos peces de cuerpo pequeño —que viven en hábitats de agua dulce y presentan movilidad limitada— suelen presentar poblaciones aisladas a lo largo de distintos paisajes y son sujetos a las típicas amenazas que enfrentan las especies endémicas que se encuentran en contacto directo con los impactos antropogénicos como la contaminación, alteración de hábitat e introducción de especies no nativas. Aquí se resume el conocimiento actual acerca de la distribución, relaciones filogenéticas, ecología y estado de conservación de cada especie de lucio, incluyendo aquellas que son de ocurrencia y distribución no nativa. También se identifican las principales amenazas a nivel género o especie y se hacen recomendaciones para investigaciones futuras encaminadas a promover tanto el conocimiento como la atención de conservación hacia este grupo.*

coasts of North America, and Alaska/Siberia (“Beringia”; Figure 1). Mudminnows are small-bodied (<20 cm) fish typically found in wetlands, stream and river margins, bogs, lakes, and marshes. Historically, the five species were classified and referred to as a monophyletic family Umbridae, but phylogenetic evidence accumulated over several decades has led to recent reclassification with their closest relatives, the Esocidae (pike and pickerel; Box 1). Mudminnows are thought to have diverged into their three recognized genera (*Umbr*, *Novumbr*, and *Dallia*) prior to the Oligocene (Cavender 1969; Gaudant 2012). Their historical biogeography is known by only a small number of fossil records, but current populations are generally considered to be relicts of larger historical distributions (Cavender 1969; Gaudant 2012; Campbell and López 2014).

The five species of mudminnows present not only an interesting case study into the challenges that face many highly endemic freshwater species in a changing world but a fascinating snapshot into components of biodiversity and adaptation. Over the years, mudminnow species have often excited (local) research interest due to curious physiological and life history adaptations that allow them to make use of underutilized habitats. Stories by indigenous peoples in Alaska attributed Alaska Blackfish with the ability to revive after being frozen (Brown et al. 2010); although this particular legend has been proved false, mudminnows are very cold tolerant (Peckham and Dineen 1957; Meldrim 1968). Their ability to withstand harsh winters is



Figure 1. Generalized distributions of mudminnow species worldwide, including the nonnative distribution of Eastern Mudminnow in Europe. Species distributions are shown as follows: Central Mudminnow (*Umbra limi*); Eastern Mudminnow (*Umbra pygmaea*); European Mudminnow (*Umbra krameri*); Alaska Blackfish (*Dallia pectoralis*); Olympic Mudminnow (*Novumbra hubbsi*). Distributional data sources are Becker (1983; *U. limi*), Verreycken et al. (2010; *U. pygmaea*, native and nonnative ranges), Wanzenböck (2004; *U. krameri*), Campbell (2011; *D. pectoralis*), and Harris (1974; *N. hubbsi*).

BOX 1. Mudminnow phylogeny: from Umbridae to Esocidae

The two high school students (Edward Frazer and William Prince) taking part in a summer science camp in central Oregon in 1964 likely had no idea that the fossil specimens (later named *Novumbra oregonensis*) they discovered would spark a 50-year phylogenetic debate on inter- and intrarelationships of mudminnow species. Interest in evolutionary relationships of mudminnows to each other and within the order Esociformes has proved as intense as it has been problematic, however, with our literature review resulting in no less than 12 (out of a total 69) peer-reviewed articles, with evidence ranging from morphological to molecular.

Soon after the Oligocene fossil remnants of *Novumbra* were found—determined as the oldest North American fossil of any Umbridae species—they were described by Cavender (1969) in a paper that also discussed the “problem” of relationships within the suborder Esocoidei. Though Cavender concluded that the fossil evidence was too slim to put forth a true phylogenetic hypothesis, he placed *Novumbra* and *Dallia* closest together and intermediate to *Esox* and *Umbra* spp. A more definite attempt to construct the relationships of mudminnows was published by Nelson (1972) based on examination of the cephalic sensory system. Nelson placed *Dallia* closer to *Umbra* and suggested that *Novumbra* constitute its own subfamily as a sister group of *Esox*.

Nelson’s hypothesis was largely corroborated by Wilson and Veilleux’s (1982) osteological study of mudminnows, but genetic work that appears in this same time period began upending prior osteological and morphological evidence. Based on karyotypic and DNA values for all *Esox* and Umbridae spp., Beamish et al. (1971:1) bluntly stated that the grouping of mudminnows into the single family Umbridae was “ill-advised.” Crossman and Ráb (1996, 2001)—on the basis of chromosome banding work on *Dallia* and *Novumbra*—suggested strong divisions between these two genera and *Umbra* spp. Most recently, López et al. (2004) and Campbell et al. (2013) examined mitochondrial DNA and nuclear genomes of Esociformes and multiple outgroups and (1) concluded that Nelson’s widely accepted hypothesis of relationships was not supported and (2) strongly rejected the monophyly of the family Umbridae. The intrarelationships proposed by López et al. (2004) place *Novumbra* and *Dallia* in a clade with *Esox*, to the exclusion of *Umbra* spp.

Though ongoing paleontological and molecular work on mudminnows is likely to result in new insights on the evolutionary history of this group of Esociformes, the family name of Umbridae seems conclusively outdated. Thus, while the historical family name appears in most references for mudminnow species, the American Fisheries Society and many other researchers now recommend classification of mudminnow species in the family Esocidae (López et al. 2004; Campbell et al. 2013) or that Umbridae be used only in reference to the three known *Umbra* spp. (Gaudant 2012).

not only a function of coldwater resistance, but four of the five species have been documented as utilizing forms of supplemental aerial respiration, allowing survival in oxygen-depleted conditions that can occur during winter and summer in shallow bog, marsh, and pond habitats. Winter feeding and growth—atypical in most fishes—has also been documented in at least three species (Martin-Bergmann and Gee 1985; Panek and Weis 2013). Finally, several studies have revealed considerable behavioral flexibility of mudminnows, particularly in regard to foraging, courtship, and spawning (Hagen et al. 1972; Paszkowski 1984). Across the five species, evidence suggests that although mudminnows are restricted in their dispersal ability and may be particularly vulnerable to many human-derived pressures, they nonetheless exhibit many characteristics of a flexible, adaptable species that can take advantage of habitats considered unsuitable for other fish species (Rahel and Magnuson 1983; Martin-Bergmann and Gee 1985; Dederen et al. 1986).

In light of the largely scattered literature on mudminnows, we argue that it is timely to synthesize current knowledge and advocate for a more systematic approach to future research and management. The conservation status of mudminnows is presently difficult to assess and generalize—where mudminnows are found, they can be highly abundant or even dominant (Becker 1983); however, their occurrence is notoriously rare, patchy, and highly localized for some species (Harris 1974; Povž 1995; Wanzenböck and Spindler 1995). The extent to which distributions and population connectivity are limited by specialization in shallow, densely vegetated areas is currently not clear. Lastly, although mudminnows are hardy and relatively easy to study in captivity, the research that exists is typically local in scale and includes few cross-species comparisons. For these reasons, many smaller studies spanning several decades are ripe for analysis to summarize characteristics of biology, ecology, distribution, and conservation status across the group.

Here we summarize the available knowledge of the five mudminnow species, including local distributions and known population status. Notable aspects of biology and ecology are presented for each species, but we particularly focus on habitat constraints or life history requirements that may influence conservation status. We reviewed primary and secondary literature to summarize general ecological patterns across species, as well as to identify research gaps that may exist. Our protocols for search and selection generally followed those outlined by Pullin and Stewart (2006) for systematic review. We used Thomson ISI's Web of Science, Science Direct, JSTOR, and Google Scholar search engine to generate a database of publications through 2012 (Note: Some primary studies on European Mudminnow [*Umbra krameri*] were not available in English and may have reduced the amount of information reported herein for that species.) We screened

references produced from our search and included 58 papers with a principal focus on one or more species of mudminnow and specifically relating to ecology, biology, or conservation. Although not a primary goal of this article, this review also includes a summary of additional articles that reflect changing knowledge of the phylogenetic relationships between mudminnow species (see Box 1). We conclude by reviewing the environmental issues that may pose particular conservation threats to mudminnows and outline recommendations for future research based on identified knowledge gaps and the most likely sources of threat to populations or species.

MUDMINNOW SPECIES

Central Mudminnow (*Umbra limi*)

Relative to the other species, the Central Mudminnow (*Umbra limi*) is comprehensively studied (Table 1), with at least two in-depth ecological studies documenting seasonal habitat use, diet, age structure, and spawning activities (Peckham and Dineen 1957; Martin-Bergmann and Gee 1985). To this are added numerous studies on individual aspects of biology, distribution, and behavior. The Central Mudminnow is also the most broadly distributed species, with a range extending from west of the Appalachian mountains northward to the Great Lakes region and extending into southern Ontario (Figure 1; Becker 1983). Extensions to this historical range have been documented with apparent introductions in Maine (Schilling et al. 2006) and New York (Schofield and Driscoll 1987), most likely resulting from baitfish releases. Their use as baitfish is widespread because they are common and often highly abundant, tolerant of harsh conditions, and attractive to other fish (predator) species (Becker 1983).

A characteristic of the Central Mudminnow that has attracted significant attention is the use of the swim bladder for supplemental respiration (Gee 1981), as well as the use of bubbles (composed of air and other gas mixtures) trapped under ice (Magnuson et al. 1983). This adaptation, along with consistent evidence of being generalist, opportunistic foragers in terms of both a versatile diet (Table 2) and flexible foraging strategies (Paszkowski 1984), is thought to broaden their ecological niche and allow *U. limi* to take advantage of and persist in specialized habitats that are subject to large fluctuations in dissolved oxygen. For example, use of supplemental oxygen has been shown to enhance foraging by mudminnows

Table 1. Summary of the number of existing research studies that report on aspects of mudminnow ecology by species and subtopic.

Species	Topic						
	Distribution	Phylogeny	Biology	Ecology	Life history	Behavior	Conservation
<i>Umbra limi</i>	2	7	2	4	2	4	1
<i>Umbra pygmaea</i>	1	7	1	4	1	—	—
<i>Umbra krameri</i>	8	5	2	4	1	1	5
<i>Dallia pectoralis</i>	—	8	1	4	1	—	—
<i>Novumbra hubbsi</i>	4	7	1	2	1	1	—

in (lethally) hypoxic waters (Rahel and Nutzman 1994) and is also believed to help avoid some effects of winterkill in small ponds and lakes (Martin-Bergmann and Gee 1985). This may allow compensation to some extent for both competition and predation from other fish species, notably Yellow Perch (*Perca flavescens*; Tonn and Paszkowski 1986).

Information on spawning habits and behaviors seems to be incomplete. The reported temperature range (2.8°C) for spawning (Becker 1983) is quite narrow compared to other species (Table 2), and there is little data on the length of time over which spawning occurs. Migrations to areas suitable for spawning (often lateral movements to flooded stream margins) are well documented (Peckham and Dineen 1957; Martin-Bergmann and Gee 1985) however, and guarding of nests by females is suggested by one source (Becker 1983).

Eastern Mudminnow (*Umbra pygmaea*)

Separated from their closest relatives *U. limi* by the Appalachian range, the Eastern Mudminnow (*Umbra pygmaea*) inhabits lowland waters with little to no streamflow between southern New York and northern Florida (Jenkins and Burkhead 1994). Although much less well-studied than Central Mudminnow (Table 1), strong similarities to their westward relatives are apparent. Eastern Mudminnows across the range exhibit very broad diets consisting of up to 13–17 distinct prey classes in a single season, with significant feeding occurring during the winter (Panek and Weis 2013). Like Central Mudminnow, their diet will even include fish, but where Central Mudminnows are thought to primarily feed on other fish species during winter months (Martin-Bergmann and Gee 1985), Eastern Mudminnows have been documented using cannibalism to augment their diet in summer (the period with the most empty stomachs; Panek and Weis 2013). Although cannibalism is not uncommon in fishes, this points to diverse diets (Table 2) as well as flexible and context-dependent foraging strategies for this group of species.

Eastern Mudminnows appear to exhibit flexible—and perhaps more complex—spawning habits, although this may simply be due to a lack of investigation into these patterns for Central Mudminnows. Migration to shallow spawning sites, such as backwater areas in streams, is documented (Breder and Rosen 1966; Jenkins and Burkhead 1994). Courtship by males and nest building are known to occur; nests are variable, including cavities in algae, under loose rocks, in depressions in sand, or scattered (Breder and Rosen 1966). Females have been observed guarding and occasionally fanning the nest; males may also be engaged in guarding, but this has not been observed conclusively (Breder and Rosen 1966).

Eastern Mudminnows have gained some notoriety since their introduction and spread to six European countries over the course of the 20th century as a result of intermittent popularity in the aquaculture and aquarium trades (Jenkins and Burkhead 1994; Verreycken et al. 2010). Conservation efforts for vulnerable species (i.e., European Mudminnow) can be undermined when closely related species (i.e., Eastern Mudminnow) are invasive in the same region; therefore, it is important to distinguish the human and/or ecological basis for invasion. In The Netherlands, notice of Eastern Mudminnows surviving in areas unsuitable for any native fish sparked investigations into the hypothesis of extreme acid tolerance. It was found that *U. pygmaea* tolerated exceptionally low (3.0) pH with no mortality, with optimal growth at pH 4.5, a level detrimental if not lethal for most fish species (Wendelaar Bonga et al. 1990); in field studies they were found to frequently inhabit areas of low pH that excluded other species (Dederen et al. 1986). Consistent with the hypothesis of acid tolerance underlying invasion dynamics, an assessment of Eastern Mudminnows in Europe found that the bulk of the nonnative distribution was in two countries—Belgium and The Netherlands—where acidification of shallow waters has significantly impacted fish communities (Verreycken et al. 2010). Combined with the fact that dispersal in other countries seems largely human mediated and their

Table 2. Mean ± SD of key habitat, environmental, and life history characteristics reported in published studies that focused on one or more species of mudminnow. N/A indicates that no reported values were found for this species, and a missing SD value indicates that only a single study was available. “DO” refers to “Dissolved Oxygen,” ♀ designates female and ♂ designates males of species. Maximum lengths were summarized from studies reporting total (T) lengths only. Food groups are the number of micro- and macrofaunal items reported in mudminnow diets at the order (or higher) level of taxonomic classification.

Genus, Species	Habitat and environment					Reproduction				Other
	Maximum lengthT (mm)	Maximum age (years)	Minimum DO (ppm)	Minimum pH	Food groups (#)	Age at maturity	Fecundity (max)	Spawning temperature (°C range)	Reproductive behaviors	
<i>Umbra limi</i>	117.6 ± 14.5	5.8 ± 2.4	1.6 ± 0.9	6.0 ± 0.7	12.3 ± 0.5	1.8 ± 0.4	1,496 ± 10	12.9–15.6	Migration	Yes
<i>Umbra pygmaea</i>	124.0 ± 12.5	5.5 ± 0.7	2.0 ± 1.9	4.0 ± 0.9	13.0 ± 4.2	1.7 ± 0.3	1,978 ± 703	9.0–15.0	Migration Courtship Nest-building (♀) Guarding (♀) Fanning (♀)	Yes
<i>Umbra krameri</i>	107.6 ± 4.8	4.6 ± 0.8	1.0 ± 0.6	7.0 ± 0.4	16	1.3 ± 0.5	1,983 ± 1,201	11.8–16.4	Nest-building (♀) Guarding (♀) Fanning (♀)	Yes
<i>Dallia pectoralis</i>	154.0 ± 36.7	6.6 ± 2.3	2.3	6.8	10.5 ± 0.7	2.3 ± 1.1	316	9.2–16.8	N/A	Yes
<i>Novumbra hubbsi</i>	89.1 ± 1.3	N/A	2.5 ± 1.5	3.8 ± 1.1	10	N/A	N/A	10.0–17.9	Courtship Guarding (♂)	N/A

presence is limited to small numbers of sites, Verreycken et al. (2010) reported Eastern Mudminnow as low-medium risk for invasiveness.

A high degree of acid tolerance has also been found to exist in *U. limi* (Rahel and Magnuson 1983). Our own review of pH values reported in field studies (Table 2) indicates that this extreme tolerance may not be similarly shared across all mudminnow species, but further study is indicated for a robust comparison across species.

European Mudminnow (*Umbra krameri*)

Although the current name was not adopted until 1792, *U. krameri* has been reported as inhabiting lowland habitats of the Danube River basin since 1726, when it was first described by Marsili (Wanzenböck 1995). Of the five species of mudminnow, the fossil records for the European Mudminnow are the most complete, offering the greatest insight into paleontological history. A primitive form of umbrids (*Palaeoesox*) have existed since the Paleocene (approximately 62 Ma), with forms of the more recent genus *Umbra* recorded since the late Oligocene (approximately 25 Ma)—it has been determined that the two genera coexisted in Europe until the Middle Miocene, or a period of 10–20 Ma (Gaudant 2012).

The present-day distribution of European Mudminnow is focused in the Danube River, with some populations in the neighboring Prut and Dniester basins. Of the 10 nations found along the Danube River (i.e., Germany, Austria, Slovakia, Hungary, Croatia, Serbia, Romania, Bulgaria, Moldova, and the Ukraine), European Mudminnows occur in all except Germany. In addition, of several nations for which part of their territory belongs to the Danube catchment, European Mudminnows have been found in two of those, namely, Slovenia and Bosnia and Herzegovina (Wanzenböck 1995; Velkov et al. 2004; Sekulić et al. 2013). Out of concern for population declines that seemed to be occurring across the range, in 1995 an international workshop was held to assess the current population and research status. In the workshop proceedings, all countries presented evidence of population declines since the early 1900s, varying from moderate in Hungary and the Ukraine (Keresztessy 1995; Movchan 1995) to near extinction in Austria (Wanzenböck and Spindler 1995) or reported that the available data was insufficient to determine changes in historical abundance and distribution (Bănărescu et al. 1995; Leiner 1995). Insufficient data made it challenging to pinpoint causes of decline in individual countries, but the research as a whole overwhelmingly pointed to the negative impacts of water regulation, with habitat loss through draining of wetlands and bogs, as well as loss of floodplain and oxbow habitats (Guti 1995; Keresztessy 1995; Povž 1995). Pollution and high nutrient loads were indicated as a secondary threat (Bíró and Paulovits 1995; Wanzenböck and Spindler 1995; Sekulić et al. 1998), though unlike with water regulation, the causal mechanisms were not as well understood. Based on these known conservation threats and an estimated population decline of 30% over the past several decades, *U. krameri* has been assessed as Vulnerable (VU A2c)

by the International Union for Conservation of Nature (IUCN) since 1996 (Freyhof 2011). It is also on national red lists or has some protected status in 9 of the 11 countries where it occurs (Wanzenböck 1995; Freyhof 2011). European Mudminnows do appear to respond favorably to habitat restoration (in the form of dredging oxbows and natural reestablishment of wetlands) where it has been tried (Povž 1995; Trombitsky et al. 2001), indicating the potential for focused conservation programs to revive populations.

European Mudminnows exhibit similar specialization in shallow and densely vegetated habitats as their North American relatives, but have one of the shorter reported life spans (Table 2). Despite numerous studies, there seems to be little agreement in fecundity estimates (Table 2); however, in a review of multiple spawning experiments for *U. krameri*, Kováč (1997) described absolute fecundity as “relatively low” and suggested that this attribute, along with complex mating behavior and a long period of parental care by females, increases the vulnerability of this species to human-induced habitat disturbance. This hypothesis was to some extent supported by a 3-year study of European Mudminnow in Hungary’s Kis-Balaton region before and after flooding to fill a reservoir. Although mudminnows were found in newly flooded areas, 2 years of sampling failed to find any yearling fish, suggesting reproductive failure due to loss of shallow spawning habitat (Keresztessy 1995). Unlike with Eastern Mudminnow (invasive in Europe but not currently overlapping in range), there have been no laboratory studies into extreme acid tolerance in *U. krameri*, but values reported in field studies do not seem to support similar extreme tolerances (Table 2). Wanzenböck and Spindler (1995:455), however, did conclude that suitable habitat for *U. krameri* showed “pronounced oxygen deficiencies,” supporting the idea that mudminnows can take advantage of some habitats underutilized by other fish species.

Alaska Blackfish (*Dallia pectoralis*)

The largest species of mudminnow (Table 2) with an extensive geographic range (Figure 1, Figure 2D) is the Alaska Blackfish (*Dallia pectoralis*), yet this species competes with Eastern and Olympic Mudminnow for the smallest number of studies conducted, particularly in terms of behavior and distribution (Table 1). Their relatively large area of documented occurrence ranges from the coastal Chukotka Peninsula in Siberia and in Alaskan coastal areas from the north Arctic all the way southward to Chignik. The distribution also reaches well inland into the Yukon River Basin. Two known fossil records exist, both of which are outside the current distribution, suggesting a historically larger range that was constrained by periods of glaciation during the Pleistocene. The older fossil from the Late Miocene was discovered on the Kenai Peninsula (Cavender 1969), 200 km east of today’s range, and a more recent fossil (Middle Pleistocene) in northeastern Siberia lies approximately 800 km west of the current distribution (Campbell 2011). The current distribution maps closely to the glacial refugia of the most recent Wisconsin period, including populations on islands between Alaska and Russia that formed part of the Beringian land bridge during that period (Campbell and López 2014). This

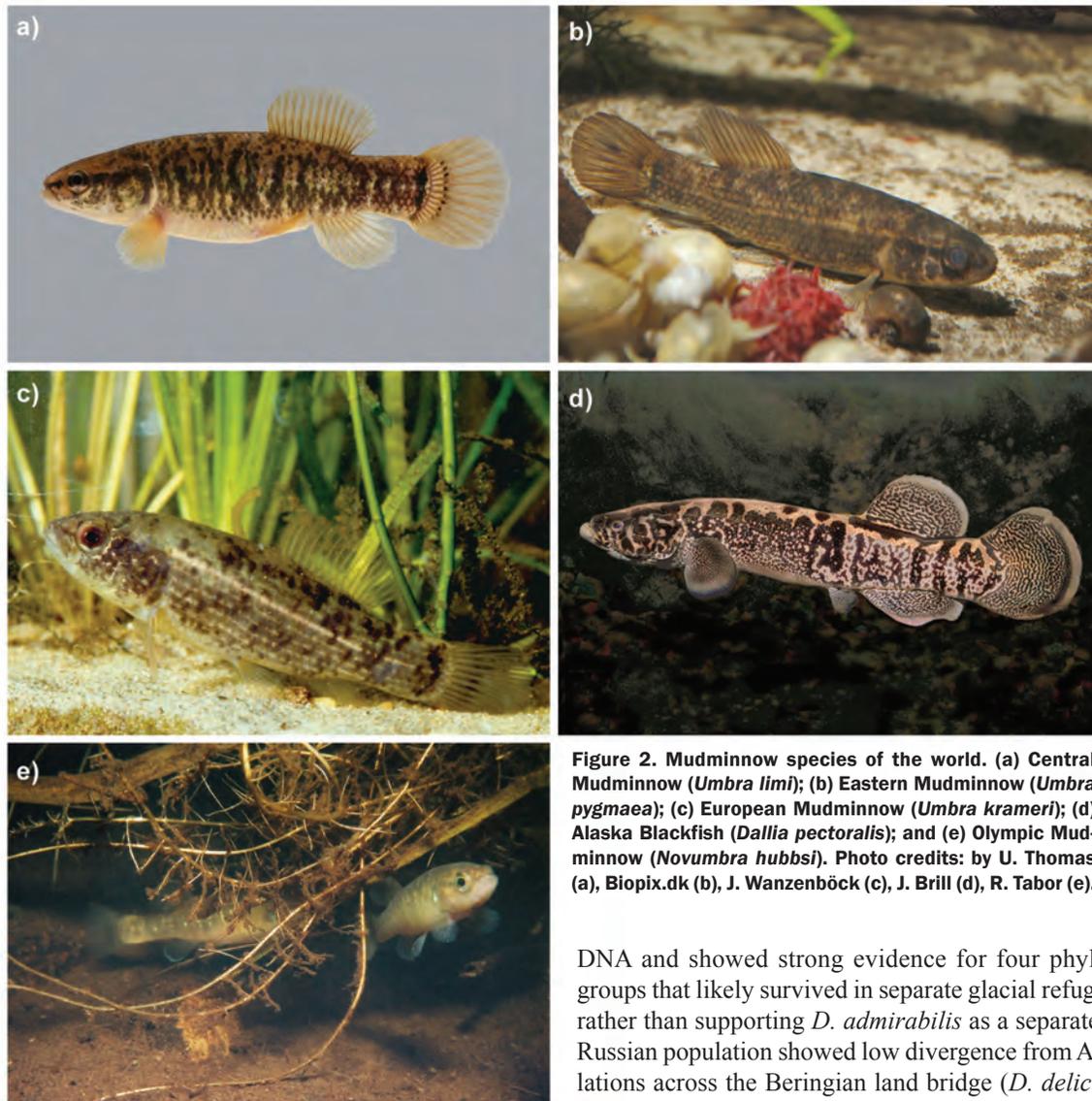


Figure 2. Mudminnow species of the world. (a) Central Mudminnow (*Umbra limi*); (b) Eastern Mudminnow (*Umbra pygmaea*); (c) European Mudminnow (*Umbra krameri*); (d) Alaska Blackfish (*Dallia pectoralis*); and (e) Olympic Mudminnow (*Novumbra hubbsi*). Photo credits: by U. Thomas (a), Biopix.dk (b), J. Wanzenböck (c), J. Brill (d), R. Tabor (e).

is not surprising, perhaps, given the limited dispersal ability and low tolerance for salinity found within the family.

A surprising proportion of the available research on Alaska Blackfish is related to phylogeny and taxonomy (Table 1). Since *D. pectoralis* was first described in 1880, up to three species of *Dallia* have been proposed. *D. delicatissima* from the northeastern Chukotka (part of Siberia) was recognized briefly in 1881 but shortly deemed a dwarf version of *D. pectoralis*, which was then considered the sole representative of the genus for nearly a century. In 1981, Chereshnev and Balushkin described a new Chukotka species based on morphology—*D. admirabilis*—and simultaneously revived *D. delicatissima*, with the hypothesis that morphological distinctions arose from survival in distinct glacial refugia. This suggested that north Arctic slope populations might be more closely related to the two Russian species than to *D. pectoralis*. Karyotypic comparison of Arctic slope and central Alaska populations was ambiguous, showing distinct chromosomal—but no morphological differences—between the two (Crossman and Ráb 1996). More recently, Campbell and López (2014) conducted an extensive biogeographical study across the full range of Alaska Blackfish using mitochondrial

DNA and showed strong evidence for four phylogeographic groups that likely survived in separate glacial refugia. However, rather than supporting *D. admirabilis* as a separate species, the Russian population showed low divergence from Alaskan populations across the Beringian land bridge (*D. delicatissima* was not examined). There was greater evidence supporting potential reproductive isolation of the north Arctic slope populations, leaving the question of multiple *Dallia* species still unresolved.

The existence of divergent *Dallia* populations across the landscape may explain puzzling inconsistencies in life history and growth rate that have been found in studies (albeit small in number) of life history and ecology (Table 3). In a detailed study of spawning characteristics of a lake population near Bristol Bay, Aspinwall (1965) documented a maximum age of 8 years and maturity at 3 years of age. Spawning was determined to occur over a relatively short 2-week period in July. By contrast, Blackett (1962) found the maximum age in an interior Yukon population to be 3–4 years old with maturity reached at age 1–2 but at much larger lengths than Aspinwall (1965) reported (Table 3). It was also concluded that spawning was a highly protracted event, possibly over several months from May to August (but this conclusion was difficult to fully support because no samples were collected in July). In support of the findings of Aspinwall (1965), Gudkov (1998) found the maximum age to be 8 years for populations in 13 Russian lakes but with highly variable length distributions (and age structure) depending on winter conditions and the presence of Arctic Char

(*Salvelinus alpinus taranetzi*) and Least Cisco (*Coregonus sardinella*) competitors (Table 3). Whether this variability across the range reflects study design (particularly the use of scales for aging, a technique that has been proved unreliable for mudminnows), habitat and rearing conditions, competition, or true population and life history diversity remains unclear.

It is thought that the extreme Arctic environment drove a highly unique adaptation in Alaska Blackfish. Air-breathing has been documented in all three *Umbra* species via modification of the swim bladder (Table 2); in contrast, Blackfish have a structure that allows absorption of air through the oesophagus (Crawford 1974). This modification for respiration is known in only one other fish, *Monopterus albus*, a tropical eel native to Asia. Crawford (1974) speculated that long periods of ice cover demanded aerial respiration to compensate for low dissolved oxygen but also a greater need for neutral buoyancy (and, hence, an unmodified swim bladder). It is likely that this unique adaptation led to stories of the ability of Alaska Blackfish to withstand freezing (Brown et al. 2010). Blackfish have never been commercially harvested but were an abundant and widely available subsistence food for Native Alaskans, particularly during times of low food stores, as animal feed, or as bait for other fish (Brown et al. 2010).

Olympic Mudminnow (*Novumbra hubbsi*)

The smallest (Table 2) and most highly endemic species of the group, Olympic Mudminnows (*Novumbra hubbsi*), occur only in a single state (Washington) in the United States (Figures 1 and 2E). Within this region, their range is primarily restricted to a single large river drainage (the Chehalis River), as well as more patchy occurrences in river drainages north toward the Puget Sound estuary and lowland habitats along the Washington coast (Harris 1974). Their distribution in Washington is largely dictated by areas of glacial refugia that existed during the Pleistocene Era; morphological differences between fish across drainages suggest very limited dispersal since that time (Meldrim 1968). Recent genetic analysis of fish throughout the range supports this view and noted that the genetic variation between all sites was high in comparison to other fish with comparable life histories (DeHaan et al. 2014), indicating that individual populations even in close geographic proximity can be genetically distinct. As with other mudminnow species, Olympic Mudminnows are strongly associated with shallow areas of dense vegetation and fine substrates (Meldrim 1968).

Although much information on the basic ecology (i.e., population size, diet, age structure, fecundity, habitat use) of the Olympic Mudminnow is currently poor or lacking (Table 1), some aspects of their biology have been closely studied and allow comparisons to other species. Egg and larval development were exhaustively documented and compared to other research, with the conclusion that

development across the three mudminnow genera appeared very similar (Kendall and Mearns 1996). This same study presented intriguing evidence in the number and movement of oil globules in eggs (a stable character), which grouped *N. hubbsi* (and other umbrids) in a clade containing esociforms, osmerids, and salmonids.

Courtship and spawning behaviors of Olympic Mudminnows have been comprehensively studied in both lab and field experiments and (to our knowledge) represent the most detailed account for any species (Hagen et al. 1972). Males establish remarkably large (0.5–0.7 m²) territories for their size and actively patrol and defend these territories for up to 7 weeks of spawning. A complicated courtship ritual (the “wigwag dance”) of 5–20 minutes results in fertilization of only one or two eggs at a time (Hagen et al. 1972), which are deposited on moss or stems of vegetation. Although it is unknown whether other species engage in this level of complex spawning, these behaviors may explain why mudminnows seem to routinely migrate to or seek out separate areas for spawning that are usually shallow and more protected from predators. *N. hubbsi* has been documented in high abundance in temporary flooded wetlands of the Chehalis River during March–May (peak spawning season; Henning et al. 2007). On a larger scale, this is consistent with reports of spawning movements to flooded stream margins and backwaters for other species (Becker 1983; Jenkins and Burkhead 1994), indicating the importance of these areas for successful reproduction.

CONSERVATION THREATS AND STATUS

Biotic Interactions with Native and Nonnative Species

Given their small size and lack of any apparent defenses, it is expected that mudminnows generally would be sensitive to

Table 3. Variability in life history and growth characteristics of *Dallia pectoralis* reported by three studies across the range. Blackett (1962) reported on an interior Yukon stream population, Aspinwall (1965) studied a coastal lake population near Bristol Bay, and Gudkov (1998) sampled 13 glacial and thermokarst lakes on the southern coastal Chukotka Peninsula in Russia. Method used in length measurements is indicated as either total (T) or standard (S) lengths.

	Blackett (1962) n = 126	Aspinwall (1965) n = 1,400	Gudkov (1998) ^a n = 394
Age method	Scales	Scales	Otoliths
Maximum length (mm) Method	165 _T	135 _T	228 _S
Maximum age (years)	4	8	8
Length at age 3 (mm)	127	56	60/105 ^a
Length at maturity (mm)	80	50	—
Age at maturity (years)	1.5	3	—
Spawning temperatures (°C)	10.0–16.0	8.3–16.9	—
Spawn timing	July 15–August 1	May–August	—
Spawning duration	2 weeks	3 months	—

^aGudkov (1998) noted significant within-region differences in length at age, where blackfish in lakes with Cisco and Char competitors exhibited significantly reduced growth compared to lakes without competitors; thus the two values are reported.

impacts of predation by and competition from nonnative species (Cucherousset and Olden 2011). The difficulty of demonstrating impacts of predation and/or competition seems to be confounded by the habitat specialization (shallow, highly vegetated areas) and broad environmental tolerances (dissolved oxygen and temperature) exhibited by mudminnows. Wanzenböck and Spindler (1995) demonstrated a negative association of European Mudminnows with other fish species, but mudminnow habitats also showed “pronounced oxygen deficiencies,” making it difficult to determine whether the environment was excluding other fish or other fish excluded mudminnows. Other studies of European Mudminnows document associated fish assemblages but are qualitative in nature and result in no clear evidence of exclusion by other species (e.g., Bíró and Paulovits 1995). Although based on occurrence of nonnative Eastern Mudminnows in The Netherlands, a survey of fish assemblages reported a strongly negative association with other fish species; similar to Wanzenböck and Spindler (1995), however, these results are confounded in that mudminnows are one of very few fish species that can live (and even thrive) in the low-pH waters that were sampled (Dederen et al. 1986; Wendelaar Bonga et al. 1990).

Some compelling evidence, however, has focused on specific species interactions or mechanisms and accounted for important environmental variability. A study of Olympic Mudminnow occurrence demonstrated a strong negative relationship with nonnative fishes—in particular with Largemouth Bass (*Micropterus salmoides*)—in oxbow lakes, but the small sample size leaves room for more investigation (Beecher and Fernau 1983). In a study of Alaska Blackfish in glacial and thermokarst lakes, Gudkov (1998) demonstrated significantly reduced growth in lakes with Arctic Char and Least Cisco competitors. By far the most comprehensive and compelling research was conducted in small lakes in Wisconsin over 3 years and focused on relationships between Central Mudminnows and Yellow Perch. Tonn and Paszkowski (1986) demonstrated not only reduced densities of mudminnows in lakes where Yellow Perch co-occurred but also that only large mudminnows were found to coexist with perch, indicating size-specific predation. Furthermore, mudminnows became dominant briefly following winterkill events that affected perch more than mudminnows. This study was followed up by a laboratory experiment demonstrating superior foraging of young perch, suggesting a mechanism for negative competitive interactions (Paszkowski 1985). Although mudminnows have been found to exhibit flexible activity and feeding patterns—such as night foraging—depending on the presence of predators and competitors (Martin-Bergmann and Gee 1985; Jenkins and Burkhead 1994) and also use specialized habitats (Rahel and Magnuson 1983; Rahel and Nutzman 1994), nonnative introductions may well be a conservation concern, especially if they result (indirectly) in loss of suitable habitat. Like many aspects of mudminnow ecology, this area could bear more attention and research.

Pollution

Many studies and status review articles of European Mudminnows state that pollution is a primary and significant threat

to population persistence (Bíró and Paulovits 1995; Leiner 1995; Sekulić et al. 1998), but research demonstrating causal mechanisms, particularly problematic pollutants or sources (e.g., industrial vs. agricultural), is sparse. (Note: Studies may be available in languages other than English, but because few citations pertaining to pollution impacts were found, we suspect that this research largely remains to be done.) However, European Mudminnows in the Danube (Europe’s second largest river) and its tributaries are subject to numerous environmental pollutants associated with a large, economically important river and densely populated watershed (International Commission for the Protection of the Danube River 2009). These include high nitrogen and phosphorus loads, municipal wastewater, and hazardous substances from industrial sources.

A study in Austria demonstrated that European Mudminnows were found in side channel habitats with limited connectivity to the Danube (and greater groundwater influence) that were significantly lower in nitrate levels (Wanzenböck and Spindler 1995). A second study examined the impacts of water from the Rhine River on chromosome damage in Eastern Mudminnows; 11 days of exposure resulted in chromosome damage in 30% of cell divisions, suggesting mutagenic impacts as one mechanism by which pollution affects populations (Prein et al. 1978). Given that all mudminnow species inhabit lowland and floodplain regions that are often prime agricultural areas (e.g., the Chesapeake watershed or the Chehalis River basin in Washington State), an interesting area of research would be to determine more closely the impacts of those pollutants on habitat quality and population viability.

Water Regulation

Strongly intertwined with habitat alteration, water regulation likely poses the single largest threat to mudminnow populations, which rely on shallow and highly vegetated wetland, floodplain, and oxbow habitats. The mechanisms of impact of water management on mudminnow populations have also been the most comprehensively documented. The most obvious of these is upstream flooding of fish habitat when dams are created, inundating habitats such as isolated bog lakes or canals (Bíró and Paulovits 1995). A notable problem with this type of habitat alteration is loss of spawning areas, as Keresztessy (1995) found when mudminnows could apparently migrate to newly flooded areas but showed signs of reproductive failure in subsequent years. Even small water management projects such as those that convert small ponds to deeper lakes for recreation can result in disappearance of mudminnows from those areas (Bănărescu et al. 1995).

Complex downstream habitat is also lost to flood control measures, with drying out of side channels, floodplains, and emergent wetlands (Bunn and Arthington 2002) that provide nursery and rearing habitat for many fish, including mudminnows (Guti 1995; Henning et al. 2007). An example of this indirect effect is the disappearance of oxbow habitats in Slovenia, which become filled in with vegetation over time; upstream water regulation reduces the creation of new oxbows and this

important mudminnow habitat has been permanently lost (Povž 1995). Another interaction with hydrologic alteration was recently brought to light with research on Austria's single remaining population of mudminnow, inhabiting approximately 5 km of side channel area of the Danube. Water regulation on the Danube has lowered groundwater levels (due to channel deepening); population modeling identified prevention of further groundwater reductions as the most important factor in persistence of this population (Wanzenböck 2004).

Habitat Loss and Degradation

In addition to water regulation, threats to mudminnow habitat exist from human activities such as draining of wetlands, or dredging lakes, rivers, or small canals (Becker 1983; Wanzenböck 2004). Although mudminnows are generally found in muddy habitats, turbidity is an apparent deterrent, so activities that increase turbidity may result in reduced habitat quality (Becker 1983). For both Olympic and European Mudminnows there is evidence of strong behavioral thermoregulation during summer months (Meldrim 1968; Povž 1995), indicating that changes in habitat that increase water temperatures could negatively impact populations. Given that much research also indicates broad environmental tolerances, however, sifting out the potential impact of warming on species of mudminnows could prove an interesting area for future research.

A significant type of habitat alteration for mudminnow populations may be losses in shallow spawning habitat. Research on mudminnow species consistently report (often substantial) movements in the spring to flooded margins of creeks, backwaters, or other shallow, protected, and densely vegetated zones for spawning (Table 2; Peckham and Dineen 1957; Henning et al. 2007; Brown et al. 2010). Given studies that also document relatively complex spawning behaviors across the family, long periods of spawning, and a high investment in parental care (Table 2; Hagen et al. 1972; Kováč 1997), the potential for increased vulnerability during this period is not surprising. In fact, Kováč (1997) pointedly suggested that these characteristics were key reasons that European Mudminnows were particularly sensitive to habitat disturbance.

Data Availability and Management

At least two species of mudminnows—European and Olympic—illuminate the conservation challenge that can arise for nongame species with limited dispersal ability and patchy distributions. Since 1996, European Mudminnows have been listed as Vulnerable on the IUCN Red List due to an estimated population decline of more than 30% over the past decades; however, our literature review indicates that this listing has not led to any significant increase in published research on European Mudminnow populations since that time.

Olympic Mudminnows share several conservation characteristics of European Mudminnow in terms of having a small native range primarily centered in a single river drainage. Their highly endemic nature suggests a need for conservation con-

cern, but lack of economic value leads to a paucity of data with which to make management decisions. This was exemplified by a 1995 petition to the U.S. Department of Fish and Wildlife for listing of a local population of Olympic Mudminnow on the Endangered Species List. The petition was declined largely on the basis of insufficient information as to overall population sizes and genetic variation between populations, and the Olympic Mudminnow was ranked a Category 2 candidate species (a now defunct category that indicated a need for future research and potential for listing given additional evidence; U.S. Fish and Wildlife Service 1995).

CONCLUSION

In this review, we have sought to synthesize existing research across a unique but somewhat overlooked group of freshwater species in the scientific literature. In doing so, we have hopefully clarified the reasons why some of these species seem to be threatened or vulnerable while others are ubiquitous and abundant or—in the case of Eastern Mudminnows—may even be invasive outside of their native range. This synthesis was also intended to offer guidance to other researchers by highlighting research gaps for individual mudminnow species (Tables 1 and 2).

As a result of this review, we present the research and management priorities we believe best complement and advance the available science on mudminnow species and that also take into account current and future conservation issues. These are as follows:

Central Mudminnow:

- Improve knowledge of spawn timing, duration, and behaviors (Table 2).

Eastern Mudminnow:

- Improve basic ecological knowledge of behavior and habitat use.

European Mudminnow:

- Strong thermoregulatory behavior during summer months and an association with groundwater-fed habitats are indicated. Given that climate change may result in critical warming of rivers and lakes, as well as changes in groundwater supplies, we recommend research on temperature sensitivities and population vulnerability of European Mudminnow due to climate change.
- Determine causal mechanisms and impacts of agricultural and industrial pollutants to more specifically assess vulnerability of populations.
- Test efficacy of reconstruction and revitalization of off-channel habitats to increase populations. Management actions might include use of environmental flow regimes that promote periodic flooding and greater hydrologic connectivity in regulated systems.

Alaska Blackfish:

- Improve basic ecological knowledge of life history, behavior, and habitat use (Tables 1 and 2). Of particular interest

is whether these vary critically between populations to help identify or confirm processes of speciation across the Beringian landscape.

Olympic Mudminnow:

- Improve basic knowledge of ecology and life history, particularly age structure, fecundity, and habitat use (Tables 1 and 2).
- Determine vulnerability to nonnative fish predators.
- Establish current distribution and changes in population size in recent decades. Given that this species also inhabits the smallest geographic range, we recommend that a conservation assessment be conducted using IUCN criteria to determine whether conservation concern is warranted and to prioritize needed research.

In tackling these outstanding research questions, scientists would not only contribute to knowledge regarding a group of species that exhibit a wide array of diversity within a very small species group but would also advance understanding as to how fish utilize wetlands, which are widely acknowledged as some of the most imperiled habitats worldwide.

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