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REVIEW

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A Synthesis of the Biology and Ecology of Sculpin Species in the Laurentian Great Lakes and Implications for the Adaptive Capacity of the Benthic Ecosystem

Kelly F. Robinson[a], Charles R. Bronte[b], David B. Bunnell[c], Peter T. Euclide[d], Darryl W. Hondorp[c], John A. Janssen[e], Matthew S. Kornis[b], Derek H. Ogle[f], Will Otte[f], Stephen C. Riley[c], Mark R. Vinson[g], Shea L. Volkel[a], and Brian C. Weidel[h]

[a]Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, USA; [b]U.S. Fish and Wildlife, Green Bay Fish and Wildlife Conservation Office, New Franken, Wisconsin, USA; [c]U.S. Geological Survey, Ann Arbor, Michigan, USA; [d]Wisconsin Cooperative Fishery Research Unit, College of Natural Resources, University of Wisconsin-Stevens Point, Stevens Point, Wisconsin, USA; [e]School of Freshwater Science, University of Wisconsin-Milwaukee, Milwaukee, Wisconsin, USA; [f]Department of Natural Resources, Northland College, Ashland, Wisconsin, USA; [g]U.S. Geological Survey, Ashland, Wisconsin, USA; [h]U.S. Geological Survey, Oswego, New York, USA

ABSTRACT

The Laurentian Great Lakes have experienced recent ecosystem changes that could lead to reductions in adaptive capacity and ultimately a loss of biodiversity and production throughout the food web. Observed changes in Great Lakes benthic communities include declines of native species and widespread success of invasive species like dreissenid mussels in all but Lake Superior. Understanding the ecology of native benthic deepwater preyfish and the reasons for their declines is important for predicting future losses in adaptive capacity and diversity, as well as managing the Great Lakes ecosystem to avoid such losses. Native sculpin species (*Cottus bairdii*, *C. cognatus*, *C. ricei*, *Myoxocephalus thompsonii*) historically were among the most abundant of the Great Lakes native deepwater benthic preyfish community and are an important link between offshore benthic and pelagic food webs. With one exception, these species have declined in abundance throughout the Great Lakes in recent years, but relatively little is known about their biology and ecology. This review synthesizes the available knowledge for the Great Lakes sculpin species and provides suggestions for future research efforts, which include understanding reproductive ecology and spawning behavior, connectivity and dispersal of populations, early life history, and influences of interactions with native and non-native species.

KEYWORDS
Slimy sculpin; deepwater sculpin; mottled sculpin; spoonhead sculpin; benthic forage fish

Introduction

Recent ecosystem changes in the Laurentian Great Lakes of North America (herein, Great Lakes) have generated concerns about the potential for reductions in adaptive capacity of the ecosystem, which ultimately could lead to loss of biodiversity and production throughout the food web (McMeans et al. 2016; Ives et al. 2019). These changes, which include invasions by Ponto-Caspian dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) and round goby (*Neogobius melanostomus*), loss of invertebrate species like *Diporeia* spp. (hereafter, *Diporeia*), and declines in abundance of native benthic fishes, have particularly affected the deepwater benthos of the Great Lakes (Bunnell et al. 2014). Much of the profundal habitat of the Great Lakes lacks strong physicochemical gradients and has a low diversity of native species, which makes this environment especially susceptible to functional changes (Moyle and Light 1996; Nalepa et al. 2009), though constraints related to low water temperature, low light, and limited production could reduce susceptibility to some extent. The decline of native benthic fishes and the increasing dominance of this habitat by dreissenid mussels and round goby could lead to an "energetic bottleneck" that would affect predator production at higher trophic levels and potentially weaken connections among habitats, all of which will reduce

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CONTACT Kelly F. Robinson kfrobins@msu.edu Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA.
W. Otte is now with Department of Biology, Northern Michigan University, Marquette, MI, USA; and S. L. Volkel is now with Department of Integrative Biology, University of South Florida, Tampa, FL, USA.

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the adaptive capacity of the ecosystem (Johnson et al. 2005; Blouzdis et al. 2013; Ives et al. 2019).

Observed changes in Great Lakes benthic communities have included declines or losses of native species, like *Diporeia*, and the widespread success of invasive species like dreissenid mussels in all but Lake Superior (Nalepa et al. 2009). The round goby has been implicated in the decline of mottled sculpin (*Cottus bairdii*; Janssen and Jude 2001; Lauer et al. 2004), a nearshore benthic species, in Lake Michigan, and is suspected in the declines of other benthic fishes in deeper environments (Riley et al. 2008; Bergstrom and Mensinger 2009). These invasive species, which are replacing native species within the deepwater benthic food web, may be of less energetic value than native forage (Rosen and Trites 2000; Fagan et al. 2017; Ives et al. 2019) and could lead to other changes to the benthic community (e.g., alteration in reproductive ecology [Honeyfield et al. 2005] and energy pathways [Mills et al. 2003; Johnson et al. 2005]), ultimately resulting in a decline in adaptive capacity (Ives et al. 2019). This loss of native benthic diversity by replacement with invasive species has implications for food web dynamics, conservation, and increased sequestration of energy (Nalepa et al. 2009) in the benthic environment, but it has received much less attention than the losses of pelagic diversity in the Great Lakes.

Historically, the native deepwater fish guild of the Great Lakes was comprised of predators like lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), benthopelagic Coregonines (*Coregonus* spp.), as well as a suite of benthic forage fishes, including deepwater sculpin (*Myoxocephalus thompsonii*), slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*C. ricei*), and ninespine stickleback (*Pungitius pungitius*), among others (Argyle 1982; Spangler and Collins 1992; Riley et al. 2008). Many species were reduced or lost during the middle of the 20th century because of overfishing, the invasion of non-native species, and/or eutrophication (Smith 1968, 1972). More recently, the deepwater native fish guild in the Great Lakes has further declined in Lakes Huron, Michigan, and Superior (Bunnell et al. 2014; Vinson et al. 2018; Bunnell et al. 2019; Riley et al. 2019), with some species declining in Lake Ontario (Weidel et al. 2018). These changes in the native benthic deepwater fish guild have coincided with invasions of dreissenids and round goby, declines in *Diporeia*, oligotrophication related to dreissenids (Riley et al. 2008; Riley and Adams 2010; Evans et al. 2011), and increased consumptive demand by predators like lake trout (Bronte et al. 2003; Bunnell et al. 2014). In addition to declines in abundance, the energy density of some species, including deepwater sculpin, has decreased with the loss of *Diporeia* (Pothoven et al. 2011). Ultimately, these observed declines in native deepwater forage fish abundance and their replacement by energetically inferior non-native species could modify the deepwater food web and resultant transfer of energy among habitats (Ives et al. 2019).

Native sculpin species, in particular, have historically been among the most abundant of the Great Lakes native deepwater benthic forage fish community (Bronte et al. 2003; Owens et al. 2003; Bunnell et al. 2006; Roseman and Riley 2009), and serve as an important link between offshore benthic and pelagic food webs (Fratt et al. 1997; Madenjian et al. 1998). All sculpin species appear to be declining in abundance in the Great Lakes in recent years, with the exception of deepwater sculpin in Lake Ontario (Figure 1; Vinson et al. 2018; Weidel et al. 2018, Bunnell et al. 2019; Riley et al. 2019). Slimy sculpin comprise an important part of juvenile lake trout diets (Stewart et al. 1983; Eck and Wells 1987; Owens and Bergstedt 1994; Madenjian et al. 1998), and deepwater sculpin are an important prey item for burbot and juvenile lake trout (Madenjian et al. 2002). In Lake Superior in particular, deepwater sculpin are the primary prey fish in offshore waters (especially for juvenile siscowet lake trout) and declines in deepwater sculpin abundance could negatively affect lake trout and burbot (Gamble et al. 2011). Spoonhead sculpin have been extirpated in Lakes Erie, Huron, and Ontario (Zimmerman and Krueger 2009), have a wide distribution but lower abundance than slimy and deepwater sculpins in Lake Superior (Vinson et al. 2018; USGS 2019), and are rare in Lake Michigan (Wells and McLain 1973; Becker 1983; Potter and Fleischer 1992; Fratt et al. 1997). Despite their importance in the benthic food web and recently observed changes in population dynamics of sculpins, there are still many knowledge gaps in the life history and ecology of these species. Understanding the ecology and population dynamics of this benthic guild would fill a key knowledge gap regarding the adaptive capacity of the Great Lakes (Ives et al. 2019), which is among the most disturbed and rapidly changing ecosystems in the world. This review describes the state of knowledge of sculpins in the Great Lakes and suggests future avenues of study.

Review and synthesis of the current state of knowledge of sculpins in the Laurentian Great Lakes

Paleobiogeography

Sculpins radiated across North America during the Cenozoic era (65 million years ago to the present)

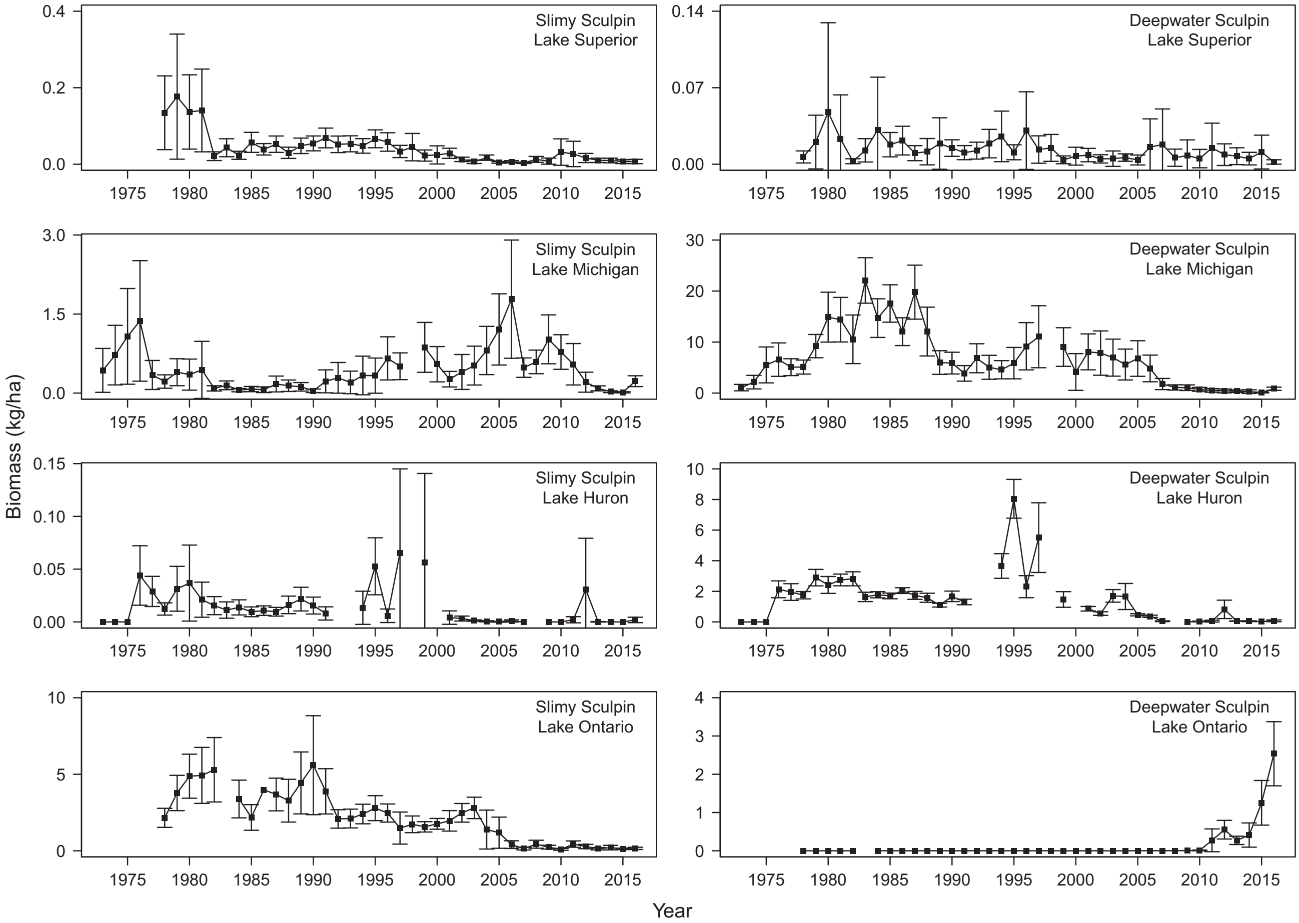

Figure 1. Biomass (kg/ha) of slimy and deepwater sculpin from U.S. Geological Survey trawl surveys in Lakes Superior, Michigan, Huron, and Ontario, 1970–2016 (beginning year depends on lake), averaged across trawl transects. Error bars represent 95% confidence intervals. Note the difference in y-axis ranges among graphs.

and likely reached the region that now contains the Great Lakes by the Miocene (23–5 million years ago) and Pleistocene eras (2.6 million–12,000 years ago) (Smith 1981). Two genera of sculpins are present in the Great Lakes, *Myoxocephalus* (sometimes still referred to as *Triglopsis*) and *Cottus*. The *Cottus* genus is comprised of a three-species flock (mottled sculpin *C. bairdii*, slimy sculpin *C. cognatus*, and spoonhead sculpin *C. ricei*) that likely speciated rapidly over the course of tens of thousands of years. Deepwater sculpin are the only member of the *Myoxocephalus* genus found in freshwater in North America (Smith 1981). Great Lakes sculpins are largely isolated by depth preference. Mottled sculpin prefer shallow water (<10 m) and streams; spoonhead and slimy sculpin share similar depth preferences (10–100 m), with spoonhead sculpin preferring slightly shallower water than slimy sculpin; and deepwater sculpin are found 70 m and deeper (Wells 1968; Scott and Crossman 1973; Selgeby 1988; Selgeby and Hoff 1996) and have been captured at depths of over 400 m in Great Slave Lake, Northwest Territories, Canada (Rawson 1951).

Connectivity, movement, and dispersal

Compared to more pelagic oriented species, sculpins are poor swimmers and lack functional swim bladders. One exception is the larvae of deepwater sculpin, which are pelagic and disperse by currents until they reach lengths of about 20–25 mm and settle to benthic habitats sometime in the first year of life (Mansfield et al. 1983; O'Gorman 1983; Geffen and Nash 1992; Roseman 2014). Adult fourhorn sculpin (*Myoxocephalus quadricornis*), which are closely related to deepwater sculpin, undertake vertical migrations to the pelagia of a lake in southern Sweden (Lake Vättern; Hammar et al. 1996), but no such behavior has been documented in adult Great Lakes sculpins. Slimy sculpin have occasionally been observed in small numbers in midwater tows in the Great Lakes (e.g., Roseman and O'Brien 2013), but they are thought to be benthic.

Many freshwater sculpins, particularly *Cottus* spp., are relatively sedentary (McCleave 1964; Hill and Grossman 1987; Goto 1998; Gray et al. 2004; Goto et al. 2015), and much of the knowledge of movements of these species comes from studies in stream systems, where dispersal is typically limited (e.g., Bailey 1952; Brown and Downhower 1982). For example, the home range of mottled sculpin in a North Carolina stream was estimated as 12.9 ± 4.7 m (Coweeta Creek; Hill and Grossman 1987) and as less than about 50 m in a Montana stream (Trout Creek; McCleave 1964). Petty and Grossman (2007) similarly reported that mottled sculpin in a North Carolina stream (Shope Fork) had home ranges of 0.92–1.02 m^2, but home range size varied annually and with fish size. These movement studies are consistent with significant genetic differentiation that has been observed among populations of mottled sculpin in streams (Lamphere and Blum 2012; Homola et al. 2016), which would suggest limited dispersal. Slimy sculpin had high site fidelity and exhibited limited movement in a New Brunswick stream (Little River; Gray et al. 2004). Despite small home ranges, 86–100 percent of slimy and mottled sculpins did not remain in approximately 30-m stream sections in northwestern lower Michigan over a season, suggesting a high rate of local movement (Shetter and Hazzard 1939). Although data are mostly lacking in the Great Lakes, δ15N stable isotope ratios of slimy sculpin mirrored ambient δ15N differences among sites in Lake Superior, suggesting that the species is relatively sedentary (Harvey and Kitchell 2000).

Although many studies suggest that most stream-dwelling sculpins are sedentary, some individuals may move relatively large distances (e.g., Schmetterling and Adams 2004; Breen et al. 2009; Hudy and Shiflet 2009; Lamphere and Blum 2012; Clarke et al. 2015; Deboer et al. 2015), and individual fish may switch between sedentary and mobile behaviors (Wells et al. 2017). Some of the evidence for limited movement of sculpins in streams, particularly in earlier studies, may have been related to methods that were not designed to detect long-distance movements (Gowan et al. 1994). Although there has been no study that explicitly evaluates the genetic connectivity of any offshore sculpin species in the Great Lakes, preliminary work in Lake Ontario has shown low genetic differentiation among slimy sculpin sampled about 200 km apart (Euclide et al. 2018), suggesting greater dispersal. Similarly, a study of the genetic origin of the deepwater sculpin resurgence in Lake Ontario found limited genetic structure across the entire basin (Welsh et al. 2017). Deepwater sculpin in the Great Lakes likely exhibit greater dispersal than *Cottus* spp. because of their pelagic larvae (Geffen and Nash 1992; Roseman 2014), and this dispersal may be somewhat predictable based on water current patterns. Evidence of larval deepwater sculpin advection derives from their occurrence in nearshore locations distant from presumed deep spawning areas (Mansfield et al. 1983; Geffen and Nash 1992), and in the western basin of Lake Erie where larvae are presumably moving "downstream" from deep water in Lake Huron (Roseman et al. 1998). Quantitative assessments of the dispersal of adult deepwater sculpin are lacking, and spoonhead sculpin dispersal has not been evaluated with genetics in the Great Lakes. Lentic and lotic populations of freshwater fishes have been shown to differ in terms of their ecology and evolution (Swain and Holtby 1989; Minns 1995; Istead et al. 2015), and the recent genetic work on population structure in Lake Champlain (Vermont and New York, USA) and Lake Ontario suggests that slimy sculpin larval dispersal may play a larger role in lentic habitats (Euclide et al. 2018). Based on these observations, more research is needed to better understand larval ecology, dispersal, and movement of Great Lakes sculpins (Euclide et al. 2018).

Habitat

Habitat partitioning and differential prey selection have long been hypothesized to maintain sculpin species diversity in the Great Lakes by lessening interspecific competition for space and food (Kraft and Kitchell 1986). Consistent with this hypothesis, bottom trawl surveys in the Great Lakes have demonstrated that abundances of different sculpin species generally peak at different depth ranges (Figure 2), although in many cases, the trawl depths likely do not capture the full range of deepwater sculpin (e.g., observations up to 350 m in Lake Superior, Boyer and Whitlatch 1989). Slimy and spoonhead sculpin, which mostly only co-occur in Lake Superior, have the greatest overlap. Although modal depths of abundance of each species vary by lake and sometimes season, the pattern of species succession by depth is remarkably consistent in the Great Lakes and in other glacial lakes (e.g., Great Bear Lake, Northwest Territories, Canada) that contain two or more species (Johnson 1975). Recently, the mean depth of capture of slimy sculpin has increased in Lakes Huron, Michigan, and Ontario (O'Brien et al. 2009; Riley and Adams 2010; Volkel 2019), potentially as a response to ecosystem changes like invasion of round goby or the decline of

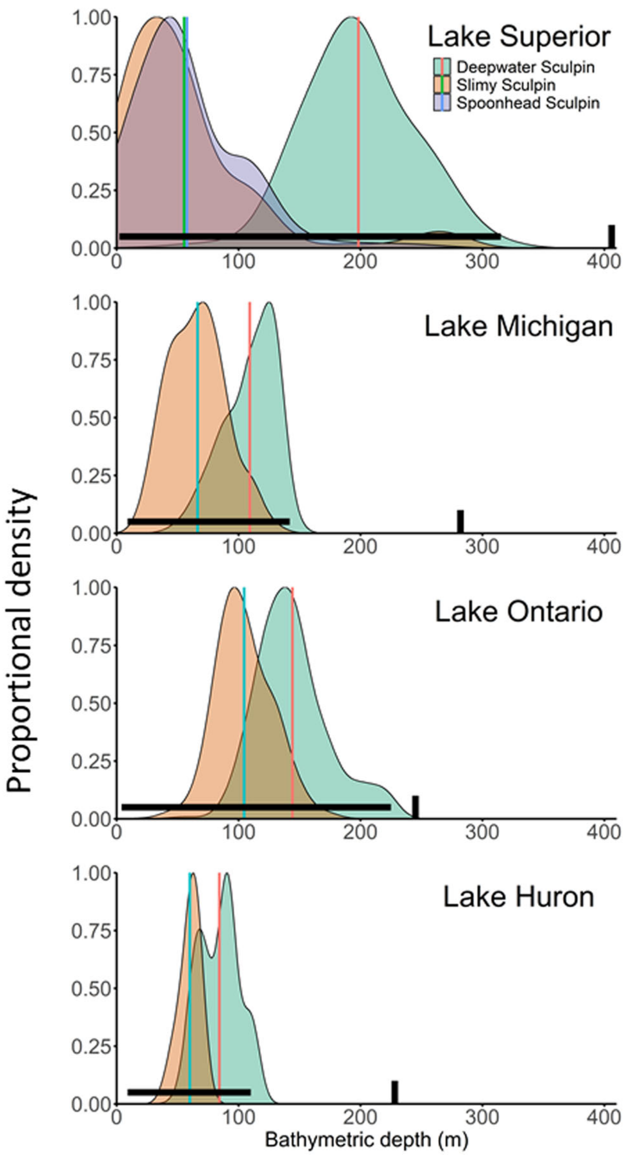

Figure 2. Proportional density plots showing depth distributions of spoonhead (Lake Superior only), slimy, and deepwater sculpins in the Laurentian Great Lakes, based on data collected by U.S. Geological Survey spring-fall bottom trawls made in 2015–2019 (Lake Ontario, 2015–2018). The horizontal black line indicates the bathymetric depths sampled in each lake and the vertical black bar indicates the maximum depth of each lake. Colored vertical lines are density weighted mean depths of capture for each species.

Diporeia. Interspecific interactions for habitat and prey selection are discussed in a later section.

Stenothermal deepwater sculpin occupy a narrow temperature range (3–7 °C) (Selgeby 1988; Sheldon 2006) which may limit distribution to the deeper parts of lakes. Slimy sculpin inhabit warmer water than deepwater sculpin, but they are rarely found in habitats with water temperatures greater than 19 °C (Gray et al. 2005; Edwards and Cunjak 2007), and species interactions may be related to temperature tolerances and the depth distributions of these species. Species-specific depth distributions may also be related to body size; in Lake Superior, smaller individuals of spoonhead, slimy, and deepwater sculpins were more abundant at depths less than 90 m while larger sculpins were more abundant at depths greater than 90 m (Gorman et al. 2012).

There have been few quantitative assessments of the importance of physical structure to sculpin populations in lake environments. Several marine sculpin species, however, have been observed in association with physical structure (Stein et al. 1992; Auster et al. 1995; Busby et al. 2012). Lane et al. (1996) reported that all four species of sculpins in the Great Lakes are associated with physical habitat structure like vegetation, logs, and rocks, but provided no supporting data. Mottled sculpin have been observed to occupy rocky habitat during the day (Figure 3A) and move to sandy and silty habitat or the tops of large rocks at night in Lakes Huron (Emery 1973) and Michigan (Hoekstra and Janssen 1985). In addition, mottled sculpin (Lyons 1987; Bailey 1952; Zarbock 1952) and slimy sculpin (Van Vliet 1964) preferred rocky or vegetated habitats in streams, and mottled sculpin presence was related to water temperature and substrate stability (Petty and Grossman 2007; Edwards and Cunjak 2007). The choice of habitat structure by slimy sculpin may change with size; older slimy sculpin have been shown to use boulders and vegetation, while young-of-the-year individuals used gravel, rubble, and vegetation in shallower water (Mundahl et al. 2012). Slimy sculpin may also bury themselves in the substrate (Emery 1973) and therefore may have less need of physical structure for cover. Greater observed catches of sculpins in nighttime versus daytime trawl tows in Lake Superior may reflect greater reliance on structural cover or a tendency to bury in sediments during the day (Janssen and Brandt 1980). In addition, the Mid-Lake Reef Complex (MLRC) in Lake Michigan, a series of deep reefs that separate the northern and southern basins of the lake, with abundant rocky habitat for shelter, can harbor seemingly high densities of slimy sculpin. For example, the densities of slimy sculpin at Sheboygan Reef, the shallowest (40-m summit) of the MLRC, were estimated to be about 3–8 m^{-2}, using an unmanned electroshocking submersible (Houghton et al. 2010).

Reproduction

Nesting behavior

Reproductive habitat and behavior of Great Lakes sculpin species are poorly described, especially for

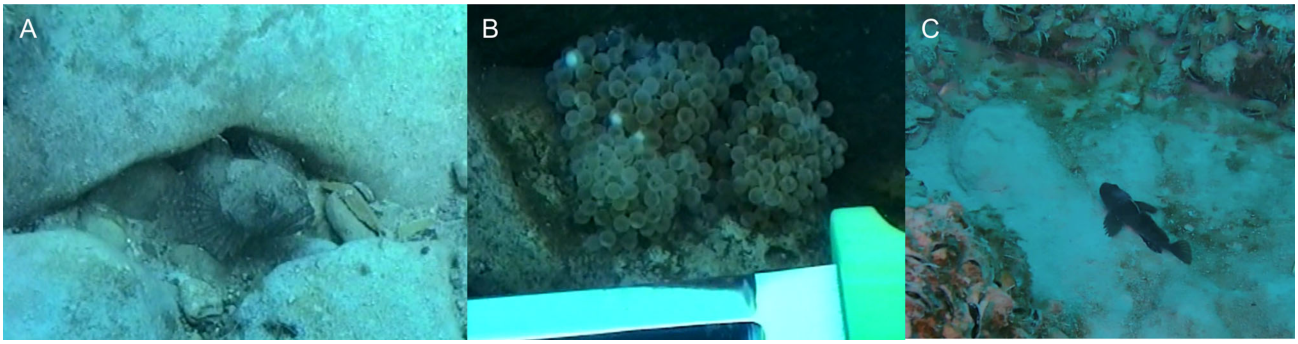

Figure 3. Photos of (A) a mottled sculpin in Lake Michigan guarding a nest in 1998, prior to decline in abundance of this species with the invasion of round goby, (B) the mottled sculpin nest being guarded by the individual shown in panel A, and (C) a male slimy sculpin in spawning coloration, Lake Michigan, 15 m depth, May, 2019. Sculpins in these photos are approximately 80–100 mm total length, and eggs in panel B are approximately 2 mm diameter. Photo credit: John Janssen, University of Wisconsin-Milwaukee.

spoonhead sculpin, and much of what is known is based on observations in smaller lakes or rivers. Males of all four Great Lakes species have been observed to select nesting habitat and guard fertilized eggs against predators, including fanning them with pectoral fins during incubation (Figure 3B; Westin 1969; Scott and Crossman 1973). In a laboratory study with fourhorn sculpin, widespread fungal infection of eggs that were not fanned was reported, with only 0.2% hatching success (Westin 1969).

Spoonhead and slimy sculpins were categorized as speleophils by Balon (1975) because they deposit adhesive eggs on a clean undersurface of a rock or ledge (Scott and Crossman 1973). Previous studies have speculated that spoonhead and slimy sculpins spawn in rocky habitat, given their rarity in bottom trawling collections over soft substrates during the putative spawning season (Selgeby 1988; Owens and Noguchi 1998). Egg masses of slimy sculpin that were adhered to logs or plastic or metal objects were collected from Lake Ontario in bottom trawls from 1988 to 1994 (Owens and Noguchi 1998) and observed in Lakes Michigan (J. Janssen, University of Wisconsin-Milwaukee, pers. obs.) and Superior (C. Bronte, USFWS, pers. obs.). In a field comparison of nest shelter selection at a small reef in Lake Michigan, mottled sculpin preferred smaller shelters (square tiles 10 and 15 cm on a side) compared to larger shelters (30 cm on a side; Wolfe 2002).

Deepwater sculpin were labeled as lithophils because their adhesive eggs are likely laid in pits dug in gravel or sand (Balon 1975). Male fourhorn sculpin dug holes for egg incubation in either algal masses or a soft bottom area free of algae in a Swedish lake at depths of 15–20 m (Westin 1970). Observations in depths as great as 350 m in Lake Superior (Boyer and Whitlatch 1989) and 100 m in Lake Michigan (Bowers et al. 1990) revealed dish-like depressions in the sand, 8–10 cm in diameter and 1–2 cm in depth, hypothesized to have been created by deepwater sculpin for egg incubation (Johnson et al. 1984), similar to the behavior observed for fourhorn sculpin.

Reproductive timing

The timing of reproduction also is poorly documented, but likely occurs over a protracted period for most species. Deepwater sculpin spawning is believed to occur in autumn, winter, and into early spring (Becker 1983; Selgeby 1988), although ripe eggs were documented in surveyed females as early as August in Lake Ontario (Dymond et al. 1929). Based on larval sampling in Lake Michigan, Geffen and Nash (1992) predicted peak deepwater sculpin hatching in March, with spawning several months prior, given expected slow incubation rates during winter. A measure of monthly gonadosomatic index (GSI, Anderson and Gutreuter 1983) of female slimy sculpin from trawls conducted in 2015–2017 (April–July and October) indicated that GSI peaked in April in Lake Champlain, indicating spring spawning in this lake (S. Volkel, Michigan State University, unpublished data; E. Marsden, University of Vermont, unpublished data). Observations of slimy sculpin in spawning colors in May in Lake Michigan corroborate a hypothesized spring spawn (Figure 3C; J. Janssen, University of Wisconsin-Milwaukee, unpublished data). In Lake Superior, spoonhead and slimy sculpin spawning occurs in spring (May), with spoonhead spawning 2–4 weeks earlier than slimy sculpin (Selgeby 1988). The most intensive study on Great Lakes sculpin reproduction focused on slimy sculpin in Lake Ontario (1988–1994; Owens and Noguchi 1998): gravid females were collected from April through October, with most females spent by July. The timing of egg mass collections suggested peak spawning in June (Owens and Noguchi 1998).

Reproductive communication

In addition to timing and habitat preference, relatively little is known about sculpin communication, particularly in terms of reproduction. Some laboratory and field studies have been conducted to understand how male and female cottids communicate. Sensory channels for communication in Cottidae include olfactory (pheromones), visual, and auditory. Male cottids from Lake Baikal, Russia, responded to female pheromones with head nods and/or shakes (Ostroumov 1992), which were associated with sound production (Ladich 1989; Whang 1992; Whang and Janssen 1994; J. Janssen, University of Wisconsin-Milwaukee, pers. obs.). The males of the species studied thus far (bullhead [*Cottus gobio*; Ladich 1989], mottled sculpin [Whang and Janssen 1994], Pygmy sculpin [*Cottus paulus*; Kierl and Johnston 2010], Kessler's sculpin [*Leocottus kesslerii*], stone sculpin [*Paracottus knerii*], and Baikal yellowfin [*Cottocomephorus grewingkii*; Whang 1992]), produce sounds below 500 Hz with peaks lower than 100 Hz. Observations of mottled sculpin via geophone suggest that communication and sensing through the substrate can enable transmission of sounds even in relatively loud riverine systems (Whang and Janssen 1994).

Early life history

Great Lakes sculpin larvae can be either benthic, pelagic, or some combination of both. Mottled sculpin and slimy sculpin appear to be mainly benthic, although *Cottus* larvae have been collected occasionally near the Lake Michigan MLRC (J. Janssen, University of Wisconsin-Milwaukee, unpublished data) and in pelagic nearshore trawls in northern Lake Huron (Roseman and O'Brien 2013). Goto et al. (2015) reviewed benthic and pelagic strategies in the Cottoidea in an evolutionary and ecological context. *Cottus* is quite variable in habitat use, indicating that understanding of larval sculpin habitats in the Great Lakes is likely incomplete. Bear Lake sculpin (*Cottus extensus*) in Bear Lake, Idaho/Utah, spawned mainly in 1–2 m depth, an area only about 0.004% of the lake, but settled fish were widespread, likely dispersed by the early pelagic stage (Ruzycki et al. 1998). Additionally, Euclide et al. (2018) found little genetic structure in slimy sculpin in Lakes Champlain and Ontario, which suggested that larval movement could be greater than previously thought.

Deepwater sculpin are demersal as juveniles and adults, but their larvae are pelagic, making them susceptible to pelagic predators like alewife (*Alosa psuedoharegnus*; Smith 1970; Wells and McLain 1973; Crowder 1980), which have been implicated in declines in deepwater sculpin abundance in Lakes Michigan (Madenjian et al. 2005) and Ontario (Mills et al. 2003). The life history stages of deepwater sculpin appear to be spatially segregated; younger and smaller post-larval individuals occupy the shallowest part of the depth range of the species (Geffen and Nash 1992; Weidel et al. 2017). In Lake Michigan, deepwater sculpin peak hatch occurs in March (consistent with Mansfield et al. 1983), but larvae can be found from November to August (Geffen and Nash 1992). The larvae, which are larger in nearshore versus offshore areas, metamorphose and become benthic beginning in July at a length of about 20 mm (Geffen and Nash 1992). The early spring peak emergence of larval deepwater sculpin suggests that size segregation may be related to the development of the thermal bar, its transition to thermal wedge, and finally to the full stratification of the deep Great Lakes. The spring thermal bar divides inshore and offshore water as areas of favorable (inshore) and less favorable (offshore) physical conditions for plankton growth (Bolgrien et al. 1995; Brett and Goldman 1996; Botte and Kay 2000). Larval deepwater sculpin sampled in Lake Michigan at the nearshore side of the thermal bar (surface temperature >4 °C, generally about 6 °C) were at greater densities, larger (consistent with Geffen and Nash 1992), and had faster growth based on daily growth rings compared to those collected on the offshore side (surface temperature <4 °C; Wang 2013). Geffen and Nash (1992) also indicated that survival from the pelagic to benthic stages for deepwater sculpin was about 0.1–0.4%.

Age and growth

Published age and growth estimates for mottled, slimy, deepwater, and spoonhead sculpin are limited for Great Lakes populations, and sporadic and dated elsewhere. Age estimates have been reported based on whole otoliths for all four species and for sectioned otoliths for slimy and deepwater sculpin, as described below. Whole otolith age estimates were similar to sectioned otolith estimates for slimy sculpin and considerably younger for deepwater sculpin. Direct comparisons between whole and sectioned otoliths have not been conducted for any of these species. Growth rates were greatest to age-1 and then declined with

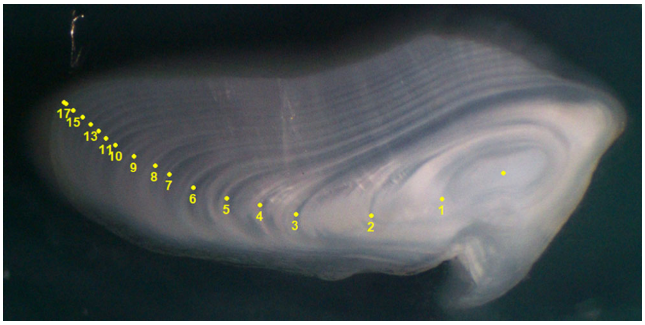

Figure 4. Sectioned otolith from a 122-mm deepwater sculpin collected from Lake Superior on 6 June 2017. Age estimate was 17 years.

age for all species (Black and Lankester 1981; Bruch 1986; Selgeby 1988; Sheldon 2006).

Mottled sculpin maximum age based on whole otoliths ranged from three to seven years for riverine populations (Koster 1936; Bailey 1952; Patten 1971; Ludwig and Lange 1975; Grossman et al. 2002), but no maximum age estimates were available from lake populations. In Lake Michigan, mottled sculpin <60 mm were designated as age-0 based on sectioned otoliths (Janssen and Jude 2001). In North Carolina, Grossman et al. (2002) observed that females grew rapidly to age 3, ∼50 mm, after which growth slowed.

Slimy sculpin maximum age estimates varied from five to eight years (Koster 1936; Van Vliet 1964; Rottiers 1965; Petrosky and Waters 1975; Craig and Wells 1976; McDonald et al. 1982; Selgeby 1988). For Great Lakes populations, the maximum age was seven years in Lake Michigan (Rottiers 1965) and five years in Lake Superior (Selgeby 1988) based on whole otoliths. Based on sectioned otoliths, maximum ages were seven and three years in unregulated and regulated tributaries to Lake Superior, respectively (Bond et al. 2016). Geffen and Nash (1992) estimated slimy sculpin growth rates at 0.12–0.15 mm/day from age-0 to age-1. Selgeby (1988) estimated mean total length at 37 mm at age-1 and 103 mm at age-5 for Lake Superior fish. A riverine population of slimy sculpin averaged 37 mm at age-1 and grew thereafter at a decreasing rate of 14–6 mm per year (Craig and Wells 1976).

Deepwater sculpin maximum estimated age varied greatly between whole and sectioned otoliths. Whole otolith maximum age estimates ranged from five to nine years (Black and Lankester 1981; Bruch 1986; Selgeby 1988). Selgeby (1988) estimated the maximum age at seven years based on whole otoliths for a Lake Superior population. As part of this review, 174 deepwater sculpin otoliths collected from Lake Superior in 2017 were sectioned and aged following the "embed and polish" method (Secor et al. 1992; Quist et al. 2012), and maximum age was estimated to be 17 years (Figure 4). Deepwater sculpin maximum age was estimated at 24 years for individuals from Wollaston Lake, Saskatchewan, Canada (Sheldon 2006), the only other aging study with sectioned otoliths. Estimated growth of deepwater sculpin was ∼50 mm by age-1, ∼7–8 mm per year at ages 2–4, ∼4–5 mm per year at ages 5–9, and <2 mm per year after age 10 in Lake Superior for fish collected in 2017. Mean total length-at-age was similar between male and female deepwater sculpin (Bruch 1986).

Spoonhead sculpin age estimates were solely available for a Lake Superior population. Selgeby (1988) reported a maximum age of six years based on whole otoliths. His estimated total lengths-at-age were 36, 58, 73, 87, 102, and 112 mm for ages one to six, respectively. These estimates were nearly identical to those reported for slimy sculpin and less than those reported for deepwater sculpin (Selgeby 1988).

Diet

Sculpin diets are generally dominated by benthic invertebrates, with some observed trophic niche overlap among species, based on the prevalence of *Diporeia* and *Mysis* in stomachs (Kraft and Kitchell 1986; Davis et al. 2007; Bunnell et al. 2015) and stable isotopes (Mumby et al. 2018). In contrast, selectivity studies have shown some differences in preference for size and type of food. Slimy sculpin had greater selectivity for *Diporeia* and chironomids, whereas deepwater sculpin had greater selectivity for *Mysis* and selected for larger animals within a given prey taxon than did slimy sculpin (Hondorp et al. 2011). Consistent with the selectivity results, historical diet studies (i.e., prior to the decline of *Diporeia* in Lakes Michigan, Huron, and Ontario) revealed that slimy sculpin generally relied more on *Diporeia* than mysids (Wells 1980; Brandt 1986a; Kraft and Kitchell 1986; Hondorp et al. 2005; Davis et al. 2007), especially at

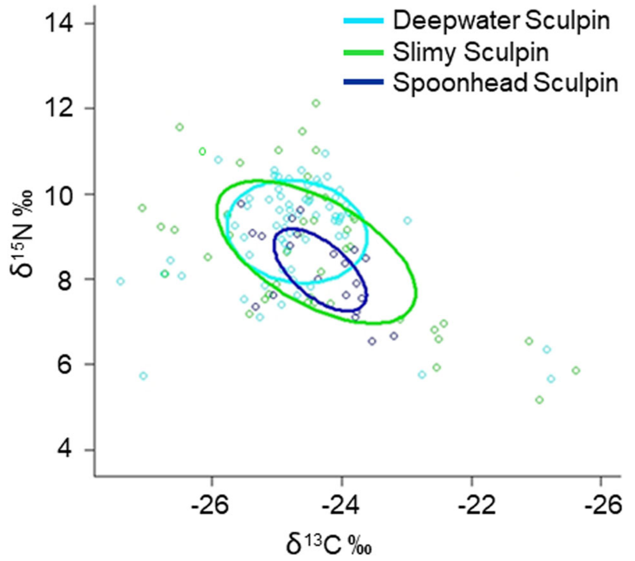

Figure 5. δ^{13}C and δ^{15}N bivariate plots for slimy, spoonhead, and deepwater sculpin collected May–September 2011 in Lake Superior. Ellipses encompass 40% of the data for each species and are drawn via a covariance matrix (for details see Jackson et al. 2011).

shallower depths (Owens and Weber 1995). As *Diporeia* has declined in these lakes, slimy sculpin diets have become more diverse and comprised of more *Mysis*, zooplankton, chironomids and oligochaetes (Owens and Dittman 2003; Walsh et al. 2008; Bunnell et al. 2015). In Lake Superior, where *Diporeia* has not declined, slimy sculpin diets continue to be dominated by *Diporeia* (Selgeby 1988; Gamble, Hrabik, Stockwell, et al. 2011; Gamble, Hrabik, Yule, et al. 2011).

Based on the prey selectivity of deepwater and slimy sculpins (Hondorp et al. 2011), slimy sculpin are predicted to be more vulnerable to the collapse of *Diporeia* than deepwater sculpin. Evidence of this is contradictory, though. For example, there is no indication of long-term declines in body condition in recent decades of slimy and deepwater sculpins in Lake Ontario and deepwater sculpin in Lake Huron (Weidel et al. 2017; Volkel 2019), which is inconsistent with declines in deepwater sculpin energy density in Lakes Huron and Michigan (Pothoven et al. 2011). In a cross-lake comparison, current (2015–2018) deepwater sculpin body condition in Lakes Huron, Michigan, and Ontario was similar to that observed in Lake Superior, despite differences in abundances of *Diporeia*, dreissenids, and round goby (Volkel 2019). Slimy sculpin body condition, however, was lower in lakes with more ecological perturbation (Lakes Michigan and Ontario) than in lakes with less ecological perturbation (Lakes Champlain and Superior; Volkel 2019).

Lake Superior sculpin trophic overlap

As part of this review, the trophic overlap of sculpins in Lake Superior was evaluated with a stable isotope analysis. The methods for this analysis are in Appendix A. One hundred and thirty-one sculpin were analyzed for δ^{13}C and δ^{15}N isotopes; 42 slimy, 21 spoonhead, and 68 deepwater sculpins (Figure 5, Table 1). The overall range in both δ^{13}C and δ^{15}N and standard ellipse area (SEAc) was highest for slimy sculpin and lowest for spoonhead sculpin; this likely reflected the broad spatial and depth distribution of slimy sculpin and the narrower distribution of spoonhead sculpin (Table 1, Figure 2). Standard ellipse area of the bivariate δ^{13}C and δ^{15}N data (Figure 5) was highest for slimy sculpin (6.7‰^{2}), intermediate for deepwater sculpin (4.1‰^{2}), and lowest for spoonhead sculpin (1.8‰^{2}). Ellipse areas were likely a reflection of the broader distribution of slimy sculpin and more narrow distribution of spoonhead sculpin. Overlap in the bivariate isotopic ellipse area ranged from 27% for slimy sculpin and deepwater sculpin occurring in spoonhead sculpin trophic space to 100% for spoonhead sculpin occupying slimy sculpin trophic space (Table 1). Coexistence of closely related fish species or morphs is common in northern lakes (Robinson and Parsons 2002) and similar levels of trophic overlap have been observed among other Lake Superior fish, including *Coregonus* species (Rosinski et al. 2020) and lake trout morphs (Sitar et al. 2020). In these fishes, feeding in different habitats or at different times was thought to reduce overall niche overlap (Rosinski et al. 2020). For Great Lakes sculpins, depth segregation appears to be a primary factor in reducing trophic overlap (Figure 2).

Species interactions

Interactions among sculpin species

Several studies have provided evidence for competitive interactions among sculpin species for space. In Lake Michigan, as deepwater sculpin increased their depth distribution, so too did slimy sculpin (Madenjian and Bunnell 2008). In Lake Ontario, following the near extirpation of deepwater sculpin during the 1980s, slimy sculpin increased their density and expanded their range into deeper water, with densities increasing at depths ≥75 m (Owens and Weber 1995). In the past decade, however, Lake Ontario deepwater sculpin have recovered (Lantry et al. 2007; Weidel et al. 2017, 2019), though the mean depth of capture of slimy sculpin appears to have been increasing in recent years (Volkel 2019). The distribution of juvenile

Table 1. Collection depths and δ^{13}C and δ^{15}N (‰) isotopic metrics for deepwater, slimy, and spoonhead sculpin collected in Lake Superior, May–September 2011.

	Deepwater Sculpin	Slimy Sculpin	Spoonhead Sculpin
Sample size	68	42	21
Collection depth (m), mean (range)	189 (31 to 337)	115 (5 to 315)	109 (25 to 220)
δ^{15}N, mean (range)	9.1 (5.7 to 11.0)	8.6 (5.2 to 12.1)	8.1 (5.5 to 9.8)
δ^{13}C, mean (range)	−24.7 (−27.4 to −20.8)	−24.4 (−27.1 to −20.4)	−24.3 (−25.5 to −23.2)
Standard Ellipse Area	4.1	6.7	1.8
Percent ellipse area overlap			
Deepwater Sculpin	—	58	63
Slimy Sculpin	94	—	100
Spoonhead Sculpin	27	27	—

Corrected Standard Ellipse Areas are visualized in Figure 5. Percent trophic overlap pairings are presented as the percent of the ellipse area of the species listed in the column that is overlapped by the ellipse area of the species listed in the row.

deepwater sculpin is limited to depths shallower than those occupied by adults (and to the depths of peak slimy sculpin abundance), indicating that the presence of adults inhibits successful recruitment by juvenile conspecifics to demersal habitats (Geffen and Nash 1992). Likewise, only larger male slimy sculpin are likely to reproduce in areas where nest habitat is limited, potentially affecting the distribution of smaller individuals (Mousseau and Collins 1987). In addition, unlike observations from trawlable habitat, sculpin species may overlap in rocky habitats, which are preferred at least for spawning and nesting by mottled and slimy sculpin (Scott and Crossman 1973; Mousseau et al. 1988; Gray et al. 2018), if not during other times of the year as well. In inland Canadian lakes, slimy sculpin move to littoral areas to make use of rocky habitat for spawning (Mousseau et al. 1988).

The deep waters of Lakes Superior, Huron, and Michigan have diverse deep reefs that could form a habitat basis for niche partitioning, with slimy sculpin occupying the shallower portions of these structures. Lake Superior has diverse ridges and trenches at its eastern end, with putative deepwater sculpin nests close to a reef base (Boyer and Whitlatch 1989). There are likely numerous Lake Superior basalt and granite reefs not yet charted that are entirely in deep water. Slimy sculpin were observed to be abundant at East Reef and Sheboygan Reef in the Lake Michigan MLRC (J. Janssen, University of Wisconsin-Milwaukee, personal observation). There are geologically similar carbonate reefs in Lake Huron (Edsall et al. 1992), and recent images of the Alpena-Amberley Ridge, which spans Alpena, Michigan, and Point Clark, Ontario, show a cobble-boulder bottom (O’Shea and Meadows 2009; O’Shea et al. 2014).

Differential prey selection also may play a role in mediating competitive interactions among sculpin species. Consumption of *Diporeia* was significantly greater for slimy sculpin than for deepwater sculpin, and consumption of *Mysis* was greater for deepwater than for slimy sculpin, in areas where slimy and deepwater sculpin overlapped spatially (Kraft and Kitchell 1986). The same study provided evidence that food was a limiting resource, which is a necessary precondition for documenting the existence of resource competition. Size, fecundity, and energy content of female slimy sculpin at various locations in Lake Ontario were inversely related to their density, which further suggests that sculpin in the Great Lakes are food-limited (Owens and Noguchi 1998). No such evidence exists that bathymetric habitat is limiting. As previously discussed, selectivity of food type and size differs between slimy and deepwater sculpin, as well (Hondorp et al. 2011). Differences in the food habits of slimy and deepwater sculpin have also been observed elsewhere in Lake Michigan (Hondorp et al. 2005) and in Lake Superior (Selgeby 1988). It is not yet clear how the dramatic decline in *Diporeia* abundance has affected these interactions, although some studies have indicated that slimy sculpin now rely more on *Mysis* and chironomids, with *Mysis* dominating the diets in some areas of Lake Michigan (French et al. 2010; Bunnell et al. 2015).

Interactions with native predators

Studies on the effects of predation by native piscivores on sculpin abundance and distribution in the Great Lakes have focused mostly on slimy and deepwater sculpin in Lakes Michigan and Ontario and suggest that the influence of native predators is greater for slimy sculpin than for deepwater sculpin. Lean lake trout and burbot are the primary predators of sculpin in these lakes, but both piscivores appear to consume more slimy sculpin than deepwater sculpin (Elrod 1983; Elrod and O’Gorman 1991; Fratt et al. 1997; Madenjian et al. 1998). Siscowet lake trout have been observed consuming mostly deepwater sculpin in Lake Superior (C. Bronte, USFWS, unpublished data) but published studies (Conner et al. 1993; Fisher and Swanson 1996; Ray et al. 2007) do not differentiate among species found in stomachs. Biomass declines and truncation of the size distribution of slimy sculpin were attributed to lake trout predation in Lake Superior (Bronte et al. 2003). Brandt (1986b) suggested that lake trout predation on slimy sculpin facilitated coexistence between slimy and deepwater sculpin (the keystone predation hypothesis) and that extirpation of deepwater sculpin from Lake Ontario was a predictable consequence of major declines in lake trout abundance during the 1950s. After decades of intensive restocking of lake trout in Lakes Michigan and Ontario, negative correlations between the biomass of lake trout and the abundance, size, and distribution of slimy sculpin have been observed (Christie et al. 1987; Eck and Wells 1987; Owens and Bergstedt 1994; Madenjian et al. 2005). Recent diet studies from Lake Michigan have indicated that sculpin species comprise <5% of the diet by weight of adult lake trout (Leonhardt 2018; Luo et al. 2019), perhaps because of reductions in sculpin biomass combined with increased abundance of other benthic prey like round goby, or because juvenile lake trout (which were not studied) may be more common predators of slimy sculpin (Madenjian et al. 1998). Evidence from inland lakes also is consistent with predators influencing slimy sculpin, as slimy sculpin favored deep waters with high densities of chironomid forage in lakes without lake trout but shifted to rocky littoral areas that offered refuge from lake trout predation but less forage when lake trout were present (Hanson et al. 1992).

The predatory effects of native piscivores on deepwater sculpin are less obvious. Deepwater sculpin declined in Lake Michigan in the early 1960s following the collapse of lake trout (Crowder 1980), but they were not extirpated (Bunnell et al. 2019). Predation of non-native alewife on pelagic larval deepwater sculpin is the primary factor believed to regulate abundance of this species (Wells and McLain 1973; Crowder 1980; Madenjian et al. 2008). Field-based and modeling studies have shown that when deepwater sculpin are abundant they can be an important component of burbot diets (Van Oosten and Deason 1938; Fratt et al. 1997; Madenjian et al. 2005). Predation has also been suggested as more important than interspecific competition as a driver of sculpin community dynamics in Lake Michigan, because the models of environmental drivers that best predicted the biomass of slimy and deepwater sculpin did not include abundance of the competing species (e.g., the best model for slimy sculpin did not include biomass of deepwater sculpin as a factor; Madenjian et al. 2005).

Negative interactions with nonindigenous species other than round goby

Given their historic dietary importance and numeric dominance of the native benthic fish community, negative interactions among sculpins and nonindigenous species could threaten the adaptive capacity of the Great Lakes. Despite the many invasions of nonindigenous species in the Great Lakes, few studies have focused on the potential for direct interactions between sculpins and nonindigenous species, and existing studies do not allow for much generalization. Prior to the invasion of round goby (whose potential effects on sculpin are considered in a separate section), the nonindigenous species most likely to interact with sculpin were alewife, rainbow smelt (*Osmerus mordax*), and dreissenid mussels. As previously stated, the pelagic larvae of deepwater sculpin appear to be particularly vulnerable to predation by alewife (Wells and McLain 1973; Crowder 1980), and thus, when alewife abundance in Lake Michigan declined during the 1980s, bottom trawl catches of deepwater sculpin significantly increased (Madenjian et al. 2005; Bunnell et al. 2006). In contrast, catches of slimy sculpin, which are presumed to have benthic larvae, did not increase over the same time period. Interestingly, however, the recent resurgence of deepwater sculpin in Lake Ontario has occurred during a time period when alewife abundance has remained relatively high (Weidel et al. 2017). Alewife and rainbow smelt have shifted to deeper water in spring, though, potentially creating a zone where larval deepwater sculpin can avoid predation and successfully transition to benthic habitats (Weidel et al. 2017). Rainbow smelt prey on juvenile and adult slimy sculpin in Lake Ontario (Brandt and Madon 1986), but the influence of rainbow smelt predation on sculpin abundance or distribution is unclear. The potential for competition for invertebrate prey among alewife, rainbow smelt, and sculpins is relatively low, given the small degree of overlap among the diets of these fish species (Bunnell et al. 2015).

Invasive dreissenid mussels could also have negatively affected sculpin species. There was a dramatic decline in abundance of *Diporeia*, an historically important food for sculpins, in Lakes Huron (Nalepa et al. 2007) and Michigan (Nalepa et al. 2009) following the dreissenid mussel invasion, which led to declines in the energy density of deepwater sculpin in both lakes (Pothoven et al. 2011). Diet of slimy sculpin has also shifted toward lower-energy prey in some areas of Lake Michigan following dreissenid invasion and coincident declines in *Diporeia* (French et al. 2010; Bunnell et al. 2015), which could result in changes in energy transfer rates between the benthic and pelagic habitats (Ives et al. 2019). Laboratory experiments have shown that slimy sculpin foraging efficiency is reduced in habitat occupied by dreissenid mussels, but also that sculpin spent more time in zebra mussel habitat than either gravel or bare sand (Beekey et al. 2004). Slimy sculpin have been observed in and around beds of dreissenid mussels in Lake Michigan (Figure 3C). The complex habitat offered by dreissenid mussels is associated with greater density of some prey, but foraging efficiency is reduced because prey are afforded a refuge from predation (Beekey et al. 2004).

Deepwater sculpin have shifted their distribution toward deeper waters in Lake Michigan since the late 1980s (Madenjian and Bunnell 2008; Bunnell et al. 2019), coincident with the dreissenid mussel invasion. Bottom-trawl estimates of deepwater sculpin biomass declined 74% during 2003–2007, concomitant with increases in dreissenid biomass in waters deeper than 50 m, but this was attributed to the effects of dreissenid mussels on sampling gear efficiency and a distributional shift of sculpins to deeper waters not traditionally sampled (Bunnell et al. 2009).

Finally, there has been little research to understand how proliferation of dreissenid mussels may have influenced sculpin spawning habitat. Owens and Noguchi (1998) reported four occasions where slimy sculpin egg masses were collected coincident with dreissenid mussels, but never attached to them.

Interactions with round goby

Establishment and proliferation of round goby in the Great Lakes has negatively affected the native sculpin species that overlap spatially with round goby. Round goby were first detected in the Great Lakes in 1990 (Jude et al. 1992) but have since spread throughout all five lakes faster than any previous fish invader (Charlebois et al. 1997) and have reached prolific abundances in all but Lake Superior (Kornis et al. 2012). Like many sculpin species, round goby prefer rocky substrate or other structurally complex habitats (e.g., submerged aquatic vegetation, debris fields; Jude et al. 1992; Cooper et al. 2009; Kornis et al. 2012) and primarily feed on benthic invertebrates. Round goby are also found in greater densities in shallow, littoral areas compared to offshore areas (Johnson et al. 2005; Taraborelli et al. 2009), although they are expanding into ever deeper waters (e.g., Walsh et al. 2007), where density appears to be increasing (USGS 2019; J. Janssen, University of Wisconsin-Milwaukee, unpublished data).

Because of the high abundance of round goby in shallower waters, most research on sculpin interactions with round goby has focused on mottled sculpin. Mottled sculpin rapidly declined in trawl catches following the invasion of round goby in nearshore areas of southern Lake Michigan (Lauer et al. 2004) and were nearly extirpated from Calumet Harbor only four years after the discovery of round goby (Janssen and Jude 2001). Both studies suggested that spawning interference was the main mechanism of these declines, as mottled sculpin and round goby have a nearly identical reproductive strategy, which involves spawning in cavities on the underside of rocks (Figures 3A and B; Scott and Crossman 1973; Meunier et al. 2009). Although both species exhibit nest guarding behavior, laboratory experiments demonstrated that round goby will attack resident or nest guarding mottled sculpin, occupy the former sculpin nests, displace the sculpin to non-sheltered habitat, and change to spawning colors, which results in the loss of nearly all mottled sculpin eggs (Janssen and Jude 2001). Round goby also dominated forage resources in laboratory experiments with mottled sculpin, spoonhead sculpin, and logperch (*Percina caprodes*; Bergstrom and Mensinger 2009).

Expansion of round goby into deeper waters represents a potential threat to other native sculpins, but the nature and basis of goby-sculpin interactions in offshore environments (depths $\geq$9 m) is unknown. Slimy and deepwater sculpin are the offshore sculpin species most likely to interact with round goby, based on depth distribution (Figure 2; Wells 1968; Selgeby 1988). Spoonhead sculpin has a depth distribution similar to slimy sculpin (Wells 1968) but is found mostly in Lake Superior, where round goby has not become widely established (Kornis et al. 2012). Among these species, slimy sculpin uses similar spawning habitat as mottled sculpin and round goby (Scott and Crossman 1973), and thus may be particularly vulnerable to displacement from spawning habitat as round goby spread into deeper waters. Much of the round goby population returns to nearshore waters to spawn during summer, and thus slimy sculpin spawning earlier in their protracted spawning season (April through October) would be most at risk for competition with round goby. In addition, some round goby were recently observed remaining in deeper water (50–100 m) during June and July in Lake Ontario (USGS 2019); interactions during the slimy sculpin spawning season may become more prevalent if round goby continue to increase their summer use of deeper habitats. Deepwater sculpin are thought to spawn in pits dug out in gravel or sand (Balon 1975) and thus are less likely to suffer from spawning habitat competition with round goby.

The potential for round goby to compete with native sculpins for forage is relatively unstudied as well. As mentioned above, slimy and deepwater sculpin feed primarily on benthic macroinvertebrates like *Mysis*, *Diporeia*, and chironomids (Selgeby 1988; Hondorp et al. 2011). Slimy sculpin appear to be more generalist in their diets, as they also consume hypolimnetic calanoid copepods and benthic cladocerans (Bunnell et al. 2015). In the offshore waters of Lake Michigan (depths 69–128 m) where round goby, slimy sculpin, and deepwater sculpin can overlap during late fall, winter, and early spring, round goby consume some *Mysis* (Mychek-Londer et al. 2013; Bunnell et al. 2015), which could result in some level of competition with sculpins if food is limited. Forage competition between round goby and sculpins is likely to increase with water depth: during spring in Lake Ontario, the frequency of occurrence of round goby with *Mysis* in their diets increased with depth (6%, 58%, and 97% at depths of 55, 95, and 130 m), while the frequency of occurrence with dreissenid mussels decreased with depth (97%, 90%, and 20% at depths of 55, 95, and 130 m; Walsh et al. 2007). Similarly, in Lake Huron the frequency of occurrence of round goby with *Diporeia* (63.4–75.5%) and *Mysis* (21.4–57.7%) in their diets was greater at depths of 55–73 m than at 27–46 m (0–28.6% for *Diporeia* and 0–7.1% for *Mysis*; Schaeffer et al. 2005). Feeding overlap could be greater in areas with low dreissenid abundance, or for smaller round goby (e.g., <75 mm TL) that are often reported to consume greater proportions of non-dreissenid prey (Janssen and Jude 2001; Barton et al. 2005; Johnson et al. 2005; Kornis et al. 2012). Round goby also have been documented to occasionally consume eggs and small fish in offshore environments (Johnson et al. 2005; Schaeffer et al. 2005; Roseman et al. 2006; Walsh et al. 2007; Mychek-Londer et al. 2013), as have some sculpin species (Chotkowski and Marsden 1999; Hudson et al. 1995; Mychek-Londer et al. 2013). Importantly, round goby effects on sculpin species could be dependent on round goby density, as has been reported for other nonindigenous species (Latzka et al. 2016). For example, whereas mottled sculpin abundances declined dramatically over four years following round goby invasion in southern Lake Michigan (Janssen and Jude 2001; Lauer et al. 2004), mottled sculpin catch per unit effort remained unchanged in seven Lake Michigan tributaries over a four-year period despite 11-fold increases in round goby abundance, likely due at least in part to lower density of round goby in tributaries compared to the lake (Kornis et al. 2013).

Future research directions for Great Lakes sculpins

Zimmerman and Krueger (2009) synthesized five questions related to Great Lakes sculpin reestablishment; four of those are still relevant. Their question related to feasibility and risks of deepwater sculpin reintroduction to Lake Ontario is less relevant because that species returned naturally (Weidel et al. 2017). The remaining four questions are relevant and supported herein:

1. Is across basin variability in life history driven by local spawning conditions?
2. Does larval and fry habitat (benthic vs pelagic) drive dispersal and ultimately population structure, as suggested by Houde (1994)?
3. Are population dynamics driven by early life history as compared to juvenile or adult stage dynamics?
4. How will non-native species and subsequent food web changes influence sculpin?

After completing this review, an updated set of future research directions and questions for sculpin species in the Great Lakes were compiled and are described below, are summarized in Table 2, and build upon the primary questions developed by Zimmerman and Krueger (2009). These research directions will enable a better understanding of sculpin ecology, the effects of ecosystem changes on sculpins and the benthic fish guild as a whole, and ultimately how ecosystem changes will affect the adaptive capacity of the benthic and pelagic food webs of the Great Lakes.

Genetic diversity and adaptive capacity

Because so little is known about sculpin genetic diversity, population structure, or evolutionary history, there are many fruitful areas of genetic research that would have far-reaching effects on conservation of sculpins in the Great Lakes and elsewhere. While expounding on the advantages of genetic and genomic research are not the purpose of this review (but see: Bernatchez et al. 2017; Hendricks et al. 2018; Meek and Larson 2019 for reviews), there are three research objectives that could be beneficial. (1) Modern population genomic studies can provide accurate and consistent delineation of conservation units, estimates of effective population size, and evidence of historical events like re-colonization, bottlenecks, or migration (Waples et al. 2008). Although smaller scale studies have been conducted on slimy and deepwater sculpin that suggest genetic structure throughout the Great Lakes may be low (Euclide et al. 2018; Welsh et al.

Table 2. Topics (in bold) and related questions that are relevant for sculpin research in the Great Lakes, which would provide a better understanding of the adaptive capacity of the native deepwater fish community, and the Great Lakes in general.

1. **Improve understanding of genetic diversity and implications for adaptive capacity**
   a. What is the genetic diversity of these species throughout the Great Lakes?
   b. What is the effective population size for each species?
   c. What are the effects of climate and community change on sculpin species, as evidenced from genomic data?
   d. Are there populations with high genetic diversity and population abundance available for conservation or reestablishment of populations in the future?
2. **Determine the connectivity, movement, and habitat use of each species throughout the Great Lakes basin**
   a. What is the population structure and connectivity across the Great Lakes of all sculpin species?
   b. What habitats are used by each species?
   c. Are there seasonal or diel changes in habitat use?
   d. What are the ontogenetic changes in habitat use?
   e. Does habitat use affect interactions among sculpin species?
   f. How and when do fish disperse among habitats?
   g. What is the source of the resurgence of deepwater sculpin in Lake Ontario?
   h. How can sculpin species in deep and rocky habitats be best and most effectively sampled?
3. **Improve understanding of sculpin reproductive ecology and early life history in the Great Lakes**
   a. When and where do sculpin species in the Great Lakes spawn, and what variables are associated with spawning?
   b. What is the fecundity of each species, and how does fecundity differ among lakes?
   c. How do species differ in terms of nest building, nest guarding, mate selection, egg deposition, egg incubation times, and post-hatch larval behavior?
   d. Is there sexual dimorphism in these sculpin species?
   e. Are slimy sculpin larvae truly benthic?
   f. How does advection affect larval dispersal?
   g. Does increased larval growth rate, as observed in nearshore habitats, suggest adverse advection?
   h. What is the recruitment of sculpin to early, juvenile, and adult stages?
4. **Adult life history**
   a. How does the age, growth, and mortality of all species differ among lakes?
   b. How can these sculpin species be aged effectively?
5. **Determine the interactions among species in a changing food web**
   a. How does habitat use change in response to changes in abundance of native predators like lake trout and burbot?
   b. How will increased stocking and natural recruitment of lake trout affect sculpins, given the observed changes in the native deepwater fish guild?
   c. How do changes in the lower benthic food web affect sculpin population dynamics?
   d. How does sculpin habitat use change in response to non-native species?
   e. How have non-indigenous species influenced the predator-prey interactions between sculpin species and the fish community of the Great Lakes?
   f. How have dreissenids affected the feeding, spawning, and habitat use of sculpins?
   g. Are round goby competing with slimy sculpin for food resources or spawning habitat?
   h. Has the introduction of non-native species affected the growth and mortality rates of sculpins?
   i. Do sculpins show signs of genetic adaptation in response to these changes?

Some topics from Zimmerman and Krueger (2009) remain relevant, and others have been identified in this review.

2017), there has not been a large-scale study focused on describing connectivity of any of the sculpin species across all the Great Lakes. Large-scale population studies of sculpins could help identify populations of conservation concern and determine the origin of recent deepwater sculpin resurgence in Lake Ontario. (2) Although sculpins were never fished, their populations have experienced substantial fluctuations and have likely adapted to the changing community and environment of the Great Lakes. Genomic techniques are already being used to evaluate ciscoes, which have evolved in response to anthropogenic changes (Ackiss et al. 2020; Bronte et al. 2017). Similar techniques could be used to increase the understanding of the effects that climate and community change in the Great Lakes have had on the native benthic community, as well as information about potential changes in adaptive capacity. (3) Finally, although deepwater sculpin are resurging in Lake Ontario, slimy sculpin abundance appears to be declining (Weidel et al. 2018). Genetic diversity and composition of slimy sculpin in Lake Ontario should be evaluated now in preparation for conservation in the future. Slimy sculpin are abundant over a broad range and inhabit both lakes and streams. Evaluating the genetic diversity and make-up of slimy sculpin in Lake Ontario now could be important for later conservation efforts or, if needed, population reestablishment through external source populations.

Connectivity, movement, and habitat use

More information is needed on specific habitat use by each Great Lakes sculpin species, seasonal, diel, and ontogenetic changes in habitat use, and dispersal among habitats. Such data would be useful in understanding interactions among sculpin species, predation risk, and the potential effects of recent large-scale changes in benthic environments on the fish community.

The large spatial extent and extreme depth of benthic habitats in the Great Lakes present enormous research challenges to studying habitat use and dispersal of sculpins and other benthic fishes. Many common techniques like quantifying or manipulating habitat conditions, physically blocking or isolating habitats, introducing or removing fish for experimental purposes, or marking and recapturing individuals, are difficult to apply. In the Great Lakes, most data on sculpins and specimen collections are derived from bottom trawl surveys deployed from large research vessels, which provide relative abundance (Figure 1) and size and age structure information on large spatial scales but are limited to mostly soft substrates. Beam trawls and submersibles have been used on complex rocky substrates to sample slimy sculpin (Hudson et al. 1995; Janssen et al. 2006; Houghton et al. 2010) and could be used to make comparisons across a variety of substrate types under experimental designs that include measures of the physical habitat. More extensive use of beam and well-designed roller trawls, during both day and night surveys, could provide more useful information on sculpin biology at a variety of habitats with more structural complexity.

Direct observation of habitat structure, quality, and use on smaller spatial scales can be accomplished by SCUBA divers, but deepwater and slimy sculpin mostly occur in areas beyond the practical working depth range of divers (Figure 2). Data on habitat structure and use could be collected with cameras mounted at stationary positions or deployed by autonomous or remotely operated vehicles (ROVs) (e.g., O'Malley et al. 2018), but trials of this method are needed as the cryptic nature of many sculpin species and low light levels at extreme depths may limit the efficacy of such visual methods. In addition, electroshocking with a suction sampler from an ROV has been successful in capturing several sculpin species, as well as round goby, at deeper depths (Olson and Janssen 2017).

Electronic tracking technologies like acoustic telemetry (Hussey et al. 2015) or passive integrated transponder (PIT) tags (e.g., Ruetz et al. 2006; Keeler et al. 2007) might be practical methods for the study of habitat use and dispersal of adult sculpins in the Great Lakes. These techniques allow the determination and tracking of the locations of tagged fish without handling or recapture. Tag size has historically limited the application of acoustic telemetry to larger fish, but continuing miniaturization of tags (Heupel et al. 2006) may allow their use for studies of sculpins. Passive integrated transponder tags are smaller and have been widely applied to small fishes in streams, but their applicability to large lakes is unclear (e.g., Cookingham and Ruetz 2008).

Reproduction and early life history

Limited information exists on spawning and early life history of all sculpin species in the Great Lakes. The exact spawning habitat and associated environmental variables of all four species has not been identified in the Great Lakes. This information is required to make comparisons among lakes and species or to determine the effects of the changing Great Lakes ecosystem on sculpin reproductive biology. In addition, little is known about dispersal pathways and the connectivity of sculpin populations both within and among lakes, although dispersal is largely hypothesized to occur early in life through larval drift (Geffen and Nash 1992; Euclide et al. 2018).

Spawning behavior and basic reproductive ecology of the four sculpin species is also not well understood. Research on nest building, nest guarding, mate selection, egg deposition, incubation periods, and post-hatch larval behavior is required. Knowledge of these aspects of sculpin reproduction can help determine if declines in sculpin abundance are the result of competition for nesting space with non-native species, as observed for mottled sculpin (Janssen and Jude 2001). Additionally, estimates of fecundity, histological assessment of gonads, and GSI for each species would improve understanding of sculpin spawning. Some GSI data for deepwater sculpin have been collected on Lake Ontario (Weidel et al. 2017), and on Lakes Michigan, Huron, and Champlain for slimy and deepwater sculpin (S. Volkel, Michigan State University, unpublished data; E. Marsden, University of Vermont, pers. comm.). Sampling should be standardized, performed year-round, and expanded to acquire other data necessary to understand the reproductive ecology of Great Lakes sculpins.

Understanding of the post-hatch behavior and dispersal of sculpins is also needed. For instance, the role of advection in movement of transforming deepwater sculpin larvae from inshore to offshore habitats has yet to be elucidated. Does the increased growth rate that has been observed nearshore (Geffen and Nash 1992) suggest "adverse advection" (sensu Hjort 1914)? Much can be learned by indirectly evaluating dispersal behavior through population genetics. Genetic methods have been used successfully to evaluate the spatial structure and migration of other species in the Great Lakes (e.g. Stott et al. 2010; Sepulveda-Villet and Stepien 2011) and could help inform sculpin early life dispersal, evaluate migration patterns, and identify possible recolonization routes (Welsh et al. 2017). Understanding how sub-populations of sculpin are connected will inform predictions of sculpin response to habitat loss and population declines, as well as the ability of sculpins to recolonize habitats in the future.

Sculpin survival varies from one life stage to the next (Geffen and Nash 1992), and these survival rates are largely unknown. Variation in survival among sculpin life stages likely relates to their life history strategy, stochasticity in recruitment, and predation. This variation may also be affected by perturbations from invasive species (e.g., dreissenid mussels and round goby) and limited prey availability (e.g., *Diporeia* collapse). The collection of basic information about age, growth, and development of sculpin species from all lakes will enable researchers to not only better understand sculpin development among habitats and species, but to determine how early life history might be affected by changes in the Great Lakes ecosystem.

Adult life history

Information about the vital rates of adult sculpin species in the Great Lakes would be useful in understanding the changes that these populations have experienced in recent years, concurrent with ecosystem changes. For instance, age and growth estimates for all four sculpin species throughout the Great Lakes are limited and rely, at times, on either whole or sectioned otoliths, which can lead to discrepancies in maximum age estimates. Research to validate the use of otoliths, including a comparison of different methods (e.g., sectioned versus whole), to estimate age would improve understanding and certainty of sculpin population dynamics. In addition, most estimates of age and growth from the Great Lakes come from Lake Superior populations. Given the difference in the ecosystem perturbations in Lake Superior compared to other Great Lakes, efforts to estimate age, growth, and mortality of each species in each lake may indicate how sculpins have been affected by invasive-mediated changes in the benthic community, as well how these vital rates differ among lakes.

Species interactions

Sculpin community and population dynamics are influenced by numerous factors, including interactions among sculpin species, with native predators, and with nonindigenous species within the food web. Time-series analyses of trawl data have provided some of the strongest evidence of biotic interactions driving sculpin dynamics in specific lakes. Future studies, however, might benefit from cross-lake time series analyses that can take advantage of gradients in abundance of putative key interactors (e.g., lake trout, alewife, round goby, dreissenid mussels) to further test some of the current hypothesized drivers. These drivers include: predator-prey interactions between sculpin species at different life stages and lake trout, burbot, and alewife; effects of dreissenid mussels on spawning and feeding of sculpin species, and larval habitat in the thermal bar; potential effects of changes in the plankton community on sculpins; and phenology of movements and distributions related to interactions between sculpins and non-native species like round goby. Lake Superior provides an ideal field experiment for cross-lake comparisons since all three offshore species (slimy, spoonhead, deepwater) are present, the native piscivore community is largely intact, *Diporeia* remains abundant, and dreissenid mussels and round goby are rare. For example, an estimated 2/3 of the *Diporeia* biomass in Lake Superior, lies in a band between about 30 and 125 m depth, but this band occupies only 25% of the surface area (Auer et al. 2013). This suggests an opportunity for cross-lake comparisons of diet and distribution of slimy sculpin in particular. Such a study would illuminate potential mechanisms driving changes in depth distribution of sculpin. In addition, within-lake comparisons among habitats could provide useful information about interactions between sculpins and nonindigenous species. For instance, the Lake Michigan MLRC provides a unique habitat for comparison with near-shore waters, as both habitats have similar species complexes. One final research need is to examine the vulnerability of slimy sculpin to competition with round goby for food and spawning habitat and determine whether such interactions are mediated by habitat availability, given the negative effects of round goby on mottled sculpin and similarities in spawning habitat between mottled sculpin and slimy sculpin. Ideally, this could include both laboratory and *in situ* experiments.

Management and conservation implications

Sculpins, as well as ciscoes (*Coregonus artedi* sensu lato), played an important role in the diets of pre-collapse native lake trout populations in the Great Lakes, especially for juvenile lake trout (Van Oosten and Deason 1938; Dryer et al. 1965), and were far more important that other strictly benthic fishes. With the exception of Lake Superior, lake trout are no longer the principal salmonine predator in the Great Lakes and are secondary to introduced Pacific salmon (*Oncorhynchus* spp.) stocked from the mid-1960s to the present to support and diversify the sport fishery and control invasive alewife (Tanner and Tody 2002; Stewart et al. 2017). After the collapse of most pelagic and bentho-pelagic ciscoes by the 1960s (Smith 1972), non-native salmonines and lake trout principally preyed on pelagic non-native alewife and rainbow smelt, and made little use of native benthic fishes (Stewart et al. 1981; Brandt 1986a; Jude et al. 1987; Diana 1990; Conner et al. 1993). Recent re-oligotrophication (Barbiero et al. 2012), combined with salmonine predation, has resulted in lower biomass of non-native pelagic prey in Lakes Michigan and Huron (Riley et al. 2008; Bunnell et al. 2014; Madenjian et al. 2018). As a result, fisheries for alewife-obligate predators like Chinook salmon (*Oncorhynchus tshawytscha*) have collapsed in Lake Huron and are currently below historical levels in Lake Michigan (Clark et al. 2016). Steelhead (*O. mykiss*), Coho salmon (*O. kisutch*), and Chinook salmon share the same general niche space in Lakes Michigan and Ontario based on stable isotope analysis (Mumby et al. 2018; Kornis et al. 2020), although steelhead appear to forage on terrestrial invertebrates to a greater extent than the other two (Conner et al. 1993; Leonhardt 2018). In contrast, lake trout and brown trout (*Salmo trutta*) exhibit greater diet flexibility and use other non-pelagic resources. Lake trout consume round goby, especially in spring (Happel et al. 2018; Luo et al. 2019), and can exploit this relatively new benthic high-density energy subsidy, unlike Pacific salmon. Brown trout also consume round goby (Leonhardt 2018; Kornis et al. 2020). Management agencies annually evaluate and adjust salmonine stocking to maintain predator-prey balance with the residual alewife populations (Claramunt et al. 2019), and have reduced stocking of Chinook salmon and lake trout in Lakes Michigan and Ontario for this very reason. More recently, agencies have implemented greater reductions of lake trout and other species to offset continued or increased stocking of Chinook salmon based on constituent feedback (J. Wesley, Michigan Department of Natural Resources, pers. comm.).

So where is the fishery management nexus for sculpins given that lake trout, one of the few salmonines that will consume small benthic forage, is, at least at the moment, being deemphasized in an attempt to conserve alewife for use by Pacific salmon? Given that the trajectory of ecosystem change in Lake Huron is likely to play out in Lake Michigan, the sustainability of Pacific salmon is questionable due to their apparent inability to shift to alternative vertebrate and invertebrate prey (e.g., Jacobs et al. 2013; Roseman et al. 2014). Sculpins convert benthic production into edible fish biomass that can supplement energy from pelagic sources, which has been reduced by the effects of oligotrophication and predation. Sculpins also occupy a wider range of lake depths than round goby, which are typically found in nearshore habitats except during winter and early spring (e.g., Walsh et al. 2007; Kornis et al. 2012), and thus potentially provide an important source of benthic forage otherwise unavailable in some areas. In addition, the density and size composition of zooplankton in Lakes Michigan, Huron and, to some extent, Ontario is now similar to that in Lake Superior (Barbiero et al. 2019), and is more appropriate for sustaining native ciscoes than non-native planktivores (Eshenroder and Lantry 2012). Hence the future salmonine predator profile appears destined to be less diverse and composed mostly of those species, like lake trout, brown trout, and steelhead, that are able to diversify their diets and persist in a forage community largely devoid of alewife (e.g., Conner et al. 1993; Roseman et al. 2014; Kao et al. 2018; Mumby et al. 2018; Kornis et al. 2020). With lower overall primary productivity, the role of sculpins to convert benthic production to consumable fish flesh will likely be paramount to support a predator base that has a more diverse diet portfolio, particularly in deeper areas that have few other forage fish.

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ORCID

Kelly F. Robinson http://orcid.org/0000-0001-8109-9492
Peter T. Euclide http://orcid.org/0000-0002-1212-0435

Derek H. Ogle http://orcid.org/0000-0002-0370-9299
Mark R. Vinson http://orcid.org/0000-0001-5256-9539
Brian C. Weidel http://orcid.org/0000-0001-6095-2773

References

Ackiss AS, Larson WA, Stott W. 2020. Genotyping-by-sequencing illuminates high levels of divergence among sympatric forms of coregonines in the Laurentian Great Lakes. Evol Appl. 2020:1–18.

Anderson RO, Gutreuter SJ. 1983. Length, weight, and associated structural indices. In: Nielsen LA, Johnson DL, editors. Fisheries techniques. Bethesda (MD): American Fisheries Society. pp. 283–300.

Argyle RL. 1982. Alewives and rainbow smelt in Lake Huron: midwater and bottom aggregations and estimates of standing stocks. Trans Am Fish Soc. 111(3):267–285. doi:10.1577/1548-8659(1982)111<267:AARSIL>2.0.CO;2

Auer MT, Auer NA, Urban NR, Auer T. 2013. Distribution of the amphipod *Diporeia* in Lake Superior: the ring of fire. J Great Lakes Res. 39(1):33–46. doi:10.1016/j.jglr.2012.12.020

Auster PJ, Malatesta RJ, LaRosa SC. 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New England (USA) continental shelf and slope. Mar Ecol Prog Ser. 127:77–85. doi:10.3354/meps127077

Bailey JE. 1952. Life history and ecology of the sculpin *Cottus bairdi punctulatus* in southwestern Montana. Copeia. 1952(4):243–255. doi:10.2307/1439271

Balon EK. 1975. Reproductive guilds of fishes: a proposal and definition. J Fish Res Bd Can. 32(6):821–864. doi:10.1139/f75-110

Barbiero RP, Lesht BM, Warren GJ. 2012. Convergence of trophic state and the lower food web in Lakes Huron, Michigan and Superior. J Great Lakes Res. 38(2):368–380. doi:10.1016/j.jglr.2012.03.009

Barbiero RP, Rudstam LG, Watkins JM, Lesht BM. 2019. A cross-lake comparison of crustacean zooplankton communities in the Laurentian Great Lakes, 1997–2016. J Great Lakes Res. 45:672–690. doi:10.1016/j.jglr.2019.03.012

Barton DR, Johnson RA, Campbell L, Petruniak J, Patterson M. 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in Eastern Lake Erie, 2002–2004. J Great Lakes Res. 31:252–261. doi:10.1016/S0380-1330(05)70318-X

Becker GC. 1983. Fishes of Wisconsin. Madison (WI): University of Wisconsin Press.

Beekey MA, McCabe DJ, Marsden JE. 2004. Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. Oecologia. 141(1):164–170. doi:10.1007/s00442-004-1632-1

Bergstrom MA, Mensinger AF. 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. Trans Am Fish Soc. 138(5):1009–1017. doi:10.1577/T08-095.1

Bernatchez L, Wellenreuther M, Araneda C, Ashton DT, Barth JMI, Beacham TD, Maes GE, Martinsohn JT, Miller KM, Naish KA, et al. 2017. Harnessing the power of genomics to secure the future of seafood. Trends Ecol Evol (Amst). 32(9):665–680. doi:10.1016/j.tree.2017.06.010

Black GA, Lankester MW. 1981. The biology and parasites of Deepwater Sculpin, *Myoxocephalus quadricornis thompsonii* (Girard), in Burchell Lake. *Ontario*. Can J Zool. 59(7):1454–1457. doi:10.1139/z81-196

Blouzdis C, Ivan L, Pothoven S, Roswell C, Foley C, T. Höök T. 2013. A trophic bottleneck?: The ecological role of trout-perch *Percopsis omiscomaycus* in Saginaw Bay, Lake Huron. J Appl Ichthyol. 29(2):416–424. doi:10.1111/jai.12023

Bolgrien DW, Granin NG, Levin L. 1995. Surface temperature dynamics of Lake Baikal observed from AVHRR images. Photogramm Eng Rem Sens. 61:211–216.

Bond MJ, Jones NE, Haxton TJ. 2016. Growth and life history patterns of a small-bodied stream fish, *Cottus cognatus*, in hydropeaking and natural rivers of northern Ontario. River Res Appl. 32(4):721–733. doi:10.1002/rra.2886

Botte V, Kay A. 2000. A numerical study of plankton population dynamics in a deep lake during the passage of the spring thermal bar. J Marine Syst. 26(3–4):367–386. doi:10.1016/S0924-7963(00)00046-4

Bowers JA, Cooper WE, Hall DJ. 1990. Midwater and epibenthic behaviors of *Mysis relicta* Loven: observations from the Johnson-Sea-Link II submersible in Lake Superior and from a remotely operated vehicle in northern Lake Michigan. J Plankton Res. 12(6):1279–1286. doi:10.1093/plankt/12.6.1279

Boyer LF, Whitlatch RB. 1989. In situ studies of organism-sediment relationships in the Caribou Island Basin, Lake Superior. J Great Lakes Res. 15(1):147–155. doi:10.1016/S0380-1330(89)71469-6

Brandt SB. 1986a. Ontogenetic shifts in habitat, diet, and diel-feeding periodicity of slimy sculpin in Lake Ontario. Trans Am Fish Soc. 115(5):711–715. doi:10.1577/1548-8659(1986)115<711:OSIHDA>2.0.CO;2

Brandt SB. 1986b. Disappearance of the deepwater sculpin (*Myoxocephalus thompsoni*) from Lake Ontario: The keystone predator hypothesis. J Great Lakes Res. 12(1):18–24. doi:10.1016/S0380-1330(86)71696-1

Brandt SB, Madon SP. 1986. Rainbow smelt (*Osmerus mordax*) predation on slimy sculpin (*Cottus cognatus*) in Lake Ontario. J Great Lakes Res. 12(4):322–325. doi:10.1016/S0380-1330(86)71732-2

Breen MJ, Ruetz CR, III, Thompson KJ, Kohler SL. 2009. Movements of mottled sculpin (*Cottus bairdii*) in a Michigan stream: how restricted are they? Can J Fish Aquat Sci. 66(1):31–41. doi:10.1139/F08-189

Brett MT, Goldman CR. 1996. A meta-analysis of the freshwater trophic cascade. Proc Natl Acad Sci USA. 93(15):7723–7726. doi:10.1073/pnas.93.15.7723

Bronte CR, Ebener MP, Schreiner DR, DeVault DS, Petzold MM, Jensen DA, Richards C, Lozano SJ. 2003. Fish community change in Lake Superior, 1970–2000. Can J Fish Aquat Sci. 60(12):1552–1574. doi:10.1139/f03-136

Bronte CR, Bunnell DB, David SR, Gordon R, Gorsky D, Millard MJ, Rea J, Stein RA, Vaccaro L. 2017. Report from the Workshop on Coregonine Restoration Science: U.S. Geological Survey Open-File Report 2017–1081. p. 23. 10.3133/ofr20171081.

Brown L, Downhower JF. 1982. Summer movements of mottled sculpins, *Cottus bairdi* (Pisces: Cottidae). Copeia. 1982(2):450–453. doi:10.2307/1444629

Bruch RM. 1986. Age and growth, mortality, reproductive cycle and fecundity of the deepwater sculpin, *Myoxocephalus thompsoni* (Girard), in Lake Michigan. M.S., University of Wisconsin-Milwaukee, Milwaukee, WI.

Bunnell DB, Barbiero RP, Ludsin SA, Madenjian CP, Warren GJ, Dolan DM, Brenden TO, Briland R, Gorman OT, He JX, et al. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. BioScience. 64(1):26–39. doi:10.1093/biosci/bit001

Bunnell DB, Davis BM, Chriscinske MA, Keeler KM, Mychek-Londer JG. 2015. Diet shifts by planktivorous and benthivorous fishes in northern Lake Michigan in response to ecosystem changes. J Great Lakes Res. 41(Suppl 3):161–171. doi:10.1016/j.jglr.2015.07.011

Bunnell DB, Madenjian CP, Claramunt RM. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). Can J Fish Aquat Sci. 63(11):2434–2446. doi:10.1139/f06-132

Bunnell DB, Madenjian CP, Desorcie TJ, Armenio P, Adams JV. 2019. Status and trends of prey fish populations in Lake Michigan, 2018. Report to the Great Lakes Fishery Commission, Lake Michigan Committee Meeting, Ypsilanti, MI. p. 17.

Bunnell DB, Madenjian CP, Holuszko JD, Adams JV, French JRP. 2009. Expansion of *Dreissena* into offshore waters of Lake Michigan and potential impacts on fish populations. J Great Lakes Res. 35(1):74–80. doi:10.1016/j.jglr.2008.10.002

Busby MS, Blood DM, Fleischer AJ, Nichol DG. 2012. Egg deposition and development of eggs and larvae of Bigmouth Sculpin (*Hemitripterus bolini*). Northwest Nat. 93(1):1–16. doi:10.1898/11-13.1

Charlebois PM, Marsden JE, Goettel RG, Wolfe RK, Jude DJ, Rudnika S. 1997. The round goby, *Neogobius melanostomus* (Pallas), a review of European and North American literature. Zion (IL): Illinois-Indiana Sea Grant Program and Illinois Natural History Survey.

Chotkowski MA, Marsden JE. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: field predictions from laboratory experiments. J Great Lakes Res. 25(1):26–35. doi:10.1016/S0380-1330(99)70714-8

Christie WJ, Scott KA, Sly PG, Strus RH. 1987. Recent changes in the aquatic food web of eastern Lake Ontario. Can J Fish Aquat Sci. 44(S2):S37–S52. doi:10.1139/f87-307

Claramunt RM, Warner DM, Madenjian CP, Kornis MS, Bronte CR, Legler ND. 2019. State of the Lake Michigan pelagic fish community in 2016 In: Madenjian CP, editor. The state of Lake Michigan in 2016. Ann Arbor (MI): Great Lakes Fishery Commission, Special Publication 2019-01. http://www.glfc.org/pubs/SpecialPubs/Sp19_01.pdf.

Clarke AD, Telmer KH, Shrimpton JM. 2015. Movement patterns of fish revealed by otolith microchemistry: a comparison of putative migratory and resident species. Environ Biol Fish. 98(6):1583–1597. doi:10.1007/s10641-015-0384-6

Clark RD, Jr, Bence JR, Claramunt RM, Johnson JE, Gonder D, Legler ND, Robillard SR, Dickinson BD. 2016. A spatially explicit assessment of changes in Chinook Salmon fisheries in lakes Michigan and Huron from 1986 to 2011. N Am J Fish Manag. 36(5):1068–1083. doi:10.1080/02755947.2016.1185060

Conner DJ, Bronte CR, Selgeby JH, Collins HL. 1993. Food of salmonine predators in Lake Superior, 1981-87 1. Great Lakes Fishery Commission. Technical Report 59: 1–19.

Cookingham MN, Ruetz CR III. 2008. Evaluating passive integrated transponder tags for tracking movements of round gobies. Ecol Freshwater Fish. 17(2):303–311. doi:10.1111/j.1600-0633.2007.00282.x

Cooper MJ, Ruetz CR, Uzarski DG, Shafer BM. 2009. III. Habitat use and diet of the round goby (*Neogobius melanostomus*) in coastal areas of Lake Michigan and Lake Huron. J Freshw Ecol. 24(3):477–488. doi:10.1080/02705060.2009.9664321

Craig PC, Wells J. 1976. Life history notes for a population of slimy sculpin (*Cottus cognatus*) in an Alaskan arctic stream. J Fish Res Bd Can. 33(7):1639–1642. doi:10.1139/f76-206

Crowder LB. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? Environ Biol Fish. 5(3):225–233. doi:10.1007/BF00005356

Davis BM, Savino JF, L. M. Ogilvie LM. 2007. Diet niches of major forage fish in Lake Michigan. Arch Hydrobiol. 60:259–273. Special issues of Adv Limnol.

Deboer JA, Holtgren JM, Ogren SA, Snyder EB. 2015. Movement and habitat use by mottled sculpin after restoration of a sand-dominated 1st-order stream. Am Midl Nat. 173(2):335–345. doi:10.1674/amid-173-02-335-345.1

Diana JS. 1990. Food habits of angler-caught salmonines in western Lake Huron. J Great Lakes Res. 16(2):271–278. doi:10.1016/S0380-1330(90)71420-7

Dryer WR, Erkkila LF, Tetzloff CL. 1965. Food of lake trout in Lake Superior. Trans Am Fish Soc. 94(2):169–176. doi:10.1577/1548-8659(1965)94[169:FOLTIL]2.0.CO;2

Dymond JR, Hart JL, A. L. Pritchard AL. 1929. The fishes of the Canadian waters of Lake Ontario. University of Toronto Studies. Pub. Ont. Fish. Res. Lab. No. 37.

Eck GW, Wells L. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa pseudoharengus*). Can J Fish Aquat Sci. 44(S2):S53–S60. doi:10.1139/f87-308

Edsall TA, Brown CL, Kennedy GW, Poe TP. 1992. Lake trout spawning habitat in the Six Fathom Bank-Yankee Reef lake trout sanctuary, Lake Huron. J Great Lakes Res. 18(1):70–90. doi:10.1016/S0380-1330(92)71276-3

Edwards PA, Cunjak RA. 2007. Influence of water temperature and streambed stability on the abundance and distribution of slimy sculpin (*Cottus cognatus*). Environ Biol Fish. 80(1):9–22. doi:10.1007/s10641-006-9102-8

Elrod JH. 1983. Seasonal food of juvenile lake trout in U.S. Waters of Lake Ontario. J Great Lakes Res. 9(3):396–402. doi:10.1016/S0380-1330(83)71911-8

Elrod JH, O'Gorman R. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979–1987. Trans Am Fish Soc. 120(3):

290–302. doi:10.1577/1548-8659(1991)120<0290:DOJLTI>2.3.CO;2

Emery AR. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J Fish Res Bd Can. 30(6):761–774. doi:10.1139/f73-131

Eshenroder RL, Lantry BF. 2012. Recent changes in successional state of the deep-water fish communities of lakes Michigan, Huron, and Ontario and management implications. In: Taylor WW, Lynch AJ, Leonard NJ, editors. Great Lakes Fisheries policy and management: a binational perspective. 2nd ed. East Lansing (MI): Michigan State University Press. p. 137–165.

Euclide PT, Flores NM, Wargo MJ, Kilpatrick CW, Marsden JE. 2018. Lack of genetic population structure of slimy sculpin in a large, fragmented lake. Ecol Freshw Fish. 27(3):699–709. doi:10.1111/eff.12385

Evans MA, Fahnenstiel G, Scavia D. 2011. Incidental oligotrophication of North American Great Lakes. Environ Sci Technol. 45(8):3297–3303. doi:10.1021/es103892w

Fagan KA, Koops MA, Arts MT, Sutton TM, Kinnunen RE, Muir AM, Power M. 2017. Lake whitefish (*Coregonus clupeaformis*) energy and nutrient partitioning in lakes Michigan, Erie and Superior. J Great Lakes Res. 43(1): 144–154. doi:10.1016/j.jglr.2016.10.007

Fisher SJ, Swanson BL. 1996. Diets of siscowet lake trout from the Apostle Islands region of Lake Superior, 1993. J Great Lakes Res. 22(2):463–468. doi:10.1016/S0380-1330(96)70970-X

Fratt TW, Coble DW, Copes F, Bruesewitz RE. 1997. Diet of burbot in Green Bay and western Lake Michigan with comparison to other waters. J Great Lakes Res. 23(1): 1–10. doi:10.1016/S0380-1330(97)70880-3

French JRP III, Stickel RG, Stockdale BA, Black MG. 2010. A short-term look at potential changes in Lake Michigan slimy sculpin diets. J Great Lakes Res. 36(2):376–379. doi: 10.1016/j.jglr.2010.01.007

Gamble AE, Hrabik TR, Stockwell JD, Yule DL. 2011. Trophic connections in Lake Superior Part I: the offshore fish community. J Great Lakes Res. 37(3):541–549. doi:10.1016/j.jglr.2011.06.003

Gamble AE, Hrabik TR, Yule DL, Stockwell JD. 2011. Trophic connections in Lake Superior Part II: the nearshore fish community. J Great Lakes Res. 37(3):550–560. doi:10.1016/j.jglr.2011.06.008

Geffen AJ, Nash RDM. 1992. The life-history strategy of deepwater sculpin, *Myoxocephalus thompsoni* (Girard), in Lake Michigan: dispersal and settlement patterns during the first year of life. J Fish Biol. 41(sb):101–110. doi:10.1111/j.1095-8649.1992.tb03872.x

Gorman OT, Yule DL, Stockwell JD. 2012. Habitat use by fishes of Lake Superior. I. Diel patterns of habitat use in nearshore and offshore waters of the Apostle Islands region. Aquat Ecosyst Health Manage. 15(3):333–354. doi:10.1080/14634988.2012.715972

Goto A. 1998. Life-history variations in the fluvial sculpin, *Cottus nozawae* (Cottidae), along the course of a small mountain stream. Environ Biol Fish. 52(1/3):203–212. doi:10.1023/A:1007347631573

Goto A, Yokoyama R, Sideleva VG. 2015. Evolutionary diversification in freshwater sculpins (Cottoidea): a review of two major adaptive radiations. Environ Biol Fish. 98(1):307–335. doi:10.1007/s10641-014-0262-7

Gowan C, Young MK, Fausch KD, Riley SC. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can J Fish Aquat Sci. 51(11):2626–2637. doi:10.1139/f94-262

Gray MA, Cunjak RA, Munkittrick KR. 2004. Site fidelity of slimy sculpin (*Cottus cognatus*): insights from stable carbon and nitrogen analysis. Can J Fish Aquat Sci. 61(9): 1717–1722. doi:10.1139/f04-108

Gray MA, Curry RA, Arciszewski TJ, Munkittrick KR, Brasfield SM. 2018. The biology and ecology of slimy sculpin: a recipe for effective environmental monitoring. FACETS. 3(1):103–127. doi:10.1139/facets-2017-0069

Gray MA, Curry RA, Munkittrick KR. 2005. Impacts of nonpoint inputs from potato farming on populations of slimy sculpin (*Cottus cognatus*). Environ Toxicol Chem. 24(9):2291–2298. doi:10.1897/04-615r.1

Grossman GD, McDaniel K, Ratajczak RE. 2002. Demographic characteristics of female mottled sculpin, *Cottus bairdi*, in the Coweeta Creek drainage, North Carolina. Environ Biol Fish. 63(3):299–308. doi:10.1023/A:1014315623637

Hammar J, Bergstrand E, Enderlein O. 1996. Why do juvenile fourhorn sculpin, *Triglopsis quadricornis*, appear in the pelagic habitat at night? *Environ*. Environ Biol Fish. 46(2):185–195. doi:10.1007/BF00005221

Hanson KL, Hershey AE, McDonald ME. 1992. A comparison of slimy sculpin (*Cottus cognatus*) populations in arctic lakes with and without piscivorous predators. Hydrobiologia. 240(1–3):189–201. doi:10.1007/BF00013460

Happel A, Jonas JL, McKenna PR, Rinchard J, He JX, Czesny SJ. 2018. Spatial variability of lake trout diets in Lakes Huron and Michigan revealed by stomach content and fatty acid profiles. Can J Fish Aquat Sci. 75(1): 95–105. doi:10.1139/cjfas-2016-0202

Harvey CJ, Kitchell JF. 2000. A stable isotope evaluation of the structure and spatial heterogeneity of a Lake Superior food web. Can J Fish Aquat Sci. 57(7):1395–1403. doi:10.1139/f00-072

Hendricks S, Anderson EC, Antao T, Bernatchez L, Forester BR, Garner B, Hand BK, Hohenlohe PA, Kardos M, Koop B, et al. 2018. Recent advances in conservation and population genomics data analysis. Evol Appl. 11(8): 1197–1211. doi:10.1111/eva.12659

Heupel MR, Semmens JM, Hobday AJ. 2006. Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Mar Freshwater Res. 57(1):1–13. doi:10.1071/MF05091

Hill J, Grossman GD. 1987. Home range estimates for three North American stream fishes. Copeia. 1987(2):376–380. doi:10.2307/1445773

Hjort J. 1914. Fluctuations in the great fisheries of Northern Europe. Rapports et Procés-Verbaux. 20:1–228.

Hoekstra D, Janssen J. 1985. Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi*, in Lake Michigan. Environ Biol Fish. 12(2):111–117. doi:10.1007/BF00002763

Hoffman JC, Sierszen ME, Cotter AM. 2015. Fish tissue lipid-C:N relationships for correcting δ^{13}C values and estimating lipid content in aquatic food-web studies. Rapid Commun Mass Spectrom. 29(21):2069–2077. doi: 10.1002/rcm.7367

Homola JJ, Ruetz CR III, Kohler SL, Thum RA. 2016. Complex postglacial recolonization inferred from population genetic structure of mottled sculpin *Cottus bairdii* in tributaries of eastern Lake Michigan, U.S.A. J Fish Biol. 89(5):2234–2250. doi:10.1111/jfb.13101

Hondorp DW, Pothoven SA, Brandt SB. 2005. Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. Trans Am Fish Soc. 134(3):588–601. doi:10.1577/T04-107.1

Hondorp DW, Pothoven SA, Brandt SB. 2011. Feeding selectivity of slimy sculpin *Cottus cognatus* and deepwater sculpin *Myoxocephalus thompsonii* in southeast Lake Michigan: implications for species coexistence. J Great Lakes Res. 37(1):165–172. doi:10.1016/j.jglr.2010.11.010

Honeyfield DC, Hinterkopf J, Fitzsimons JD, Tillitt DE, Zajicek JL, Brown SB. 2005. Development of thiamine deficiencies and early mortality syndrome in lake trout by feeding experimental and feral fish diets containing thiaminase using natural diet. J Aquat Anim Health. 17(1):4–12. doi:10.1577/H03-078.1

Houde ED. 1994. Differences between marine and freshwater fish larvae: implications for recruitment. ICES J Mar Sci. 51(1):91–97. doi:10.1006/jmsc.1994.1008

Houghton CJ, Bronte CR, Paddock RW, Janssen J. 2010. Evidence for allochthonous prey delivery to Lake Michigan's Mid-Lake Reef Complex: Are deep reefs analogs to oceanic sea mounts? J Great Lakes Res. 36(4): 666–673. doi:10.1016/j.jglr.2010.07.003

Hudson PL, Savino JF, Bronte CR. 1995. Predator-prey relations and competition for food between age-0 lake trout and slimy sculpins in the Apostle Island region of Lake Superior. J Great Lakes Res. 21:445–457. doi:10.1016/S0380-1330(95)71116-9

Hudy M, Shiflet J. 2009. Movement and recolonization of Potomac sculpin in a Virginia stream. N Am J Fish Manage. 29(1):196–204. doi:10.1577/M07-101.1

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, et al. 2015. Aquatic animal telemetry: a panoramic window into the underwater world. Science. 348(6240): 1255642. doi:10.1126/science.1255642

Istead AE, Yavno S, Fox MG. 2015. Morphological change and phenotypic plasticity in response to water velocity in three species of centrarchidae. Can J Zool. 93(11): 879–888. doi:10.1139/cjz-2015-0096

Ives JT, McMeans BC, McCann KS, Fisk AT, Johnson TB, Bunnell DB, Frank KT, Muir AM. 2019. Food-web structure and ecosystem function in the Laurentian Great Lakes—toward a conceptual model. Freshw Biol. 64(1): 1–23. doi:10.1111/fwb.13203

Jackson AL, Inger R, Parnell AC, Bearhop S. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. J Anim Ecol. 80(3):595–602. doi:10.1111/j.1365-2656.2011.01806.x

Jacobs GR, Madenjian CP, Bunnell DB, Warner DM, Claramunt RM. 2013. Chinook salmon foraging pattern in a changing Lake Michigan. Trans Amer Fish Soc. 142(2):362–372. doi:10.1080/00028487.2012.739981

Janssen J, Brandt SB. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can J Fish Aquat Sci. 37(2):177–184. doi:10.1139/f80-023

Janssen J, Jude DJ. 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J Great Lakes Res. 27(3): 319–328. doi:10.1016/S0380-1330(01)70647-8

Janssen J, Jude DJ, Edsall TA, Paddock RW, Wattrus N, Toneys M, McKee P. 2006. Evidence of lake trout reproduction at Lake Michigan's mid-lake reef complex. J Great Lakes Res. 32(4):749–763. doi:10.3394/0380-1330(2006)32[749:EOLTRA]2.0.CO;2

Johnson L. 1975. Distribution of fish species in Great Bear Lake, Northwest Territories, with reference to zooplankton, benthic invertebrates, and environmental conditions. J Fish Res Bd Can. 32(11):1989–2004. doi:10.1139/f75-235

Johnson TB, Bunnell DB, Knight CT. 2005. A potential new energy pathway in Central Lake Erie: the round goby connection. J Great Lakes Res. 31(suppl 2):238–225. doi:10.1016/S0380-1330(05)70317-8

Johnson TC, Halfman JD, Busch WH, Flood RD. 1984. Effects of bottom currents and fish on sedimentation in a deep-water, lacustrine environment. Geol Soc Am Bull. 95(12):1425–1436. doi:10.1130/0016-7606(1984)95<1425:EOBCAF>2.0.CO;2

Jude DJ, Reider RH, Smith GR. 1992. Establishment of Gobiidae in the Great Lakes basin. Can J Fish Aquat Sci. 49(2):416–421. doi:10.1139/f92-047

Jude DJ, Tesar FJ, Deboe SF, Miller TJ. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. Trans Am Fish Soc. 116(5):677–691. doi:10.1577/1548-8659(1987)116<677:DASOMP>2.0.CO;2

Kao Y, Rogers MW, Bunnell DB. 2018. Evaluating stocking efficiency in an ecosystem undergoing oligotrophication. Ecosystems. 21(4):600–618. doi:10.1007/s10021-017-0173-5

Keeler RA, Breton AR, Peterson DP, Cunjak RA. 2007. Apparent survival and detection estimates for PIT-tagged slimy sculpin in five small New Brunswick streams. Trans Am Fish Soc. 136(1):281–292. doi:10.1577/T05-131.1

Kierl NC, Johnston CE. 2010. Sound production in the pygmy sculpin *Cottus paulus* (Cottidae) during courtship and agonistic behaviours. J Fish Biol. 77(6):1268–1281. doi:10.1111/j.1095-8649.2010.02745.x

Kornis MS, Bunnell DB, Swanson HK, Bronte CR. 2020. Spatiotemporal patterns in trophic niche overlap among five salmonines in Lake Michigan, USA. Can J Fish Aquat Sci. 77(6):1059–1075. doi:10.1139/cjfas-2019-0288

Kornis MS, Mercado-Silva N, Vander Zanden MJ. 2012. Twenty years of invasion: a review of round goby Neogobius melanostomus biology, spread and ecological implications. J Fish Biol. 80(2):235–285. doi:10.1111/j.1095-8649.2011.03157.x

Kornis MS, Sharma S, Vander Zanden MJ. 2013. Invasion success and impact of an invasive fish, round goby, in Great Lakes tributaries. Divers Distrib. 19(2):184–198. doi:10.1111/ddi.12001

Koster WJ. 1936. The life history and ecology of the sculpins (Cottidae) in Central New York. Doctoral dissertation, Cornell University, Ithaca, NY.

Kraft CE, Kitchell JF. 1986. Partitioning of food resources by sculpins in Lake Michigan. Environ Biol Fish. 16(4): 309–316. doi:10.1007/BF00842986

Ladich F. 1989. Sound production by the river bullhead, *Cottus gobio* L. (Cottidae, Teleostei). J Fish Biol. 35(4): 531–538. doi:10.1111/j.1095-8649.1989.tb03004.x

Lamphere BA, Blum MJ. 2012. Genetic estimates of population structure and dispersal in a benthic stream fish. Ecol Freshw Fish. 21(1):75–86. doi:10.1111/j.1600-0633.2011.00525.x

Lane JA, Port CB, Mins CK. 1996. Adult habitat characteristics of Great Lakes fishes. Can J Fish Aquat Sci. 53(S1): 35–44. doi:10.1139/f95-271

Lantry BF, O'Gorman R, Walsh MG, Casselman JM, Hoyle JA, Keir MJ, Lantry JR. 2007. Reappearance of deepwater sculpin in Lake Ontario: resurgence or last gasp of a doomed population? J Great Lakes Res. 33(sp1):34–45. doi:10.3394/0380-1330(2007)33[34:RODSIL]2.0.CO;2

Latzka AW, Hansen GJ, Kornis M, Vander Zanden MJ. 2016. Spatial heterogeneity in invasive species impacts at the landscape scale. Ecosphere. 7(3):e01311. doi:10.1002/ecs2.1311

Lauer TE, Allen PJ, McComish TS. 2004. Changes in mottled sculpin and johnny darter trawl catches after the appearance of round gobies in the Indiana waters of Lake Michigan. Trans Am Fish Soc. 133(1):185–189. doi:10.1577/T02-123

Layman CA. 2007. What can stable isotope ratios reveal about mangroves as fish habitat? Bull Mar Sci. 80: 513–527.

Leonhardt BS. 2018. Evaluating methods to describe dietary patterns of Lake Michigan Salmonids. MSc thesis, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN.

Ludwig GM, Lange EL. 1975. The relationship of length, age, and age-length interaction to the fecundity of the northern mottled sculpin, *Cottus b. bairdi*. Trans Am Fish Soc. 104(1):64–67. doi:10.1577/1548-8659(1975)104<64:TROLAA>2.0.CO;2

Luo MK, Madenjian CP, Diana JS, Kornis MS, Bronte CR. 2019. Shifting diets of lake trout in northeastern Lake Michigan. North Am J Fish Manage. 39(4):793–806. doi:10.1002/nafm.10318

Lyons J. 1987. Distribution, abundance, and mortality of small littoral-zone fishes in Sparkling Lake. Environ Biol Fish. 18(2):93–107. doi:10.1007/BF00002598

Madenjian CP, Bunnell DB. 2008. Depth distribution dynamics of the sculpin community in Lake Michigan. Trans Am Fish Soc. 137(5):1346–1357. doi:10.1577/T07-001.1

Madenjian CP, Bunnell DB, Desorcie TJ, Armenio P, Adams JV. 2018. Status and trends of prey fish populations in Lake Michigan, 2017. In Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys 2017 [online]. http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2 018.pdf.

Madenjian CP, Desorcie TJ, Stedman RM. 1998. Ontogenic and spatial patterns in diet and growth of lake trout in Lake Michigan. Trans Am Fish Soc. 127(2):236–252. doi:10.1577/1548-8659(1998)127<0236:OASPID>2.0.CO;2

Madenjian CP, Fahnenstiel GL, Johengen TH, Nalepa TF, Vanderploeg HA, Fleischer GW, Schneeberger PJ, Benjamin DM, Smith EB, Bence JR, et al. 2002. Dynamics of the Lake Michigan food web, 1970-2000. Can J Fish Aquat Sci. 59(4):736–753. doi:10.1139/f02-044

Madenjian CP, Hondorp DW, Desorcie TJ, Holuszko JD. 2005. Sculpin community dynamics in Lake Michigan. J Great Lakes Res. 31(3):267–276. doi:10.1016/S0380-1330(05)70258-6

Madenjian CP, O'Gorman R, Bunnell DB, Argyle RL, Roseman EF, Warner DM, Stockwell JD, Stapanian MA. 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. North Am J Fish Manage. 28(1): 263–282. doi:10.1577/M07-012.1

Mansfield PJ, Jude DJ, Michaud DT, Brazo DC, Gulvas J. 1983. Distribution and abundance of larval burbot and deepwater sculpin in Lake Michigan. Trans Am Fish Soc. 112(2A):162–172. doi:10.1577/1548-8659(1983)112<162:DAAOLB>2.0.CO;2

McCleave JD. 1964. Movement and population of the mottled sculpin (*Cottus biardi* Girard) in a small Montana stream. Copeia. 1964(3):506–513. doi:10.2307/1441514

McDonald ME, Cuker BE, Mozley SC. 1982. Distribution, production, and age structure of slimy sculpin in an arctic lake. Environ Biol Fish. 7(2):171–176. doi:10.1007/BF00001788

McMeans B, McCann K, Tunney T, Fisk A, Muir A, Lester N, Shuter B, Rooney N. 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. Ecol Monogr. 86(1):4–19. doi:10.1890/15-0288.1

Meek MH, Larson WA. 2019. The future is now: Amplicon sequencing and sequence capture usher in the conservation genomics era. Mol Ecol Resour. 19(4):795–803. doi:10.1111/1755-0998.12998

Meunier B, Yavno S, Ahmed S, Corkum LD. 2009. First documentation of spawning and nest guarding in the laboratory by the invasive fish, the round goby (*Neogobius melanostomus*). J Great Lakes Res. 35(4): 608–612. doi:10.1016/j.jglr.2009.08.012

Mills EL, Casselman JM, Dermott R, Fitzsimons JD, Gal G, Holeck KT, Hoyle JA, Johannsson OE, Lantry BF, Makarewicz JC, et al. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Can J Fish Aquat Sci. 60(4):471–490. doi:10.1139/f03-033

Minns CK. 1995. Allometry of home range size in lake and river fishes. Can J Fish Aquat Sci. 52(7):1499–1508. doi:10.1139/f95-144

Mousseau TA, Collins NC. 1987. Polygyny and nest site abundance in the slimy sculpin (*Cottus cognatus*). Can J Zool. 65(11):2827–2829. doi:10.1139/z87-429

Mousseau TA, Collins NC, Cabana G. 1988. A comparative study of sexual selection and reproductive investment in the slimy sculpin, *Cottus cognatus*. OIKOS. 51(2): 156–162. doi:10.2307/3565637

Moyle PB, Light T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biol Cons. 78(1–2): 149–161. doi:10.1016/0006-3207(96)00024-9

Mumby JA, Johnson TB, Stewart TJ, Halfyard EA, Weidel BC, Walsh MG, Lantry JR, Fisk AT. 2018. Feeding ecology and niche overlap of Lake Ontario offshore forage fish assessed with stable isotopes. Can J Fish Aquat Sci. 75(5):759–771. doi:10.1139/cjfas-2016-0150

Mundahl ND, Thomas KN, Mundahl ED. 2012. Selected Habitats of slimy sculpin in coldwater tributaries of the upper Mississippi River in Minnesota. Am Midl Nat. 168(1):144–161. doi:10.1674/0003-0031-168.1.144

Mychek-Londer JG, Bunnell DB, Stott W, Diana JS, French JRP, Chriscinske MA. 2013. Using diets to reveal overlap and egg predation among benthivorous fishes in Lake Michigan. Trans Am Fish Soc. 142(2):492–504. doi:10.1080/00028487.2012.756431

Nalepa TF, Fanslow DL, Lang GA. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from native amphipod *Diporeia* spp. to invasive mussel *Dreissena rostriformis bugensis*. Freshw Biol. 54(3): 466–479. doi:10.1111/j.1365-2427.2008.02123.x

Nalepa TF, Fanslow DL, Pothoven SA, Foley AJ III, Lang GA. 2007. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. J Great Lakes Res. 33(2):421–436. doi:10.3394/0380-1330(2007)33[421:LTIBMP]2.0.CO;2

O'Brien TP, Roseman EF, Kiley CS, Schaeffer JS. 2009. Fall diet and bathymetric distribution of deepwater sculpin (*Myoxocephalus thompsonii*) in Lake Huron. J Great Lakes Res. 35(3):464–472. doi:10.1016/j.jglr.2009.05.006

O'Gorman R. 1983. Distribution and abundance of larval fish in the nearshore waters of western Lake Huron. J Great Lakes Res. 9(1):14–22. doi:10.1016/S0380-1330(83)71867-8

Olson DS, Janssen J. 2017. Early feeding of round goby (*Neogobius melanostomus*) fry. J Great Lakes Res. 43(4): 728–736. doi:10.1016/j.jglr.2017.04.006

O'Malley BP, Dillon RA, Paddock RW, Hansson S, Stockwell JD. 2018. An underwater video system to assess abundance and behavior of epibenthic Mysis. Limnol Oceanogr Methods. 16(12):868–880. doi:10.1002/lom3.10289

O'Shea JM, Lemke AK, Sonnenburg EP, Reynolds RG, Abbott BD. 2014. A 9,000-year-old caribou hunting structure beneath Lake Huron. Proc Natl Acad Sci USA. 111(19):6911–6915. doi:10.1073/pnas.1404404111

O'Shea JM, Meadows GA. 2009. Evidence for early hunters beneath the Great Lakes. Proc Natl Acad Sci USA. 106(25):10120–10123. doi:10.1073/pnas.0902785106

Ostroumov VA. 1992. Interspecific effects of sex pheromones in fish. In: Doty RL, Miller-Schwartz D, editors. Chemical signals in vertebrates. Vol. 6. New York (NY): Plenum Press. p. 371–374.

Owens RW, Bergstedt RA. 1994. Response of slimy sculpins to predation by juvenile lake trout in southern Lake Ontario. Trans Am Fish Soc. 123(1):28–36. doi:10.1577/1548-8659(1994)123<0028:ROSSTP>2.3.CO;2

Owens RW, Dittman DE. 2003. Shifts in the diet of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod Diporeia. Aquat Ecosyst Health Manage. 6(3):311–323. doi:10.1080/14634980301487

Owens RW, Noguchi GE. 1998. Intra-lake variation in maturity, fecundity, and spawning of slimy sculpins (*Cottus cognatus*) in southern Lake Ontario. J Great Lakes Res. 24(2):383–391. doi:10.1016/S0380-1330(98)70829-9

Owens RW, O'Gorman R, Eckert TH, Lantry BF. 2003. The offshore fish community in southern Lake Ontario, 1972–1998. In: Munawar M, editor. The State of Lake Ontario: past, present, and future. Ecovision World Monograph Series. Burlington, ON: Aquatic Ecosystem Health and Management Society. pp. 407–442.

Owens RW, Weber PG. 1995. Predation on *Mysis relicta* by slimy sculpins (*Cottus cognatus*) in southern Lake Ontario. J Fish Res Board Can. 21(2):275–283. doi:10.1016/S0380-1330(95)71037-1

Patten BG. 1971. Spawning and fecundity of seven species of northwest American *Cottus*. Am Midl Nat. 85(2): 493–506. doi:10.2307/2423771

Petrosky CE, Waters TF. 1975. Annual production by the slimy sculpin population in a small Minnesota trout stream. Trans Am Fish Soc. 104(2):237–244. doi:10.1577/1548-8659(1975)104<237:APBTSS>2.0.CO;2

Petty JT, Grossman GD. 2007. Size-dependent territoriality of mottled sculpin in a southern Appalachian stream. Trans Am Fish Soc. 136(6):1750–1761. doi:10.1577/T06-034.1

Pothoven SA, Hondorp DW, Nalepa TF. 2011. Declines in deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia* spp. in lakes Huron and Michigan. Ecol Freshw Fish. 20(1):14–22. doi:10.1111/j.1600-0633.2010.00447.x

Potter RL, Fleischer GW. 1992. Reappearance of spoonhead sculpins (*Cottus ricei*) in Lake Michigan. J Great Lakes Res. 18(4):755–758. doi:10.1016/S0380-1330(92)71334-3

Quist MC, Pegg MA, DeVries DR. 2012. Age and growth. In: Zale AV, Parrish DL, Sutton TM, editors. Fisheries techniques. 3rd ed. Bethesda (MD): American Fisheries Society. p 677–731.

R Core Team. 2020. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. https://www.R-project.org/.

Rawson DS. 1951. Studies of the fish of Great Slave Lake. J Fish Res Bd Can. 8b(4):207–240. doi:10.1139/f50-014

Ray BA, Hrabik TR, Ebener MP, Gorman OT, Schreiner DR, Schram ST, Sitar SP, Mattes WP, Bronte CR. 2007. Diet and prey selection by Lake Superior lake trout during spring, 1986–2001. J Great Lakes Res. 33(1):104–113. doi:10.3394/0380-1330(2007)33[104:DAPSBL]2.0.CO;2

Riley SC, Adams JV. 2010. Long-term trends in habitat use of offshore demersal fishes in western Lake Huron suggest large-scale ecosystem change. Trans Am Fish Soc. 139(5):1322–1334. doi:10.1577/T09-090.1

Riley SC, Roseman EF, Nichols SJ, O'Brien TP, Kiley CS, Schaeffer JS. 2008. Deepwater demersal fish community collapse in Lake Huron. Trans Am Fish Soc. 137(6): 1879–1890. doi:10.1577/T07-141.1

Riley SC, Hondorp DW, Roseman EF, Chriscinski MA, Phillips K. 2019. Status and trends of the Lake Huron offshore demersal fish community, 1976–2018. Ann Arbor (MI): U.S. Geological Survey, Great Lakes Science Center.

Robinson BW, Parsons KJ. 2002. Changing times, spaces, and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. Can J Fish Aquat Sci. 59(11):1819–1833. doi:10.1139/f02-144

Roseman EF. 2014. Diet and habitat use by age-0 deepwater sculpins in northern Lake Huron, Michigan and the Detroit River. J Great Lakes Res. 40:110–117. doi:10.1016/j.jglr.2013.07.004

Roseman EF, Jude DJ, Raths MK, Coon TG, Taylor WW. 1998. Occurrence of the deepwater sculpin (*Myoxocephalus thompsoni*) in western Lake Erie. J Great Lakes Res. 24(2): 479–483. doi:10.1016/S0380-1330(98)70838-X

Roseman EF, O'Brien TP. 2013. Spatial distribution of pelagic fish larvae in the northern main basin of Lake Huron. Aquat Ecosyst Health Manage. 16(3):311–321. doi:10.1080/14634988.2013.824348

Roseman EF, Riley SC. 2009. Biomass of deepwater demersal forage fishes in Lake Huron, 1994-2007: Implications for offshore predators. Aquat Ecosyst Health Manage. 12(1):29–36. doi:10.1080/14634980802711786

Roseman EF, Schaeffer JS, Bright E, Fielder DG. 2014. Angler-caught piscivore diets reflect fish community changes in Lake Huron. Trans Am Fish Soc. 143(6): 1419–1433. doi:10.1080/00028487.2014.945659

Roseman EF, Taylor WW, Hayes DB, Jones AL, Francis JT. 2006. Predation on walleye eggs by fish on reefs in western Lake Erie. J Great Lakes Res. 32(3):415–423. doi:10.3394/0380-1330(2006)32[415:POWEBF]2.0.CO;2

Rosen DA, Trites AW. 2000. Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. Can J Zool. 78(7):1243–1250. doi:10.1139/z00-060

Rosinski CL, Vinson MR, Yule DL. 2020. Niche Partitioning among native ciscoes and nonnative rainbow smelt in Lake Superior. Trans Am Fish Soc. 149(2):184–203. doi:10.1002/tafs.10219

Rottiers DV. 1965. Some aspects of the life history of *Cottus cognatus* in Lake Michigan. Doctoral dissertation, University of Michigan, Ann Arbor, MI.

Ruetz CR III, Earl BM, Kohler SL. 2006. Evaluating passive integrated transponder tags for marking mottled sculpins: effects on growth and mortality. Trans Am Fish Soc. 135(6):1456–1461. doi:10.1577/T05-295.1

Ruzycki JR, Wurtsbaugh WA, Lay C. 1998. Reproductive ecology and early life history of a lacustrine sculpin, *Cottus extensus* (Teleostei, Cottidae). Environ Biol Fish. 53(2):117–127. doi:10.1023/A:1007436502285

Schaeffer JS, Bowen A, Thomas M, French JRP, Curtis GL. 2005. Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in Western Lake Huron, USA. J Great Lakes Res. 31(4):414–425. doi:10.1016/S0380-1330(05)70273-2

Schmetterling DA, Adams SB. 2004. Summer movements within the fish community of a small montane stream. N Am J Fish Manage. 24(4):1163–1172. doi:10.1577/M03-025.1

Scott WB, Crossman EJ. 1973. Freshwater fishes of Canada. Bulletin 184. Fisheries Research Board of Canada, Ottawa.

Secor DH, Dean JM, Laban EH. 1992. Otolith removal and preparation for microstructural examination. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences. 117:19–57.

Selgeby JH. 1988. Comparative biology of the sculpins of Lake Superior. J Great Lakes Res. 14(1):44–51. doi:10.1016/S0380-1330(88)71531-2

Selgeby JH, Hoff M. 1996. Seasonal bathymetric distributions of 16 fishes in Lake Superior. Nat Biol Serv Biol Rep. 7:1958–1975.

Sepulveda-Villet OJ, Stepien CA. 2011. Fine-scale population genetic structure of the yellow perch *Perca flavescens* in Lake Erie. Can J Fish Aquat Sci. 68(8):1435–1453. doi:10.1139/f2011-077

Sheldon TA. 2006. Ecology and evolution of the deepwater sculpin (*Myoxocephalus thompsonii*): conservation of a glacial relict. MS thesis, University of Manitoba, Winnipeg, Canada.

Shetter DS, Hazzard AS. 1939. Species composition by age groups and stability of fish populations in sections of three Michigan trout streams during the summer of 1937. Trans Am Fish Soc. 68(1):281–302. doi:10.1577/1548-8659(1938)68[281:SCBAGA]2.0.CO;2

Sitar S, Goetz F, Jasonowicz A, Seider M. 2020. Lipid levels and diet compositions in lake charr ecotypes at Isle Royale in northern Lake Superior. J Great Lakes Res. 46(3):569–577. doi:10.1016/j.jglr.2020.03.001

Smith GR. 1981. Late cenozoic freshwater fishes of North America. Annu Rev Ecol Syst. 12(1):163–193. doi:10.1146/annurev.es.12.110181.001115

Smith SH. 1968. Species succession and fishery exploitation in the Great Lakes. J Fish Res Bd Can. 25(4):667–693. doi:10.1139/f68-063

Smith SH. 1970. Species interactions of the alewife in the Great Lakes. Trans Am Fish Soc. 99(4):754–765. doi:10.1577/1548-8659(1970)99<754:SIOTAI>2.0.CO;2

Smith SH. 1972. Factors of ecologic succession in oligotrophic fish communities of the Laurentian Great Lakes. J Fish Res Bd Can. 29(6):717–730. doi:10.1139/f72-117

Spangler GR, Collins JJ. 1992. Lake Huron fish community structure based on gill-net catches corrected for selectivity and encounter probability. N Am J Fish Manage. 12(3): 585–597. doi:10.1577/1548-8675(1992)012<0585:LHFCSB>2.3.CO;2

Stein DL, Tissot BN, Hixon MA, Barss W. 1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish Bull. 90:540–551.

Stewart DJ, Kitchell JF, Crowder LB. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans Am Fish Soc. 110(6):751–763. doi:10.1577/1548-8659(1981)110<751:FFATSP > 2.0.CO;2

Stewart DJ, Weininger D, Rottiers DV, Edsall TA. 1983. An energetics model for lake trout, Salvelinus namaycush: application to the Lake Michigan population. Can J Fish Aquat Sci. 40(6):681–698. doi:10.1139/f83-091

Stewart TJ, Todd A, LaPan S. 2017. Fish community objectives for Lake Ontario [online]. www.glfc.org/pubs/FisheryMgmtDocs/Fmd17-01.pdf.

Stott W, VanDeHey JA, Justin JA. 2010. Genetic diversity of lake whitefish in lakes Michigan and Huron; sampling, standardization, and research priorities. J Great Lakes Res. 36:59–65. doi:10.1016/j.jglr.2010.01.004

Swain DP, Holtby LB. 1989. Differences in morphology and behavior between juvenile Coho salmon (*Oncorhynchus kisutch*) rearing in a lake and its tributary system. Can J Fish Aquat Sci. 46(8):1406–1414. doi:10.1139/f89-180

Tanner HA, Tody WH. 2002. History of the Great Lakes salmon fishery: a Michigan perspective. In: Lynch KD, Jones ML, Taylor WW, editors. Sustaining North American salmon: perspectives across regions and disciplines. Bethesda (MD): American Fisheries Society. p. 139–154.

Taraborelli AC, Fox MG, Schaner T, Johnson TB. 2009. Density and habitat use by the round goby (*Apollonia melanostoma*) in the Bay of Quinte, Lake Ontario. J Great Lakes Res. 35(2):266–271. doi:10.1016/j.jglr.2008.12.004

U.S. Geological Survey (USGS). 2019. Great Lakes Science Center, 2019. Great Lakes Research Vessel Operations 1958-2018 (ver. 3.0, April). U.S. Geological Survey data release. 10.5066/F75M63X0.

Van Oosten J, Deason HJ. 1938. The food of the lake trout (*Cristivomer namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan. Trans Am Fish Soc. 67(1):155–177. doi:10.1577/1548-8659(1937)67[155:TFOTLT]2.0.CO;2

Van Vliet WH. 1964. An ecological study of *Cottus cognatus* Richardson in Northern Saskatchewan. Doctoral dissertation, University of Saskatchewan, Saskatoon, Canada.

Vanderklift MA, Ponsard S. 2003. Sources of variation in consumer-diet delta 15N enrichment: a meta-analysis. Oecologia. 136(2):169–182. doi:10.1007/s00442-003-1270-z

Vinson MR, Evrard LM, Gorman OT, Yule DL. 2018. Status and trends in the Lake Superior Fish Community, 2017. In Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys 2017 [online]. http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2018.pdf.

Volkel SL. 2019. Evaluation of changes in sculpin populations in the Great Lakes associated with shifts in benthic species composition. MS thesis, Michigan State University, East Lansing, MI.

Walsh MG, Dittman DE, O'Gorman R. 2007. Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. J Great Lakes Res. 33(1):83–92. doi:10.3394/0380-1330(2007)33[83:OAFHOT]2.0.CO;2

Walsh MG, O'Gorman R, Strang T, Edwards WH, Rudstam LG. 2008. Fall diets of alewife, rainbow smelt, and slimy sculpin in the profundal zone of southern Lake Ontario during 1994–2005 with an emphasis on occurrence of *Mysis relicta*. Aquat Ecosyst Health Manage. 11(4):368–376. doi:10.1080/14634980802516128

Wang Y. 2013. Lake Michigan hydrodynamics: mysis and larval fish interactions. Doctoral dissertation, University of Wisconsin-Milwaukee, Milwaukee, WI.

Waples RS, Punt AE, Cope JM. 2008. Integrating genetic data into management of marine resources: how can we do it better? Fish Fish. 9(4):423–449. doi:10.1111/j.1467-2979.2008.00303.x

Weidel BC, Connerton MJ, Walsh MG, Holden JP, Holeck KT, Lantry BE. 2019. Lake Ontario deepwater sculpin recovery: an unexpected outcome of ecosystem change. In: Kreuger C, Taylor WW, Youn S, editors. From catastrophe to recovery: stories of fishery management success. Bethesda (MD): American Fisheries Society. p. 467–484.

Weidel BC, Connerton MJ, Holden JP. 2018. Bottom trawl assessment of Lake Ontario prey fishes. In Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys 2017 [online]. http://www.glfc.org/pubs/lake_committees/common_docs/CompiledReportsfromUSGS2 018.pdf.

Weidel BC, Walsh MG, Connerton MJ, Lantry BF, Lantry JR, Holden JP, Yuille MJ, Hoyle JA. 2017. Deepwater sculpin status and recovery in Lake Ontario. J Great Lakes Res. 43(5):854–862. doi:10.1016/j.jglr.2016.12.011

Wells L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. Fish Bull. 67:1–15.

Wells L. 1980. Food of alewives, yellow perch, spottail shiners, trout-perch, and slimy and fourhorn sculpins in southeastern Lake Michigan. Technical papers of the U.S. Fish and Wildlife Service 12:98.

Wells L, McLain AL. 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fish. Comm. Tech. Rept. No. 20, p. 55.

Wells WG, Johnson TC, Gebhard AE, Paine RTR, Hix LA, Ferrell HN, Engle AN, Perkin JS. 2017. March of the sculpin: measuring and predicting short-term movement of banded sculpin *Cottus carolinae*. Ecol Freshw Fish. 26(2):280–291. doi:10.1111/eff.12274

Welsh AB, Scribner K, Stott W, Walsh MG. 2017. A population on the rise: The origin of deepwater sculpin in Lake Ontario. J Great Lakes Res. 43(5):863–870. doi:10.1016/j.jglr.2017.04.009

Westin L. 1969. The mode of fertilization, parental behavior, and time of egg development in fourhorn sculpin, *Myoxocephalus quadricornis* (L.). Rep Inst Freshw Res Drottningholm. 49:175–182.

Westin L. 1970. Observations on the nest digging of fourhorn sculpin *Myoxocephalus quadricornis* (L.). Rep Inst Freshw Res Drottningholm. 50:211–214.

Whang A. 1992. Hydromechanical communication during reproductive behavior in three species of sculpin (Cottidae). MS thesis, Loyola University of Chicago, Chicago, IL.

Whang A, Janssen J. 1994. Sound production through the substrate during reproduction in the mottled sculpin, Cottus bairdi (Cottidae). Environ Biol Fish. 40(2):141–148. doi:10.1007/BF00002540

Wolfe RK. 2002. Reproductive behavior of the round goby (*Neogobius melanostomus*). MS thesis, Loyola University of Chicago, Chicago, IL.

Zarbock WM. 1952. Life history of the Utah sculpin, *Cottus bairdi semiscaber* (Cope), in Logan River, Utah. Trans Am Fish Soc. 81:249–259. doi:10.1577/1548-8659(1951)81[249:LHOTUS]2.0.CO;2

Zimmerman MS, Krueger CC. 2009. An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. N Am J Fish Manage. 29(5):1352–1371. doi:10.1577/M08-194.1

Appendix A: Stable isotope analysis methods

As part of this review, the trophic overlap of sculpins in Lake Superior was evaluated with a stable isotope analysis. Fish were collected at 56 locations, with a depth range of 5–311 m, distributed throughout Lake Superior from July through September 2011, using bottom trawls fished on-contour from the U.S. Geological Survey (USGS) Research Vessel *Kiyi* (Rosinski et al. 2020). Sites were selected using a spatially balanced random probability design. Total length was measured, and a skinless white muscle tissue sample was collected from behind the dorsal fin and frozen. Thawed skinless white muscle tissue was rinsed in deionized water, dried at 50–60 °C, ground, and 0.5–1.0 mg was packed into tin capsules. Samples were analyzed for δ^{13}C and δ^{15}N at the University of California—Davis Stable Isotope Facility (UCDSIF; http://stableisotopefacility.ucdavis.

edu/) using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The UCDSIF also interspersed samples with several replicates of at least two different laboratory standards and provided final δ^{13}C and δ^{15}N values relative to international standards Vienna PeeDee Belemnite for carbon and atmospheric air for nitrogen.

Data for δ^{13}C and δ^{15}N were used to compare niche breadth and to estimate trophic overlap among species. Values of δ^{13}C were normalized for lipid content following Hoffman et al. (2015). Niche breadth and trophic overlap were assessed using metrics developed by Layman (2007) and were computed using a multivariate Bayesian package in R (Stable Isotope Bayesian Ellipses in R-SIBER; v2.1.3, Jackson et al. 2011; R Core Team 2020). Niche breadth was estimated based on (1) the range in δ^{13}C and δ^{15}N; and (2) the standard ellipse area (SEA) of the bivariate δ^{13}C and δ^{15}N data. Range in δ^{13}C is an indicator of diet diversity, and range in δ^{15}N is an indicator of the range of trophic levels that the population uses (Vanderklift and Ponsard 2003; Layman 2007). A transformed version of SEA, SEAc, which provides an unbiased correction for small sample sizes (see Jackson et al. 2011 for details, functions groupMetricsML, plotSiberObject), was used in the analyses to determine the degree of trophic overlap among species. Percent overlap between ellipses was calculated using the maxLikOverlap function.