1   A synthesis of the biology and ecology of sculpin species in the Laurentian Great Lakes and implications

2   for the adaptive capacity of the benthic ecosystem

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37   **Abstract**

38   The Laurentian Great Lakes have experienced recent ecosystem changes that could lead to reductions in

39   adaptive capacity and ultimately a loss of biodiversity and production throughout the food web. Observed

40   changes in Great Lakes benthic communities include declines of native species and widespread success of

41   invasive species like dreissenid mussels in all but Lake Superior. Understanding the ecology of native

42   benthic deepwater preyfish and the reasons for their declines is important for predicting future losses in

43   adaptive capacity and diversity, as well as managing the Great Lakes ecosystem to avoid such losses.

44   Native sculpin species (*Cottus bairdii*, *C. cognatus*, *C. ricei*, *Myoxocephalus thompsonii*) historically

45   were among the most abundant of the Great Lakes native deepwater benthic preyfish community and are

46   an important link between offshore benthic and pelagic food webs. With one exception, these species

47   have declined in abundance throughout the Great Lakes in recent years, but relatively little is known

48   about their biology and ecology. This review synthesizes the available knowledge for the Great Lakes

49   sculpin species and provides suggestions for future research efforts, which include understanding

50   reproductive ecology and spawning behavior, connectivity and dispersal of populations, early life history,

51   and influences of interactions with native and non-native species.

Introduction

52 **Introduction**

53   Recent ecosystem changes in the Laurentian Great Lakes of North America (herein, Great Lakes)

54 have generated concerns about the potential for reductions in adaptive capacity of the ecosystem, which

55 ultimately could lead to loss of biodiversity and production throughout the food web (McMeans et al.,

56 2016; Ives et al., 2019). These changes, which include invasions by Ponto-Caspian dreissenid mussels

57 (*Dreissena polymorpha* and *D. bugensis*) and round goby (*Neogobius melanostomus*), loss of invertebrate

58 species like *Diporeia* spp. (hereafter, *Diporeia*), and declines in abundance of native benthic fishes, have

59 particularly affected the deepwater benthos of the Great Lakes (Bunnell et al., 2014). Much of the

60 profundal habitat of the Great Lakes lacks strong physicochemical gradients and has a low diversity of

61 native species, which makes this environment especially susceptible to functional changes (Moyle and

62 Light, 1996; Nalepa et al., 2009), though constraints related to low water temperature, low light, and

63 limited production could reduce susceptibility to some extent. The decline of native benthic fishes and the

64 increasing dominance of this habitat by dreissenid mussels and round goby could lead to an "energetic

65 bottleneck" that would affect predator production at higher trophic levels and potentially weaken

66 connections among habitats, all of which will reduce the adaptive capacity of the ecosystem (Blouzdis et

67 al., 2013; Johnson et al., 2005; Ives et al., 2019).

68   Observed changes in Great Lakes benthic communities have included declines or losses of native

69 species, like *Diporeia*, and the widespread success of invasive species like dreissenid mussels in all but

70 Lake Superior (Nalepa et al., 2009). The round goby has been implicated in the decline of mottled sculpin

71 (*Cottus bairdii*; Janssen and Jude, 2001; Lauer et al., 2004), a nearshore benthic species, in Lake

72 Michigan, and is suspected in the declines of other benthic fishes in deeper environments (Riley et al.,

73 2008; Bergstrom and Mensinger, 2009). These invasive species, which are replacing native species within

74 the deepwater benthic food web, may be of less energetic value than native forage (Fagan et al., 2017;

75 Rosen and Trites, 2000; Ives et al., 2019) and could lead to other changes to the benthic community (e.g.,

76 alteration in reproductive ecology [Honeyfield et al., 2005] and energy pathways [Mills et al., 2003;

77 Johnson et al., 2005]), ultimately resulting in a decline in adaptive capacity (Ives et al., 2019). This loss of

78 native benthic diversity by replacement with invasive species has implications for food web dynamics,

79 conservation, and increased sequestration of energy (Nalepa et al., 2009) in the benthic environment, but

80 it has received much less attention than the losses of pelagic diversity in the Great Lakes.

81   Historically, the native deepwater fish guild of the Great Lakes was comprised of predators like

82 lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), bentho-pelagic Coregonines (*Coregonus* spp.),

83 as well as a suite of benthic forage fishes, including deepwater sculpin (*Myoxocephalus thompsonii*),

84 slimy sculpin (*Cottus cognatus*), spoonhead sculpin (*C. ricei*), and ninespine stickleback (*Pungitius*

85 *pungitius*), among others (Argyle, 1982; Riley et al., 2008; Spangler and Collins, 1992). Many species

86 were reduced or lost during the middle of the 20th century because of overfishing, the invasion of non-

87 native species, and/or eutrophication (Smith, 1968, 1972). More recently, the deepwater native fish guild

88 in the Great Lakes has further declined in Lakes Huron, Michigan, and Superior (Bunnell et al., 2014;

89 Bunnell et al., 2019; Riley et al., 2019; Vinson et al., 2018), with some species declining in Lake Ontario

90 (Weidel et al., 2018). These changes in the native benthic deepwater fish guild have coincided with

91 invasions of dreissenids and round goby, declines in *Diporeia*, oligotrophication related to dreissenids

92 (Riley et al., 2008; Riley and Adams, 2010; Evans et al. 2011), and increased consumptive demand by

93 predators like lake trout (Bronte et al., 2003; Bunnell et al., 2014). In addition to declines in abundance,

94 the energy density of some species, including deepwater sculpin, has decreased with the loss of *Diporeia*

95 (Pothoven et al., 2011). Ultimately, these observed declines in native deepwater forage fish abundance

96 and their replacement by energetically inferior non-native species could modify the deepwater food web

97 and resultant transfer of energy among habitats (Ives et al., 2019).

98   Native sculpin species, in particular, have historically been among the most abundant of the Great

99 Lakes native deepwater benthic forage fish community (Bronte et al., 2003; Bunnell et al., 2006; Owens

100 et al., 2003; Roseman and Riley, 2009), and serve as an important link between offshore benthic and

101 pelagic food webs (Fratt et al., 1997; Madenjian et al., 1998). All sculpin species appear to be declining in

102 abundance in the Great Lakes in recent years, with the exception of deepwater sculpin in Lake Ontario

103 (Figure 1; Vinson et al., 2018; Weidel et al., 2018, Bunnell et al., 2019; Riley et al., 2019). Slimy sculpin

104 comprise an important part of juvenile lake trout diets (Stewart et al., 1983; Eck and Wells, 1987;

105 Madenjian et al., 1998; Owens and Bergstedt, 1994), and deepwater sculpin are an important prey item

106 for burbot and juvenile lake trout (Madenjian et al., 2002). In Lake Superior in particular, deepwater

107 sculpin are the primary prey fish in offshore waters (especially for juvenile siscowet lake trout) and

108 declines in deepwater sculpin abundance could negatively affect lake trout and burbot (Gamble et al.,

109 2011a). Spoonhead sculpin have been extirpated in Lakes Erie, Huron, and Ontario (Zimmerman and

110 Krueger, 2009), have a wide distribution but lower abundance than slimy and deepwater sculpins in Lake

111 Superior (Vinson et al., 2018; USGS, 2019), and are rare in Lake Michigan (Wells and McLain, 1973;

112 Potter and Fleischer, 1992; Becker, 1983; Fratt et al., 1997). Despite their importance in the benthic food

113 web and recently observed changes in population dynamics of sculpins, there are still many knowledge

114 gaps in the life history and ecology of these species. Understanding the ecology and population dynamics

115 of this benthic guild would fill a key knowledge gap regarding the adaptive capacity of the Great Lakes

116 (Ives et al., 2019), which is among the most disturbed and rapidly changing ecosystems in the world. This

117 review describes the state of knowledge of sculpins in the Great Lakes and suggests future avenues of

118 study.

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

120 *Paleobiogeography*

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

122 present) and likely reached the region that now contains the Great Lakes by the Miocene (23–5 million

123 years ago) and Pleistocene eras (2.6 million–12,000 years ago) (Smith, 1981). Two genera of sculpins are

124 present in the Great Lakes, *Myoxocephalus* (sometimes still referred to as *Triglopsis*) and *Cottus*. The

125 *Cottus* genus is comprised of a three-species flock (mottled sculpin *C. bairdii*, slimy sculpin *C. cognatus*,

126 and spoonhead sculpin *C. ricei*) that likely speciated rapidly over the course of tens of thousands of years.

127 Deepwater sculpin are the only member of the *Myoxocephalus* genus found in freshwater in North

128 America (Smith, 1981). Great Lakes sculpins are largely isolated by depth preference. Mottled sculpin

129 prefer shallow water (<10 m) and streams; spoonhead and slimy sculpin share similar depth preferences

130   (10–100 m), with spoonhead sculpin preferring slightly shallower water than slimy sculpin; and

131   deepwater sculpin are found 70 m and deeper (Wells, 1968; Scott and Crossman, 1973; Selgeby, 1988;

132   Selgeby and Hoff, 1996) and have been captured at depths of over 400 m in Great Slave Lake, Northwest

133   Territories, Canada (Rawson, 1951).

134   ***Connectivity, Movement, and Dispersal***

135   Compared to more pelagic oriented species, sculpins are poor swimmers and lack functional

136   swim bladders. One exception is the larvae of deepwater sculpin, which are pelagic and disperse by

137   currents until they reach lengths of about 20–25 mm and settle to benthic habitats sometime in the first

138   year of life (Mansfield et al., 1983; O'Gorman, 1983; Geffen and Nash, 1992; Roseman, 2014). Adult

139   fourhorn sculpin (*Myoxocephalus quadricornis*), which are closely related to deepwater sculpin,

140   undertake vertical migrations to the pelagia of a lake in southern Sweden (Lake Vättern; Hammar et al.,

141   1996), but no such behavior has been documented in adult Great Lakes sculpins. Slimy sculpin have

142   occasionally been observed in small numbers in midwater tows in the Great Lakes (e.g., Roseman and

143   O'Brien, 2013), but they are thought to be benthic.

144   Many freshwater sculpins, particularly *Cottus* spp., are relatively sedentary (McCleave, 1964;

145   Hill and Grossman, 1987; Goto, 1998; Gray et al., 2004; Goto et al., 2015), and much of the knowledge

146   of movements of these species comes from studies in stream systems, where dispersal is typically limited

147   (e.g., Bailey 1952; Brown and Downhower 1982). For example, the home range of mottled sculpin in a

148   North Carolina stream was estimated as 12.9 ± 4.7 m (Coweeta Creek; Hill and Grossman, 1987) and as

149   less than about 50 m in a Montana stream (Trout Creek; McCleave, 1964). Petty and Grossman (2007)

150   similarly reported that mottled sculpin in a North Carolina stream (Shope Fork) had home ranges of 0.92–

151   1.02 m^2, but home range size varied annually and with fish size. These movement studies are consistent

152   with significant genetic differentiation that has been observed among populations of mottled sculpin in

153   streams (Lamphere and Blum, 2012; Homola et al., 2016), which would suggest limited dispersal. Slimy

154   sculpin had high site fidelity and exhibited limited movement in a New Brunswick stream (Little River;

155   Gray et al., 2004). Despite small home ranges, 86–100 percent of slimy and mottled sculpins did not

156   remain in approximately 30-m stream sections in northwestern lower Michigan over a season, suggesting

157   a high rate of local movement (Shetter and Hazzard 1939). Although data are mostly lacking in the Great

158   Lakes, δ15N stable isotope ratios of slimy sculpin mirrored ambient δ15N differences among sites in

159   Lake Superior, suggesting that the species is relatively sedentary (Harvey and Kitchell, 2000).

160   Although many studies suggest that most stream-dwelling sculpins are sedentary, some

161   individuals may move relatively large distances (e.g., Schmetterling and Adams, 2004; Breen et al., 2009;

162   Hudy and Shiflet, 2009; Lamphere and Blum, 2012; Clarke et al., 2015; Deboer et al., 2015), and

163   individual fish may switch between sedentary and mobile behaviors (Wells et al., 2017). Some of the

164   evidence for limited movement of sculpins in streams, particularly in earlier studies, may have been

165   related to methods that were not designed to detect long-distance movements (Gowan et al., 1994).

166   Although there has been no study that explicitly evaluates the genetic connectivity of any offshore sculpin

167   species in the Great Lakes, preliminary work in Lake Ontario has shown low genetic differentiation

168   among slimy sculpin sampled about 200 km apart (Euclide et al., 2018), suggesting greater dispersal.

169   Similarly, a study of the genetic origin of the deepwater sculpin resurgence in Lake Ontario found limited

170   genetic structure across the entire basin (Welsh et al., 2017). Deepwater sculpin in the Great Lakes likely

171   exhibit greater dispersal than *Cottus* spp. because of their pelagic larvae (Geffen and Nash, 1992;

172   Roseman, 2014), and this dispersal may be somewhat predictable based on water current patterns.

173   Evidence of larval deepwater sculpin advection derives from their occurrence in nearshore locations

174   distant from presumed deep spawning areas (Geffen and Nash, 1992; Mansfield et al., 1983), and in the

175   western basin of Lake Erie where larvae are presumably moving "downstream" from deep water in Lake

176   Huron (Roseman et al., 1998). Quantitative assessments of the dispersal of adult deepwater sculpin are

177   lacking, and spoonhead sculpin dispersal has not been evaluated with genetics in the Great Lakes. Lentic

178   and lotic populations of freshwater fishes have been shown to differ in terms of their ecology and

179   evolution (Swain and Holtby, 1989; Minns, 1995; Istead et al., 2015), and the recent genetic work on

180   population structure in Lake Champlain (Vermont and New York, USA) and Lake Ontario suggests that

181   slimy sculpin larval dispersal may play a larger role in lentic habitats (Euclide et al., 2018). Based on

182   these observations, more research is needed to better understand larval ecology, dispersal, and movement

183   of Great Lakes sculpins (Euclide et al., 2018).

184   ***Habitat***

185   Habitat partitioning and differential prey selection have long been hypothesized to maintain

186   sculpin species diversity in the Great Lakes by lessening interspecific competition for space and food

187   (Kraft and Kitchell, 1986). Consistent with this hypothesis, bottom trawl surveys in the Great Lakes have

188   demonstrated that abundances of different sculpin species generally peak at different depth ranges (Figure

189   2), although in many cases, the trawl depths likely do not capture the full range of deepwater sculpin (e.g.,

190   observations up to 350 m in Lake Superior, Boyer and Whitlatch, 1989). Slimy and spoonhead sculpin,

191   which mostly only co-occur in Lake Superior, have the greatest overlap. Although modal depths of

192   abundance of each species vary by lake and sometimes season, the pattern of species succession by depth

193   is remarkably consistent in the Great Lakes and in other glacial lakes (e.g., Great Bear Lake, Northwest

194   Territories, Canada) that contain two or more species (Johnson, 1975). Recently, the mean depth of

195   capture of slimy sculpin has increased in Lakes Huron, Michigan, and Ontario (O'Brien et al., 2009; Riley

196   and Adams, 2010; Volkel, 2019), potentially as a response to ecosystem changes like invasion of round

197   goby or the decline of *Diporeia*. Interspecific interactions for habitat and prey selection are discussed in a

198   later section.

199   Stenothermal deepwater sculpin occupy a narrow temperature range (3–7 °C) (Selgeby, 1988;

200   Sheldon, 2006) which may limit distribution to the deeper parts of lakes. Slimy sculpin inhabit warmer

201   water than deepwater sculpin, but they are rarely found in habitats with water temperatures greater than

202   19 °C (Gray et al., 2005; Edwards and Cunjak, 2007), and species interactions may be related to

203   temperature tolerances and the depth distributions of these species. Species-specific depth distributions

204   may also be related to body size; in Lake Superior, smaller individuals of spoonhead, slimy, and

205   deepwater sculpins were more abundant at depths less than 90 m while larger sculpins were more

206   abundant at depths greater than 90 m (Gorman et al., 2012).

207　　　　There have been few quantitative assessments of the importance of physical structure to sculpin

208　　populations in lake environments. Several marine sculpin species, however, have been observed in

209　　association with physical structure (Stein et al., 1992; Auster et al., 1995; Busby et al., 2012). Lane et al.

210　　(1996) reported that all four species of sculpins in the Great Lakes are associated with physical habitat

211　　structure like vegetation, logs, and rocks, but provided no supporting data. Mottled sculpin have been

212　　observed to occupy rocky habitat during the day (Figure 3A) and move to sandy and silty habitat or the

213　　tops of large rocks at night in Lakes Huron (Emery, 1973) and Michigan (Hoekstra and Janssen, 1985). In

214　　addition, mottled sculpin (Bailey, 1952; Zarbock, 1952; Lyons, 1987) and slimy sculpin (Van Vliet, 1964)

215　　preferred rocky or vegetated habitats in streams, and mottled sculpin presence was related to water

216　　temperature and substrate stability (Petty and Grossman, 2007; Edwards and Cunjak, 2007). The choice

217　　of habitat structure by slimy sculpin may change with size; older slimy sculpin have been shown to use

218　　boulders and vegetation, while young-of-the-year individuals used gravel, rubble, and vegetation in

219　　shallower water (Mundahl et al., 2012). Slimy sculpin may also bury themselves in the substrate (Emery,

220　　1973) and therefore may have less need of physical structure for cover. Greater observed catches of

221　　sculpins in nighttime versus daytime trawl tows in Lake Superior may reflect greater reliance on

222　　structural cover or a tendency to bury in sediments during the day (Janssen and Brandt, 1980). In addition,

223　　the Mid-Lake Reef Complex (MLRC) in Lake Michigan, a series of deep reefs that separate the northern

224　　and southern basins of the lake, with abundant rocky habitat for shelter, can harbor seemingly high

225　　densities of slimy sculpin. For example, the densities of slimy sculpin at Sheboygan Reef, the shallowest

226　　(40-m summit) of the MLRC, were estimated to be about 3–8 m^{-2}, using an unmanned electroshocking

227　　submersible (Houghton and Janssen, 2010).

228　　***Reproduction***

229　　*Nesting behavior*

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

231　　for spoonhead sculpin, and much of what is known is based on observations in smaller lakes or rivers.

232　　Males of all four Great Lakes species have been observed to select nesting habitat and guard fertilized

233 eggs against predators, including fanning them with pectoral fins during incubation (Figure 3B; Scott and

234 Crossman, 1973; Westin, 1969). In a laboratory study with fourhorn sculpin, widespread fungal infection

235 of eggs that were not fanned was reported, with only 0.2% hatching success (Westin, 1969).

236 Spoonhead and slimy sculpins were categorized as speleophils by Balon (1975) because they

237 deposit adhesive eggs on a clean undersurface of a rock or ledge (Scott and Crossman, 1973). Previous

238 studies have speculated that spoonhead and slimy sculpins spawn in rocky habitat, given their rarity in

239 bottom trawling collections over soft substrates during the putative spawning season (Selgeby, 1988;

240 Owens and Noguchi, 1998). Egg masses of slimy sculpin that were adhered to logs or plastic or metal

241 objects were collected from Lake Ontario in bottom trawls from 1988–1994 (Owens and Noguchi, 1998)

242 and observed in Lakes Michigan (J. Janssen, University of Wisconsin-Milwaukee, pers. obs.) and

243 Superior (C. Bronte, USFWS, pers. obs.). In a field comparison of nest shelter selection at a small reef in

244 Lake Michigan, mottled sculpin preferred smaller shelters (square tiles 10 and 15 cm on a side) compared

245 to larger shelters (30 cm on a side; Wolfe, 2002).

246 Deepwater sculpin were labeled as lithophils because their adhesive eggs are likely laid in pits

247 dug in gravel or sand (Balon, 1975). Male fourhorn sculpin dug holes for egg incubation in either algal

248 masses or a soft bottom area free of algae in a Swedish lake at depths of 15–20 m (Westin 1970).

249 Observations in depths as great as 350 m in Lake Superior (Boyer and Whitlatch, 1989) and 100 m in

250 Lake Michigan (Bowers et al., 1990) revealed dish-like depressions in the sand, 8–10 cm in diameter and

251 1–2 cm in depth, hypothesized to have been created by deepwater sculpin for egg incubation (Johnson et

252 al., 1984), similar to the behavior observed for fourhorn sculpin.

253 *Reproductive timing*

254 The timing of reproduction also is poorly documented, but likely occurs over a protracted period

255 for most species. Deepwater sculpin spawning is believed to occur in autumn, winter, and into early

256 spring (Becker, 1983; Selgeby, 1988), although ripe eggs were documented in surveyed females as early

257 as August in Lake Ontario (Dymond et al., 1929). Based on larval sampling in Lake Michigan, Geffen

258 and Nash (1992) predicted peak deepwater sculpin hatching in March, with spawning several months

259 prior, given expected slow incubation rates during winter. A measure of monthly gonadosomatic index

260 (GSI, Anderson and Gutreuter, 1983) of female slimy sculpin from trawls conducted in 2015–2017

261 (April–July and October) indicated that GSI peaked in April in Lake Champlain, indicating spring

262 spawning in this lake (S. Volkel, Michigan State University, unpublished data; E. Marsden, University of

263 Vermont, unpublished data). Observations of slimy sculpin in spawning colors in May in Lake Michigan

264 corroborate a hypothesized spring spawn (Figure 3C; J. Janssen, University of Wisconsin-Milwaukee,

265 unpublished data). In Lake Superior, spoonhead and slimy sculpin spawning occurs in spring (May), with

266 spoonhead spawning 2–4 weeks earlier than slimy sculpin (Selgeby, 1988). The most intensive study on

267 Great Lakes sculpin reproduction focused on slimy sculpin in Lake Ontario (1988–1994; Owens and

268 Noguchi, 1998): gravid females were collected from April through October, with most females spent by

269 July. The timing of egg mass collections suggested peak spawning in June (Owens and Noguchi, 1998).

270 *Reproductive communication*

271   In addition to timing and habitat preference, relatively little is known about sculpin

272 communication, particularly in terms of reproduction. Some laboratory and field studies have been

273 conducted to understand how male and female cottids communicate. Sensory channels for communication

274 in Cottidae include olfactory (pheromones), visual, and auditory. Male cottids from Lake Baikal, Russia,

275 responded to female pheromones with head nods and/or shakes (Ostroumov, 1992), which were

276 associated with sound production (Ladich, 1989; Whang, 1992; Whang and Janssen, 1994; J. Janssen,

277 University of Wisconsin-Milwaukee, pers. obs.). The males of the species studied thus far (bullhead

278 [*Cottus gobio*; Ladich, 1989], mottled sculpin [Whang and Janssen, 1994], Pygmy sculpin [*Cottus paulus*;

279 Kierl and Johnston, 2010], Kessler's sculpin [*Leocottus kesslerii*], stone sculpin [*Paracottus knerii*], and

280 Baikal yellowfin [*Cottocomephorus grewingkii*; Whang, 1992]), produce sounds below 500 Hz with

281 peaks lower than 100 Hz. Observations of mottled sculpin via geophone suggest that communication and

282 sensing through the substrate can enable transmission of sounds even in relatively loud riverine systems

283 (Whang and Janssen 1994).

284 **Early life history**

285   Great Lakes sculpin larvae can be either benthic, pelagic, or some combination of both. Mottled

286   sculpin and slimy sculpin appear to be mainly benthic, although *Cottus* larvae have been collected

287   occasionally near the Lake Michigan MLRC (J. Janssen, University of Wisconsin-Milwaukee,

288   unpublished data) and in pelagic nearshore trawls in northern Lake Huron (Roseman and O'Brien, 2013).

289   Goto et al. (2015) reviewed benthic and pelagic strategies in the Cottoidea in an evolutionary and

290   ecological context. *Cottus* is quite variable in habitat use, indicating that understanding of larval sculpin

291   habitats in the Great Lakes is likely incomplete. Bear Lake sculpin (*Cottus extensus*) in Bear Lake,

292   Idaho/Utah, spawned mainly in 1–2 m depth, an area only about 0.004% of the lake, but settled fish were

293   widespread, likely dispersed by the early pelagic stage (Ruzycki et al. 1998). Additionally, Euclide et al.

294   (2018) found little genetic structure in slimy sculpin in Lakes Champlain and Ontario, which suggested

295   that larval movement could be greater than previously thought.

296   Deepwater sculpin are demersal as juveniles and adults, but their larvae are pelagic, making them

297   susceptible to pelagic predators like alewife (*Alosa psuedoharegnus*; Smith, 1970; Wells and McLain,

298   1973; Crowder, 1980), which have been implicated in declines in deepwater sculpin abundance in Lakes

299   Michigan (Madenjian et al., 2005) and Ontario (Mills et al., 2003). The life history stages of deepwater

300   sculpin appear to be spatially segregated; younger and smaller post-larval individuals occupy the

301   shallowest part of the depth range of the species (Geffen and Nash, 1992; Weidel et al., 2017). In Lake

302   Michigan, deepwater sculpin peak hatch occurs in March (consistent with Mansfield et al., 1983), but

303   larvae can be found from November to August (Geffen and Nash, 1992). The larvae, which are larger in

304   nearshore versus offshore areas, metamorphose and become benthic beginning in July at a length of about

305   20 mm (Geffen and Nash, 1992). The early spring peak emergence of larval deepwater sculpin suggests

306   that size segregation may be related to the development of the thermal bar, its transition to thermal wedge,

307   and finally to the full stratification of the deep Great Lakes. The spring thermal bar divides inshore and

308   offshore water as areas of favorable (inshore) and less favorable (offshore) physical conditions for

309   plankton growth (Bolgrien et al., 1995; Brett and Goldman, 1996; Botte and Kay, 2000). Larval

310   deepwater sculpin sampled in Lake Michigan at the nearshore side of the thermal bar (surface temperature

311   > 4 °C, generally about 6 °C) were at greater densities, larger (consistent with Geffen and Nash, 1992),

312   and had faster growth based on daily growth rings compared to those collected on the offshore side

313   (surface temperature < 4 °C; Wang 2013). Geffen and Nash (1992) also indicated that survival from the

314   pelagic to benthic stages for deepwater sculpin was about 0.1–0.4%.

315   *Age and growth*

316   Published age and growth estimates for mottled, slimy, deepwater, and spoonhead sculpin are

317   limited for Great Lakes populations, and sporadic and dated elsewhere. Age estimates have been reported

318   based on whole otoliths for all four species and for sectioned otoliths for slimy and deepwater sculpin, as

319   described below. Whole otolith age estimates were similar to sectioned otolith estimates for slimy sculpin

320   and considerably younger for deepwater sculpin. Direct comparisons between whole and sectioned

321   otoliths have not been conducted for any of these species. Growth rates were greatest to age-1 and then

322   declined with age for all species (Black and Lankester, 1981; Bruch, 1986; Selgeby, 1988; Sheldon,

323   2006).

324   Mottled sculpin maximum age based on whole otoliths ranged from three to seven years for

325   riverine populations (Koster, 1936; Bailey, 1952; Patten, 1971; Ludwig and Lange, 1975; Grossman et

326   al., 2002), but no maximum age estimates were available from lake populations. In Lake Michigan,

327   mottled sculpin <60 mm were designated as age-0 based on sectioned otoliths (Janssen and Jude, 2001).

328   In North Carolina, Grossman et al. (2002) observed that females grew rapidly to age 3, ~50 mm, after

329   which growth slowed.

330   Slimy sculpin maximum age estimates varied from five to eight years (Koster, 1936; Van Vliet,

331   1964; Rottiers, 1965; Petrosky and Waters, 1975; Craig and Wells, 1976; McDonald et al., 1982; Selgeby,

332   1988). For Great Lakes populations, the maximum age was seven years in Lake Michigan (Rottiers, 1965)

333   and five years in Lake Superior (Selgeby, 1988) based on whole otoliths. Based on sectioned otoliths,

334   maximum ages were seven and three years in unregulated and regulated tributaries to Lake Superior,

335   respectively (Bond et al., 2016). Geffen and Nash (1992) estimated slimy sculpin growth rates at 0.12–

336 0.15 mm/day from age-0 to age-1. Selgeby (1988) estimated mean total length at 37 mm at age-1 and 103

337 mm at age-5 for Lake Superior fish. A riverine population of slimy sculpin averaged 37 mm at age-1 and

338 grew thereafter at a decreasing rate of 14 to 6 mm per year (Craig and Wells, 1976).

339   Deepwater sculpin maximum estimated age varied greatly between whole and sectioned otoliths.

340 Whole otolith maximum age estimates ranged from five to nine years (Black and Lankester, 1981; Bruch,

341 1986; Selgeby, 1988). Selgeby (1988) estimated the maximum age at seven years based on whole otoliths

342 for a Lake Superior population. As part of this review, 174 deepwater sculpin otoliths collected from Lake

343 Superior in 2017 were sectioned and aged following the "embed and polish" method (Secor et al., 1992;

344 Quist et al., 2012), and maximum age was estimated to be 17 years (Figure 4). Deepwater sculpin

345 maximum age was estimated at 24 years for individuals from Wollaston Lake, Saskatchewan, Canada

346 (Sheldon, 2006), the only other aging study with sectioned otoliths. Estimated growth of deepwater

347 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

348 per year after age 10 in Lake Superior for fish collected in 2017. Mean total length-at-age was similar

349 between male and female deepwater sculpin (Bruch, 1986).

350   Spoonhead sculpin age estimates were solely available for a Lake Superior population. Selgeby

351 (1988) reported a maximum age of six years based on whole otoliths. His estimated total lengths-at-age

352 were 36, 58, 73, 87, 102, and 112 mm for ages one to six, respectively. These estimates were nearly

353 identical to those reported for slimy sculpin and less than those reported for deepwater sculpin (Selgeby,

354 1988).

355 *Diet*

356   Sculpin diets are generally dominated by benthic invertebrates, with some observed trophic niche

357 overlap among species, based on the prevalence of *Diporeia* and *Mysis* in stomachs (Kraft and Kitchell,

358 1996; Davis et al., 2007; Bunnell et al., 2015) and stable isotopes (Mumby et al., 2018). In contrast,

359 selectivity studies have shown some differences in preference for size and type of food. Slimy sculpin had

360 greater selectivity for *Diporeia* and chironomids, whereas deepwater sculpin had greater selectivity for

361 *Mysis* and selected for larger animals within a given prey taxon than did slimy sculpin (Hondorp et al.,

362 2011). Consistent with the selectivity results, historical diet studies (i.e., prior to the decline of *Diporeia*

363 in Lakes Michigan, Huron, and Ontario) revealed that slimy sculpin generally relied more on *Diporeia*

364 than mysids (Wells, 1980; Brandt, 1986a; Kraft and Kitchell, 1986; Hondorp et al., 2005; Davis et al.,

365 2007), especially at shallower depths (Owens and Weber, 1995). As *Diporeia* has declined in these lakes,

366 slimy sculpin diets have become more diverse and comprised of more *Mysis*, zooplankton, chironomids

367 and oligochaetes (Owens and Dittman, 2003; Walsh et al., 2008; Bunnell et al., 2015). In Lake Superior,

368 where *Diporeia* has not declined, slimy sculpin diets continue to be dominated by *Diporeia* (Selgeby,

369 1988; Gamble et al., 2011a, b).

370   Based on the prey selectivity of deepwater and slimy sculpins (Hondorp et al., 2011), slimy

371 sculpin are predicted to be more vulnerable to the collapse of *Diporeia* than deepwater sculpin. Evidence

372 of this is contradictory, though. For example, there is no indication of long-term declines in body

373 condition in recent decades of slimy and deepwater sculpins in Lake Ontario and deepwater sculpin in

374 Lake Huron (Weidel et al., 2017; Volkel, 2019), which is inconsistent with declines in deepwater sculpin

375 energy density in Lakes Huron and Michigan (Pothoven et al., 2011). In a cross-lake comparison, current

376 (2015–2018) deepwater sculpin body condition in Lakes Huron, Michigan, and Ontario was similar to

377 that observed in Lake Superior, despite differences in abundances of *Diporeia*, dreissenids, and round

378 goby (Volkel, 2019). Slimy sculpin body condition, however, was lower in lakes with more ecological

379 perturbation (Lakes Michigan and Ontario) than in lakes with less ecological perturbation (Lakes

380 Champlain and Superior; Volkel, 2019).

381 *Lake Superior sculpin trophic overlap*

382   As part of this review, the trophic overlap of sculpins in Lake Superior was evaluated with a

383 stable isotope analysis. The methods for this analysis are in Appendix A. One hundred and thirty-one

384 sculpin were analyzed for δ^{13}C and δ^{15}N isotopes; 42 slimy, 21 spoonhead, and 68 deepwater sculpins

385 (Figure 5, Table 1). The overall range in both δ^{13}C and δ^{15}N and standard ellipse area (SEAc) was highest

386 for slimy sculpin and lowest for spoonhead sculpin; this likely reflected the broad spatial and depth

387 distribution of slimy sculpin and the narrower distribution of spoonhead sculpin (Table 1, Figure 2).

388   Standard ellipse area of the bivariate $\delta^{13}C$ and $\delta^{15}N$ data (Figure 5) was highest for slimy sculpin (6.7‰^{2}),

389   intermediate for deepwater sculpin (4.1‰^{2}), and lowest for spoonhead sculpin (1.8‰^{2}). Ellipse areas were

390   likely a reflection of the broader distribution of slimy sculpin and more narrow distribution of spoonhead

391   sculpin. Overlap in the bivariate isotopic ellipse area ranged from 27% for slimy sculpin and deepwater

392   sculpin occurring in spoonhead sculpin trophic space to 100% for spoonhead sculpin occupying slimy

393   sculpin trophic space (Table 1). Coexistence of closely related fish species or morphs is common in

394   northern lakes (Robinson and Parsons 2002) and similar levels of trophic overlap have been observed

395   among other Lake Superior fish, including *Coregonus* species (Rosinski et al. 2020) and lake trout

396   morphs (Sitar et al., 2020). In these fishes, feeding in different habitats or at different times was thought

397   to reduce overall niche overlap (Rosinski et al., 2020). For Great Lakes sculpins, depth segregation

398   appears to be a primary factor in reducing trophic overlap (Figure 2).

399   ***Species interactions***

400   *Interactions among sculpin species*

401   Several studies have provided evidence for competitive interactions among sculpin species for

402   space. In Lake Michigan, as deepwater sculpin increased their depth distribution, so too did slimy sculpin

403   (Madenjian and Bunnell, 2008). In Lake Ontario, following the near extirpation of deepwater sculpin

404   during the 1980s, slimy sculpin increased their density and expanded their range into deeper water, with

405   densities increasing at depths ≥75 m (Owens and Weber, 1995). In the past decade, however, Lake

406   Ontario deepwater sculpin have recovered (Lantry et al., 2007; Weidel et al., 2017, 2019), though the

407   mean depth of capture of slimy sculpin appears to have been increasing in recent years (Volkel, 2019).

408   The distribution of juvenile deepwater sculpin is limited to depths shallower than those occupied by

409   adults (and to the depths of peak slimy sculpin abundance), indicating that the presence of adults inhibits

410   successful recruitment by juvenile conspecifics to demersal habitats (Geffen and Nash, 1992). Likewise,

411   only larger male slimy sculpin are likely to reproduce in areas where nest habitat is limited, potentially

412   affecting the distribution of smaller individuals (Mousseau and Collins, 1987). In addition, unlike

413   observations from trawlable habitat, sculpin species may overlap in rocky habitats, which are preferred at

414   least for spawning and nesting by mottled and slimy sculpin (Scott and Crossman, 1973; Mousseau et al.,

415   1988; Gray et al., 2018), if not during other times of the year as well. In inland Canadian lakes, slimy

416   sculpin move to littoral areas to make use of rocky habitat for spawning (Mousseau et al., 1988).

417   The deep waters of Lakes Superior, Huron, and Michigan have diverse deep reefs that could form

418   a habitat basis for niche partitioning, with slimy sculpin occupying the shallower portions of these

419   structures. Lake Superior has diverse ridges and trenches at its eastern end, with putative deepwater

420   sculpin nests close to a reef base (Boyer and Whitlatch, 1989). There are likely numerous Lake Superior

421   basalt and granite reefs not yet charted that are entirely in deep water. Slimy sculpin were observed to be

422   abundant at East Reef and Sheboygan Reef in the Lake Michigan MLRC (J. Janssen, University of

423   Wisconsin-Milwaukee, personal observation). There are geologically similar carbonate reefs in Lake

424   Huron (Edsall et al., 1992), and recent images of the Alpena-Amberley Ridge, which spans Alpena,

425   Michigan, and Point Clark, Ontario, show a cobble-boulder bottom (O'Shea and Meadows, 2009; O'Shea

426   et al., 2014).

427   Differential prey selection also may play a role in mediating competitive interactions among

428   sculpin species. Consumption of *Diporeia* was significantly greater for slimy sculpin than for deepwater

429   sculpin, and consumption of *Mysis* was greater for deepwater than for slimy sculpin, in areas where slimy

430   and deepwater sculpin overlapped spatially (Kraft and Kitchell 1986). The same study provided evidence

431   that food was a limiting resource, which is a necessary precondition for documenting the existence of

432   resource competition. Size, fecundity, and energy content of female slimy sculpin at various locations in

433   Lake Ontario were inversely related to their density, which further suggests that sculpin in the Great

434   Lakes are food-limited (Owens and Noguchi, 1998). No such evidence exists that bathymetric habitat is

435   limiting. As previously discussed, selectivity of food type and size differs between slimy and deepwater

436   sculpin, as well (Hondorp et al. 2011). Differences in the food habits of slimy and deepwater sculpin have

437   also been observed elsewhere in Lake Michigan (Hondorp et al., 2005) and in Lake Superior (Selgeby,

438   1988). It is not yet clear how the dramatic decline in *Diporeia* abundance has affected these interactions,

439   although some studies have indicated that slimy sculpin now rely more on *Mysis* and chironomids, with

440   *Mysis* dominating the diets in some areas of Lake Michigan (French et al., 2010; Bunnell et al., 2015).

441   *Interactions with native predators*

442   Studies on the effects of predation by native piscivores on sculpin abundance and distribution in

443   the Great Lakes have focused mostly on slimy and deepwater sculpin in Lakes Michigan and Ontario and

444   suggest that the influence of native predators is greater for slimy sculpin than for deepwater sculpin. Lean

445   lake trout and burbot are the primary predators of sculpin in these lakes, but both piscivores appear to

446   consume more slimy sculpin than deepwater sculpin (Elrod, 1983; Elrod and OʹGorman, 1991; Fratt et

447   al., 1997; Madenjian et al., 1998). Siscowet lake trout have been observed consuming mostly deepwater

448   sculpin in Lake Superior (C. Bronte, USFWS, unpublished data) but published studies (Conner et al.,

449   1993; Fisher and Swanson, 1996; Ray et al., 2007) do not differentiate among species found in stomachs.

450   Biomass declines and truncation of the size distribution of slimy sculpin were attributed to lake trout

451   predation in Lake Superior (Bronte et al., 2003). Brandt (1986b) suggested that lake trout predation on

452   slimy sculpin facilitated coexistence between slimy and deepwater sculpin (the keystone predation

453   hypothesis) and that extirpation of deepwater sculpin from Lake Ontario was a predictable consequence

454   of major declines in lake trout abundance during the 1950s. After decades of intensive restocking of lake

455   trout in Lakes Michigan and Ontario, negative correlations between the biomass of lake trout and the

456   abundance, size, and distribution of slimy sculpin have been observed (Christie et al., 1987; Eck and

457   Wells, 1987; Owens and Bergstedt, 1994; Madenjian et al., 2005). Recent diet studies from Lake

458   Michigan have indicated that sculpin species comprise < 5% of the diet by weight of adult lake trout

459   (Leonhardt 2018; Luo et al. 2019), perhaps because of reductions in sculpin biomass combined with

460   increased abundance of other benthic prey like round goby, or because juvenile lake trout (which were not

461   studied) may be more common predators of slimy sculpin (Madenjian et al., 1998). Evidence from inland

462   lakes also is consistent with predators influencing slimy sculpin, as slimy sculpin favored deep waters

463   with high densities of chironomid forage in lakes without lake trout but shifted to rocky littoral areas that

464   offered refuge from lake trout predation but less forage when lake trout were present (Hanson et al.,

465   1992).

466   The predatory effects of native piscivores on deepwater sculpin are less obvious. Deepwater

467   sculpin declined in Lake Michigan in the early 1960s following the collapse of lake trout (Crowder,

468   1980), but they were not extirpated (Bunnell et al., 2019). Predation of non-native alewife on pelagic

469   larval deepwater sculpin is the primary factor believed to regulate abundance of this species (Wells and

470   McLain, 1973; Crowder, 1980; Madenjian et al., 2008). Field-based and modeling studies have shown

471   that when deepwater sculpin are abundant they can be an important component of burbot diets (Van

472   Oosten and Deason, 1938; Fratt et al., 1997; Madenjian et al., 2005). Predation has also been suggested as

473   more important than interspecific competition as a driver of sculpin community dynamics in Lake

474   Michigan, because the models of environmental drivers that best predicted the biomass of slimy and

475   deepwater sculpin did not include abundance of the competing species (e.g., the best model for slimy

476   sculpin did not include biomass of deepwater sculpin as a factor; Madenjian et al., 2005).

477   *Negative interactions with nonindigenous species other than round goby*

478   Given their historic dietary importance and numeric dominance of the native benthic fish

479   community, negative interactions among sculpins and nonindigenous species could threaten the adaptive

480   capacity of the Great Lakes. Despite the many invasions of nonindigenous species in the Great Lakes, few

481   studies have focused on the potential for direct interactions between sculpins and nonindigenous species,

482   and existing studies do not allow for much generalization. Prior to the invasion of round goby (whose

483   potential effects on sculpin are considered in a separate section), the nonindigenous species most likely to

484   interact with sculpin were alewife, rainbow smelt (*Osmerus mordax*), and dreissenid mussels. As

485   previously stated, the pelagic larvae of deepwater sculpin appear to be particularly vulnerable to predation

486   by alewife (Wells and McLain, 1973; Crowder, 1980), and thus, when alewife abundance in Lake

487   Michigan declined during the 1980s, bottom trawl catches of deepwater sculpin significantly increased

488   (Madenjian et al., 2005; Bunnell et al., 2006). In contrast, catches of slimy sculpin, which are presumed to

489   have benthic larvae, did not increase over the same time period. Interestingly, however, the recent

490   resurgence of deepwater sculpin in Lake Ontario has occurred during a time period when alewife

491   abundance has remained relatively high (Weidel et al., 2017). Alewife and rainbow smelt have shifted to

492   deeper water in spring, though, potentially creating a zone where larval deepwater sculpin can avoid

493   predation and successfully transition to benthic habitats (Weidel et al., 2017). Rainbow smelt prey on

494   juvenile and adult slimy sculpin in Lake Ontario (Brandt and Madon, 1986), but the influence of rainbow

495   smelt predation on sculpin abundance or distribution is unclear. The potential for competition for

496   invertebrate prey among alewife, rainbow smelt, and sculpins is relatively low, given the small degree of

497   overlap among the diets of these fish species (Bunnell et al., 2015).

498   Invasive dreissenid mussels could also have negatively affected sculpin species. There was a

499   dramatic decline in abundance of *Diporeia*, an historically important food for sculpins, in Lakes Huron

500   (Nalepa et al., 2007) and Michigan (Nalepa et al., 2009) following the dreissenid mussel invasion, which

501   led to declines in the energy density of deepwater sculpin in both lakes (Pothoven et al., 2011). Diet of

502   slimy sculpin has also shifted toward lower-energy prey in some areas of Lake Michigan following

503   dreissenid invasion and coincident declines in *Diporeia* (French et al., 2010; Bunnell et al., 2015), which

504   could result in changes in energy transfer rates between the benthic and pelagic habitats (Ives et al.,

505   2019). Laboratory experiments have shown that slimy sculpin foraging efficiency is reduced in habitat

506   occupied by dreissenid mussels, but also that sculpin spent more time in zebra mussel habitat than either

507   gravel or bare sand (Beekey et al., 2004). Slimy sculpin have been observed in and around beds of

508   dreissenid mussels in Lake Michigan (Figure 3C). The complex habitat offered by dreissenid mussels is

509   associated with greater density of some prey, but foraging efficiency is reduced because prey are afforded

510   a refuge from predation (Beekey et al., 2004).

511   Deepwater sculpin have shifted their distribution toward deeper waters in Lake Michigan since

512   the late 1980s (Madenjian and Bunnell, 2008; Bunnell et al., 2019), coincident with the dreissenid mussel

513   invasion. Bottom-trawl estimates of deepwater sculpin biomass declined 74% during 2003–2007,

514   concomitant with increases in dreissenid biomass in waters deeper than 50 m, but this was attributed to

515   the effects of dreissenid mussels on sampling gear efficiency and a distributional shift of sculpins to

516   deeper waters not traditionally sampled (Bunnell et al., 2009).

517   Finally, there has been little research to understand how proliferation of dreissenid mussels may

518   have influenced sculpin spawning habitat. Owens and Noguchi (1998) reported four occasions where

519   slimy sculpin egg masses were collected coincident with dreissenid mussels, but never attached to them.

520   *Interactions with round goby*

521   Establishment and proliferation of round goby in the Great Lakes has negatively affected the

522   native sculpin species that overlap spatially with round goby. Round goby were first detected in the Great

523   Lakes in 1990 (Jude et al., 1992) but have since spread throughout all five lakes faster than any previous

524   fish invader (Charlebois et al., 1997) and have reached prolific abundances in all but Lake Superior

525   (Kornis et al., 2012). Like many sculpin species, round goby prefer rocky substrate or other structurally

526   complex habitats (e.g., submerged aquatic vegetation, debris fields; Jude et al., 1992; Cooper and Ruetz,

527   2009; Kornis et al., 2012) and primarily feed on benthic invertebrates. Round goby are also found in

528   greater densities in shallow, littoral areas compared to offshore areas (Johnson et al., 2005; Taraborelli et

529   al., 2009), although they are expanding into ever deeper waters (e.g., Walsh et al., 2007), where density

530   appears to be increasing (USGS, 2019; J. Janssen, University of Wisconsin-Milwaukee, unpublished

531   data).

532   Because of the high abundance of round goby in shallower waters, most research on sculpin

533   interactions with round goby has focused on mottled sculpin. Mottled sculpin rapidly declined in trawl

534   catches following the invasion of round goby in nearshore areas of southern Lake Michigan (Lauer et al.,

535   2004) and were nearly extirpated from Calumet Harbor only four years after the discovery of round goby

536   (Janssen and Jude, 2001). Both studies suggested that spawning interference was the main mechanism of

537   these declines, as mottled sculpin and round goby have a nearly identical reproductive strategy, which

538   involves spawning in cavities on the underside of rocks (Figures 3A and 3B; Scott and Crossman, 1973;

539   Meunier et al., 2009). Although both species exhibit nest guarding behavior, laboratory experiments

540   demonstrated that round goby will attack resident or nest guarding mottled sculpin, occupy the former

541   sculpin nests, displace the sculpin to non-sheltered habitat, and change to spawning colors, which results

542   in the loss of nearly all mottled sculpin eggs (Janssen and Jude, 2001). Round goby also dominated forage

543   resources in laboratory experiments with mottled sculpin, spoonhead sculpin, and logperch (*Percina*

544   *caprodes*; Bergstrom and Mensinger 2009).

545   Expansion of round goby into deeper waters represents a potential threat to other native sculpins,

546   but the nature and basis of goby-sculpin interactions in offshore environments (depths $\geq$ 9 m) is unknown.

547   Slimy and deepwater sculpin are the offshore sculpin species most likely to interact with round goby,

548   based on depth distribution (Figure 2; Selgeby, 1988; Wells, 1968). Spoonhead sculpin has a depth

549   distribution similar to slimy sculpin (Wells, 1968) but is found mostly in Lake Superior, where round

550   goby has not become widely established (Kornis et al., 2012). Among these species, slimy sculpin uses

551   similar spawning habitat as mottled sculpin and round goby (Scott and Crossman, 1973), and thus may be

552   particularly vulnerable to displacement from spawning habitat as round goby spread into deeper waters.

553   Much of the round goby population returns to nearshore waters to spawn during summer, and thus slimy

554   sculpin spawning earlier in their protracted spawning season (April through October) would be most at

555   risk for competition with round goby. In addition, some round goby were recently observed remaining in

556   deeper water (50–100 m) during June and July in Lake Ontario (USGS, 2019); interactions during the

557   slimy sculpin spawning season may become more prevalent if round goby continue to increase their

558   summer use of deeper habitats. Deepwater sculpin are thought to spawn in pits dug out in gravel or sand

559   (Balon, 1975) and thus are less likely to suffer from spawning habitat competition with round goby.

560   The potential for round goby to compete with native sculpins for forage is relatively unstudied as

561   well. As mentioned above, slimy and deepwater sculpin feed primarily on benthic macroinvertebrates like

562   *Mysis*, *Diporeia*, and chironomids (Selgeby, 1988; Hondorp et al., 2011). Slimy sculpin appear to be more

563   generalist in their diets, as they also consume hypolimnetic calanoid copepods and benthic cladocerans

564   (Bunnell et al., 2015). In the offshore waters of Lake Michigan (depths 69–128 m) where round goby,

565   slimy sculpin, and deepwater sculpin can overlap during late fall, winter, and early spring, round goby

566   consume some *Mysis* (Mychek-Londer et al., 2013; Bunnell et al., 2015), which could result in some level

567 of competition with sculpins if food is limited. Forage competition between round goby and sculpins is

568 likely to increase with water depth: during spring in Lake Ontario, the frequency of occurrence of round

569 goby with *Mysis* in their diets increased with depth (6%, 58%, and 97% at depths of 55, 95, and 130 m),

570 while the frequency of occurrence with dreissenid mussels decreased with depth (97%, 90%, and 20% at

571 depths of 55, 95, and 130 m; Walsh et al., 2007). Similarly, in Lake Huron the frequency of occurrence of

572 round goby with *Diporeia* (63.4–75.5 %) and *Mysis* (21.4–57.7%) in their diets was greater at depths of

573 55–73 m than at 27–46 m (0–28.6% for *Diporeia* and 0–7.1% for *Mysis*; Schaeffer et al., 2005). Feeding

574 overlap could be greater in areas with low dreissenid abundance, or for smaller round goby (e.g., < 75

575 mm TL) that are often reported to consume greater proportions of non-dreissenid prey (Janssen and Jude,

576 2001; Barton et al., 2005; Johnson et al., 2005; Kornis et al., 2012). Round goby also have been

577 documented to occasionally consume eggs and small fish in offshore environments (Johnson et al., 2005;

578 Schaeffer et al., 2005; Roseman et al., 2006; Walsh et al., 2007; Mychek-Londer et al., 2013), as have

579 some sculpin species (Chotkowski and Marsden, 1999; Hudson et al., 1995; Mychek-Londer et al., 2013).

580 Importantly, round goby effects on sculpin species could be dependent on round goby density, as has been

581 reported for other nonindigenous species (Latzka et al., 2016). For example, whereas mottled sculpin

582 abundances declined dramatically over four years following round goby invasion in southern Lake

583 Michigan (Janssen and Jude, 2001; Lauer et al., 2004), mottled sculpin catch per unit effort remained

584 unchanged in seven Lake Michigan tributaries over a four-year period despite 11-fold increases in round

585 goby abundance, likely due at least in part to lower density of round goby in tributaries compared to the

586 lake (Kornis et al., 2013).

587 **Future research directions for Great Lakes sculpins**

588 Zimmerman and Krueger (2009) synthesized five questions related to Great Lakes sculpin

589 reestablishment; four of those are still relevant. Their question related to feasibility and risks of deepwater

590 sculpin reintroduction to Lake Ontario is less relevant because that species returned naturally (Weidel et

591 al., 2017). The remaining four questions are relevant and supported herein:

592   1. Is across basin variability in life history driven by local spawning conditions?

593   2. Does larval and fry habitat (benthic vs pelagic) drive dispersal and ultimately population

594   structure, as suggested by Houde (1994)?

595   3. Are population dynamics driven by early life history as compared to juvenile or adult

596   stage dynamics?

597   4. How will non-native species and subsequent food web changes influence sculpin?

598   After completing this review, an updated set of future research directions and questions for

599   sculpin species in the Great Lakes were compiled and are described below, are summarized in Table 2,

600   and build upon the primary questions developed by Zimmerman and Krueger (2009). These research

601   directions will enable a better understanding of sculpin ecology, the effects of ecosystem changes on

602   sculpins and the benthic fish guild as a whole, and ultimately how ecosystem changes will affect the

603   adaptive capacity of the benthic and pelagic food webs of the Great Lakes.

604   ***Genetic diversity and adaptive capacity***

605   Because so little is known about sculpin genetic diversity, population structure, or evolutionary

606   history, there are many fruitful areas of genetic research that would have far-reaching effects on

607   conservation of sculpins in the Great Lakes and elsewhere. While expounding on the advantages of

608   genetic and genomic research are not the purpose of this review (but see: Bernatchez et al., 2017;

609   Hendricks et al., 2018; Meek and Larson, 2019 for reviews), there are three research objectives that could

610   be beneficial. (1) Modern population genomic studies can provide accurate and consistent delineation of

611   conservation units, estimates of effective population size, and evidence of historical events like re-

612   colonization, bottlenecks, or migration (Waples et al., 2008). Although smaller scale studies have been

613   conducted on slimy and deepwater sculpin that suggest genetic structure throughout the Great Lakes may

614   be low (Euclide et al., 2018; Welsh et al., 2017), there has not been a large-scale study focused on

615   describing connectivity of any of the sculpin species across all the Great Lakes. Large-scale population

616   studies of sculpins could help identify populations of conservation concern and determine the origin of

617   recent deepwater sculpin resurgence in Lake Ontario. (2) Although sculpins were never fished, their

618   populations have experienced substantial fluctuations and have likely adapted to the changing community

619 and environment of the Great Lakes. Genomic techniques are already being used to evaluate ciscoes,

620 which have evolved in response to anthropogenic changes (Ackiss et al., 2020; Bronte et al., 2017).

621 Similar techniques could be used to increase the understanding of the effects that climate and community

622 change in the Great Lakes have had on the native benthic community, as well as information about

623 potential changes in adaptive capacity. (3) Finally, although deepwater sculpin are resurging in Lake

624 Ontario, slimy sculpin abundance appears to be declining (Weidel et al., 2018). Genetic diversity and

625 composition of slimy sculpin in Lake Ontario should be evaluated now in preparation for conservation in

626 the future. Slimy sculpin are abundant over a broad range and inhabit both lakes and streams. Evaluating

627 the genetic diversity and make-up of slimy sculpin in Lake Ontario now could be important for later

628 conservation efforts or, if needed, population re-establishment through external source populations.

629 ***Connectivity, movement, and habitat use***

630 More information is needed on specific habitat use by each Great Lakes sculpin species, seasonal,

631 diel, and ontogenetic changes in habitat use, and dispersal among habitats. Such data would be useful in

632 understanding interactions among sculpin species, predation risk, and the potential effects of recent large-

633 scale changes in benthic environments on the fish community.

634 The large spatial extent and extreme depth of benthic habitats in the Great Lakes present

635 enormous research challenges to studying habitat use and dispersal of sculpins and other benthic fishes.

636 Many common techniques like quantifying or manipulating habitat conditions, physically blocking or

637 isolating habitats, introducing or removing fish for experimental purposes, or marking and recapturing

638 individuals, are difficult to apply. In the Great Lakes, most data on sculpins and specimen collections are

639 derived from bottom trawl surveys deployed from large research vessels, which provide relative

640 abundance (Figure 1) and size and age structure information on large spatial scales but are limited to

641 mostly soft substrates. Beam trawls and submersibles have been used on complex rocky substrates to

642 sample slimy sculpin (Hudson et al., 1995; Janssen et al. 2006; Houghton and Janssen, 2010) and could

643 be used to make comparisons across a variety of substrate types under experimental designs that include

644 measures of the physical habitat. More extensive use of beam and well-designed roller trawls, during both

645   day and night surveys, could provide more useful information on sculpin biology at a variety of habitats

646   with more structural complexity.

647   Direct observation of habitat structure, quality, and use on smaller spatial scales can be

648   accomplished by SCUBA divers, but deepwater and slimy sculpin mostly occur in areas beyond the

649   practical working depth range of divers (Figure 2). Data on habitat structure and use could be collected

650   with cameras mounted at stationary positions or deployed by autonomous or remotely operated vehicles

651   (ROVs) (e.g., O'Malley et al., 2018), but trials of this method are needed as the cryptic nature of many

652   sculpin species and low light levels at extreme depths may limit the efficacy of such visual methods. In

653   addition, electroshocking with a suction sampler from an ROV has been successful in capturing several

654   sculpin species, as well as round goby, at deeper depths (Olson and Janssen, 2017).

655   Electronic tracking technologies like acoustic telemetry (Hussey et al., 2015) or passive

656   integrated transponder (PIT) tags (e.g., Ruetz et al., 2006; Keeler et al., 2007) might be practical methods

657   for the study of habitat use and dispersal of adult sculpins in the Great Lakes. These techniques allow the

658   determination and tracking of the locations of tagged fish without handling or recapture. Tag size has

659   historically limited the application of acoustic telemetry to larger fish, but continuing miniaturization of

660   tags (Heupel et al. 2006) may allow their use for studies of sculpins. Passive integrated transponder tags

661   are smaller and have been widely applied to small fishes in streams, but their applicability to large lakes is

662   unclear (e.g., Cookingham and Ruetz, 2008).

663   ***Reproduction and early life history***

664   Limited information exists on spawning and early life history of all sculpin species in the Great

665   Lakes. The exact spawning habitat and associated environmental variables of all four species has not been

666   identified in the Great Lakes. This information is required to make comparisons among lakes and species

667   or to determine the effects of the changing Great Lakes ecosystem on sculpin reproductive biology. In

668   addition, little is known about dispersal pathways and the connectivity of sculpin populations both within

669   and among lakes, although dispersal is largely hypothesized to occur early in life through larval drift

670   (Geffen and Nash, 1992; Euclide et al., 2018).

671   Spawning behavior and basic reproductive ecology of the four sculpin species is also not well

672   understood. Research on nest building, nest guarding, mate selection, egg deposition, incubation periods,

673   and post-hatch larval behavior is required. Knowledge of these aspects of sculpin reproduction can help

674   determine if declines in sculpin abundance are the result of competition for nesting space with non-native

675   species, as observed for mottled sculpin (Janssen and Jude, 2001). Additionally, estimates of fecundity,

676   histological assessment of gonads, and GSI for each species would improve understanding of sculpin

677   spawning. Some GSI data for deepwater sculpin have been collected on Lake Ontario (Weidel et al.,

678   2017), and on Lakes Michigan, Huron, and Champlain for slimy and deepwater sculpin (S. Volkel,

679   Michigan State University, unpublished data; E. Marsden, University of Vermont, pers. comm.).

680   Sampling should be standardized, performed year-round, and expanded to acquire other data necessary to

681   understand the reproductive ecology of Great Lakes sculpins.

682   Understanding of the post-hatch behavior and dispersal of sculpins is also needed. For instance,

683   the role of advection in movement of transforming deepwater sculpin larvae from inshore to offshore

684   habitats has yet to be elucidated. Does the increased growth rate that has been observed nearshore (Geffen

685   and Nash, 1992) suggest "adverse advection" (sensu Hjort, 1914)? Much can be learned by indirectly

686   evaluating dispersal behavior through population genetics. Genetic methods have been used successfully

687   to evaluate the spatial structure and migration of other species in the Great Lakes (e.g. Stott et al., 2010;

688   Sepulveda-Villet and Stepien, 2011) and could help inform sculpin early life dispersal, evaluate migration

689   patterns, and identify possible recolonization routes (Welsh et al., 2017). Understanding how sub-

690   populations of sculpin are connected will inform predictions of sculpin response to habitat loss and

691   population declines, as well as the ability of sculpins to recolonize habitats in the future.

692   Sculpin survival varies from one life stage to the next (Geffen and Nash, 1992), and these survival

693   rates are largely unknown. Variation in survival among sculpin life stages likely relates to their life

694   history strategy, stochasticity in recruitment, and predation. This variation may also be affected by

695   perturbations from invasive species (e.g., dreissenid mussels and round goby) and limited prey

696   availability (e.g., *Diporeia* collapse). The collection of basic information about age, growth, and

697   development of sculpin species from all lakes will enable researchers to not only better understand

698   sculpin development among habitats and species, but to determine how early life history might be

699   affected by changes in the Great Lakes ecosystem.

700   ***Adult life history***

701   Information about the vital rates of adult sculpin species in the Great Lakes would be useful in

702   understanding the changes that these populations have experienced in recent years, concurrent with

703   ecosystem changes. For instance, age and growth estimates for all four sculpin species throughout the

704   Great Lakes are limited and rely, at times, on either whole or sectioned otoliths, which can lead to

705   discrepancies in maximum age estimates. Research to validate the use of otoliths, including a comparison

706   of different methods (e.g., sectioned versus whole), to estimate age would improve understanding and

707   certainty of sculpin population dynamics. In addition, most estimates of age and growth from the Great

708   Lakes come from Lake Superior populations. Given the difference in the ecosystem perturbations in Lake

709   Superior compared to other Great Lakes, efforts to estimate age, growth, and mortality of each species in

710   each lake may indicate how sculpins have been affected by invasive-mediated changes in the benthic

711   community, as well how these vital rates differ among lakes.

712   ***Species interactions***

713   Sculpin community and population dynamics are influenced by numerous factors, including

714   interactions among sculpin species, with native predators, and with nonindigenous species within the food

715   web. Time-series analyses of trawl data have provided some of the strongest evidence of biotic

716   interactions driving sculpin dynamics in specific lakes. Future studies, however, might benefit from cross-

717   lake time series analyses that can take advantage of gradients in abundance of putative key interactors

718   (e.g., lake trout, alewife, round goby, dreissenid mussels) to further test some of the current hypothesized

719   drivers. These drivers include: predator-prey interactions between sculpin species at different life stages

720   and lake trout, burbot, and alewife; effects of dreissenid mussels on spawning and feeding of sculpin

721   species, and larval habitat in the thermal bar; potential effects of changes in the plankton community on

722   sculpins; and phenology of movements and distributions related to interactions between sculpins and non-

723   native species like round goby. Lake Superior provides an ideal field experiment for cross-lake

724   comparisons since all three offshore species (slimy, spoonhead, deepwater) are present, the native

725   piscivore community is largely intact, *Diporeia* remains abundant, and dreissenid mussels and round goby

726   are rare. For example, an estimated 2/3 of the *Diporeia* biomass in Lake Superior, lies in a band between

727   about 30 and 125 m depth, but this band occupies only 25% of the surface area (Auer et al., 2013). This

728   suggests an opportunity for cross-lake comparisons of diet and distribution of slimy sculpin in particular.

729   Such a study would illuminate potential mechanisms driving changes in depth distribution of sculpin. In

730   addition, within-lake comparisons among habitats could provide useful information about interactions

731   between sculpins and nonindigenous species. For instance, the Lake Michigan MLRC provides a unique

732   habitat for comparison with near-shore waters, as both habitats have similar species complexes. One final

733   research need is to examine the vulnerability of slimy sculpin to competition with round goby for food

734   and spawning habitat and determine whether such interactions are mediated by habitat availability, given

735   the negative effects of round goby on mottled sculpin and similarities in spawning habitat between

736   mottled sculpin and slimy sculpin. Ideally, this could include both laboratory and *in situ* experiments.

737   ***Management and conservation implications***

738   Sculpins, as well as ciscoes (*Coregonus artedi* sensu lato), played an important role in the diets of

739   pre-collapse native lake trout populations in the Great Lakes, especially for juvenile lake trout (Van

740   Oosten and Deason, 1938; Dryer et al., 1965), and were far more important that other strictly benthic

741   fishes. With the exception of Lake Superior, lake trout are no longer the principal salmonine predator in

742   the Great Lakes and are secondary to introduced Pacific salmon (*Oncorhynchus* spp.) stocked from the

743   mid-1960s to the present to support and diversify the sport fishery and control invasive alewife (Tanner

744   and Tody, 2002; Stewart et al., 2017). After the collapse of most pelagic and bentho-pelagic ciscoes by

745   the 1960s (Smith, 1972), non-native salmonines and lake trout principally preyed on pelagic non-native

746   alewife and rainbow smelt, and made little use of native benthic fishes (Stewart et al., 1981; Brandt,

747   1986a; Jude et al., 1987; Diana, 1990; Conner et al., 1993). Recent re-oligotrophication (Barbiero et al.,

748   2012), combined with salmonine predation, has resulted in lower biomass of non-native pelagic prey in

749 Lakes Michigan and Huron (Riley et al., 2008; Bunnell et al., 2014; Madenjian et al., 2018). As a result,

750 fisheries for alewife-obligate predators like Chinook salmon (*Oncorhynchus tshawytscha*) have collapsed

751 in Lake Huron and are currently below historical levels in Lake Michigan (Clark et al., 2016). Steelhead

752 (*O. mykiss*), Coho salmon (*O. kisutch*), and Chinook salmon share the same general niche space in Lakes

753 Michigan and Ontario based on stable isotope analysis (Mumby et al., 2018; Kornis et al., 2020), although

754 steelhead appear to forage on terrestrial invertebrates to a greater extent than the other two (Conner et al.,

755 1993; Leonhardt, 2018). In contrast, lake trout and brown trout (*Salmo trutta*) exhibit greater diet

756 flexibility and use other non-pelagic resources. Lake trout consume round goby, especially in spring

757 (Happel et al., 2018; Luo et al., 2019), and can exploit this relatively new benthic high-density energy

758 subsidy, unlike Pacific salmon. Brown trout also consume round goby (Leonhardt, 2018; Kornis et al.,

759 2020). Management agencies annually evaluate and adjust salmonine stocking to maintain predator-prey

760 balance with the residual alewife populations (Claramunt et al., 2019), and have reduced stocking of

761 Chinook salmon and lake trout in Lakes Michigan and Ontario for this very reason. More recently,

762 agencies have implemented greater reductions of lake trout and other species to offset continued or

763 increased stocking of Chinook salmon based on constituent feedback (J. Wesley, Michigan Department of

764 Natural Resources, pers. comm.).

765 So where is the fishery management nexus for sculpins given that lake trout, one of the few

766 salmonines that will consume small benthic forage, is, at least at the moment, being deemphasized in an

767 attempt to conserve alewife for use by Pacific salmon? Given that the trajectory of ecosystem change in

768 Lake Huron is likely to play out in Lake Michigan, the sustainability of Pacific salmon is questionable

769 due to their apparent inability to shift to alternative vertebrate and invertebrate prey (e.g., Jacobs et al.,

770 2013; Roseman et al., 2014). Sculpins convert benthic production into edible fish biomass that can

771 supplement energy from pelagic sources, which has been reduced by the effects of oligotrophication and

772 predation. Sculpins also occupy a wider range of lake depths than round goby, which are typically found

773 in nearshore habitats except during winter and early spring (e.g., Walsh et al., 2007; Kornis et al., 2012),

774 and thus potentially provide an important source of benthic forage otherwise unavailable in some areas. In

775 addition, the density and size composition of zooplankton in Lakes Michigan, Huron and, to some extent,

776 Ontario is now similar to that in Lake Superior (Barberio et al., 2019), and is more appropriate for

777 sustaining native ciscoes than non-native planktivores (Eshenroder and Lantry, 2012). Hence the future

778 salmonine predator profile appears destined to be less diverse and composed mostly of those species, like

779 lake trout, brown trout, and steelhead, that are able to diversify their diets and persist in a forage

780 community largely devoid of alewife (e.g., Conner et al., 1993; Roseman et al., 2014; Kao et al., 2018;

781 Mumby et al., 2018; Kornis et al., 2020). With lower overall primary productivity, the role of sculpins to

782 convert benthic production to consumable fish flesh will likely be paramount to support a predator base

783 that has a more diverse diet portfolio, particularly in deeper areas that have few other forage fish.

784 **Acknowledgments**

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Appendix A Stable Isotope Analysis Methods

1384

1385   As part of this review, the trophic overlap of sculpins in Lake Superior was evaluated with a

1386 stable isotope analysis. Fish were collected at 56 locations, with a depth range of 5–311 m, distributed

1387 throughout Lake Superior from July through September 2011, using bottom trawls fished on-contour

1388 from the U.S. Geological Survey (USGS) Research Vessel *Kiyi* (Rosinski et al. 2020). Sites were selected

1389 using a spatially balanced random probability design. Total length was measured, and a skinless white

1390 muscle tissue sample was collected from behind the dorsal fin and frozen. Thawed skinless white muscle

1391 tissue was rinsed in deionized water, dried at 50–60 °C, ground, and 0.5–1.0 mg was packed into tin

1392 capsules. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the University of California—Davis Stable Isotope

1393 Facility (UCDSIF; http://stableisotopefacility.ucdavis.edu/) using a PDZ Europa ANCA-GSL elemental

1394 analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

1395 The UCDSIF also interspersed samples with several replicates of at least two different laboratory

1396 standards and provided final $\delta^{13}C$ and $\delta^{15}N$ values relative to international standards Vienna PeeDee

1397 Belemnite for carbon and atmospheric air for nitrogen.

1398   Data for $\delta^{13}C$ and $\delta^{15}N$ were used to compare niche breadth and to estimate trophic overlap

1399 among species. Values of $\delta^{13}C$ were normalized for lipid content following Hoffman et al. (2015). Niche

1400 breadth and trophic overlap were assessed using metrics developed by Layman et al. (2007) and were

1401 computed using a multivariate Bayesian package in R (Stable Isotope Bayesian Ellipses in R-SIBER;

1402 v2.1.3, Jackson et al. 2011; R Core Team 2020). Niche breadth was estimated based on 1) the range in

1403 $\delta^{13}C$ and $\delta^{15}N$; and 2) the standard ellipse area (SEA) of the bivariate $\delta^{13}C$ and $\delta^{15}N$ data. Range in $\delta^{13}C$ is

1404 an indicator of diet diversity, and range in $\delta^{15}N$ is an indicator of the range of trophic levels that the

1405 population uses (Vanderklift and Ponsard, 2003; Layman, 2007). A transformed version of SEA, SEAc,

1406 which provides an unbiased correction for small sample sizes (see Jackson et al., 2011 for details,

1407 functions groupMetricsML, plotSiberObject), was used in the analyses to determine the degree of trophic

1408 overlap among species. Percent overlap between ellipses was calculated using the maxLikOverlap

1409 function.

1410   **Table 1**. Collection depths and δ^{13}C and δ^{15}N (‰) isotopic metrics for deepwater, slimy, and spoonhead

1411   sculpin collected in Lake Superior, May-September 2011. Corrected Standard Ellipse Areas are visualized

1412   in Figure 5. Percent trophic overlap pairings are presented as the percent of the ellipse area of the species

1413   listed in the column that is overlapped by the ellipse area of the species listed in the row.

	Deepwater Sculpin	Slimy Sculpin	Spoonhead Sculpin
Sample size	68	42	21
Collection depth (m): mean, range	189, 31-337	115, 5-315	109, 25-220
δ^{15}N: mean, range	9.1, 5.7 — 11.0	8.6, 5.2 — 12.1	8.1, 5.5 — 9.8
δ^{13}C: mean, range	-24.7, -27.4 — -20.8	-24.4, -27.1 — -20.4	-24.3, -25.5 — -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	-

1414

1415   **Table 2** Topics (in bold) and related questions that are relevant for sculpin research in the Great Lakes,
1416   which would provide a better understanding of the adaptive capacity of the native deepwater fish
1417   community, and the Great Lakes in general. Some topics from Zimmerman and Krueger (2009) remain
1418   relevant, and others have been identified in this review.

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 re-establishment 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?

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1420

1421 **Figure 1.** Biomass (kg/ha) of slimy and deepwater sculpin from U.S. Geological Survey trawl surveys in

1422 Lakes Superior, Michigan, Huron, and Ontario, 1970s–2016 (beginning year depends on lake), averaged

1423 across trawl transects. Error bars represent 95% confidence intervals. Note the difference in y-axis ranges

1424 among graphs.

1425 **Figure 2.** Proportional density plots showing depth distributions of spoonhead (Lake Superior only),

1426 slimy, and deepwater sculpins in the Laurentian Great Lakes, based on data collected by U.S. Geological

1427 Survey spring-fall bottom trawls made in 2015–2019 (Lake Ontario, 2015–2018). The horizontal black

1428 line indicates the bathymetric depths sampled in each lake and the vertical black bar indicates the

1429 maximum depth of each lake. Colored vertical lines are density weighted mean depths of capture for each

1430 species.

1431 **Figure 3.** Photos of A) a mottled sculpin in Lake Michigan guarding a nest in 1998, prior to decline in

1432 abundance of this species with the invasion of round goby, B) the mottled sculpin nest being guarded by

1433 the individual shown in panel A, and C) a male slimy sculpin in spawning coloration, Lake Michigan,

1434 15m depth, May, 2019. Sculpins in these photos are approximately 80–100 mm total length, and eggs in

1435 panel B are approximately 2 mm diameter. Photo credit: John Janssen, University of Wisconsin-

1436 Milwaukee.

1437 **Figure 4.** Sectioned otolith from a 122-mm deepwater sculpin collected from Lake Superior on 6 June

1438 2017. Age estimate was 17 years.

1439 **Figure 5.** $\delta^{13}C$ and $\delta^{15}N$ bivariate plots for slimy, spoonhead, and deepwater sculpin collected May-

1440 September 2011 in Lake Superior. Ellipses encompass 40% of the data for each species and are drawn via

1441 a covariance matrix (for details see Jackson et al. 2011).

1442   **Figure 1**

1443
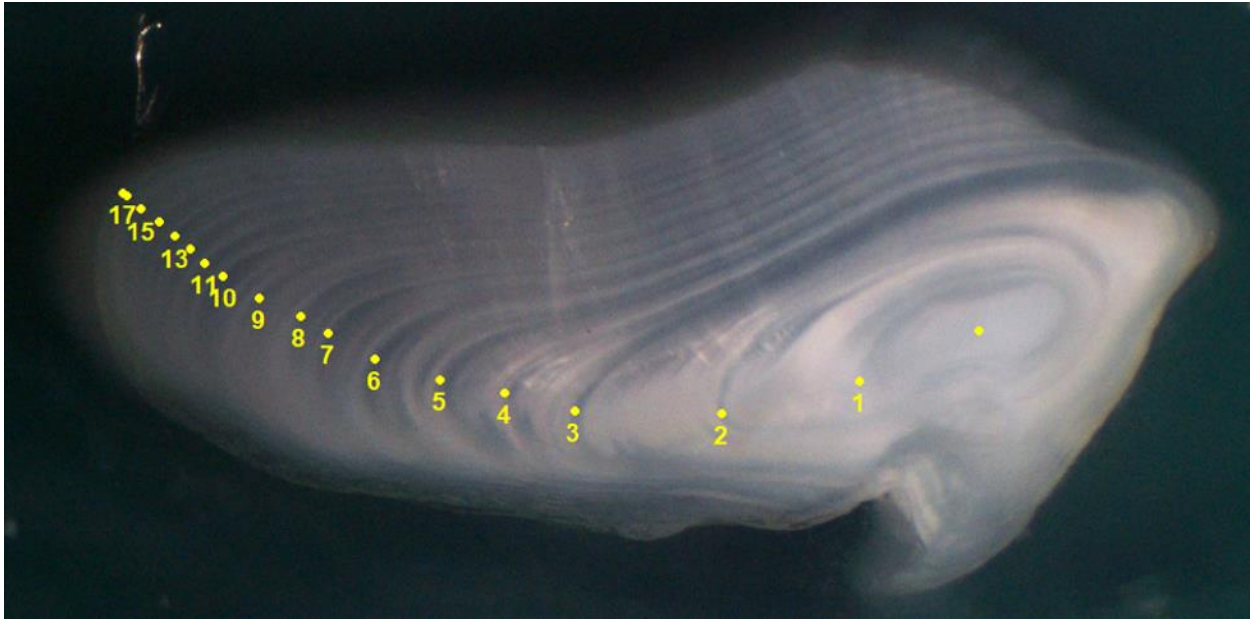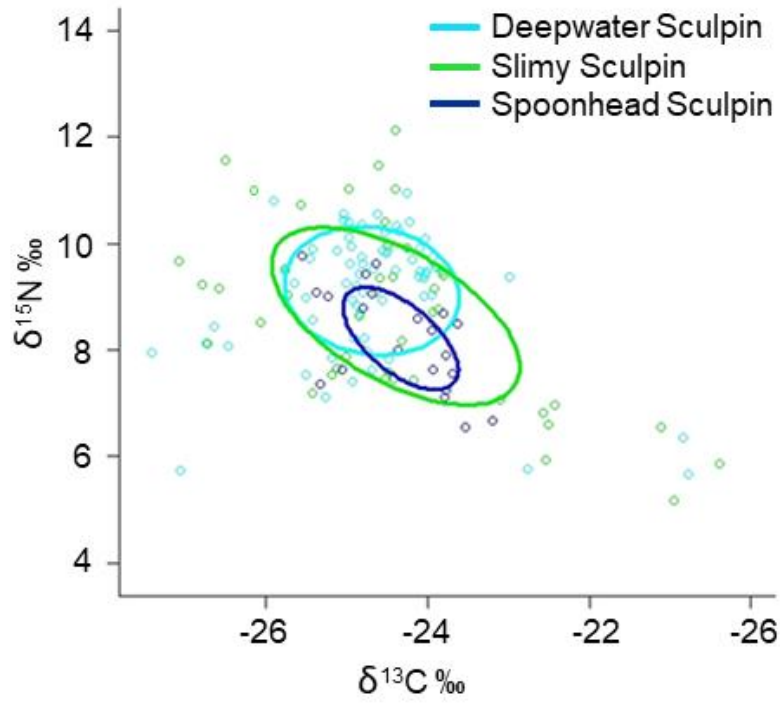
1444   **Figure 2**

1445
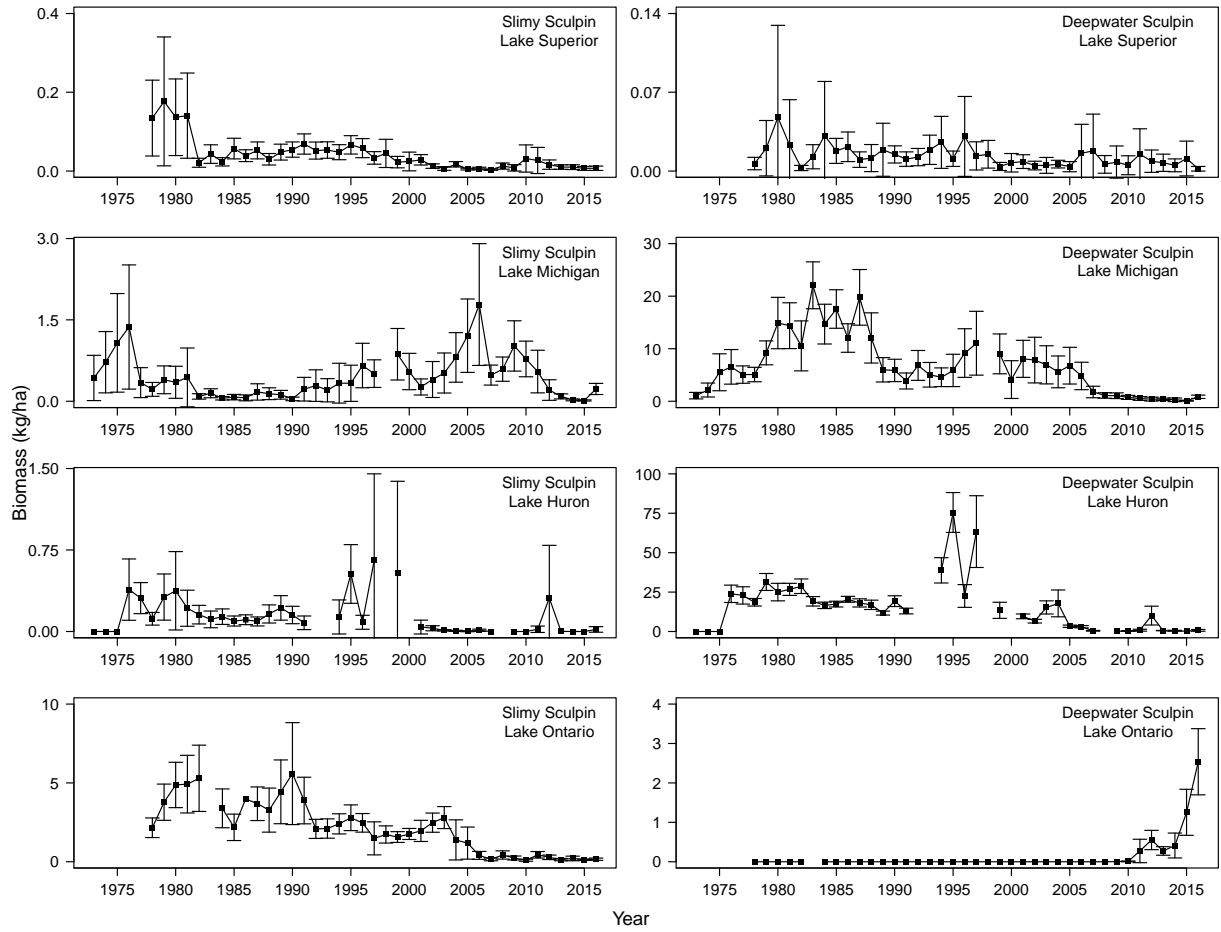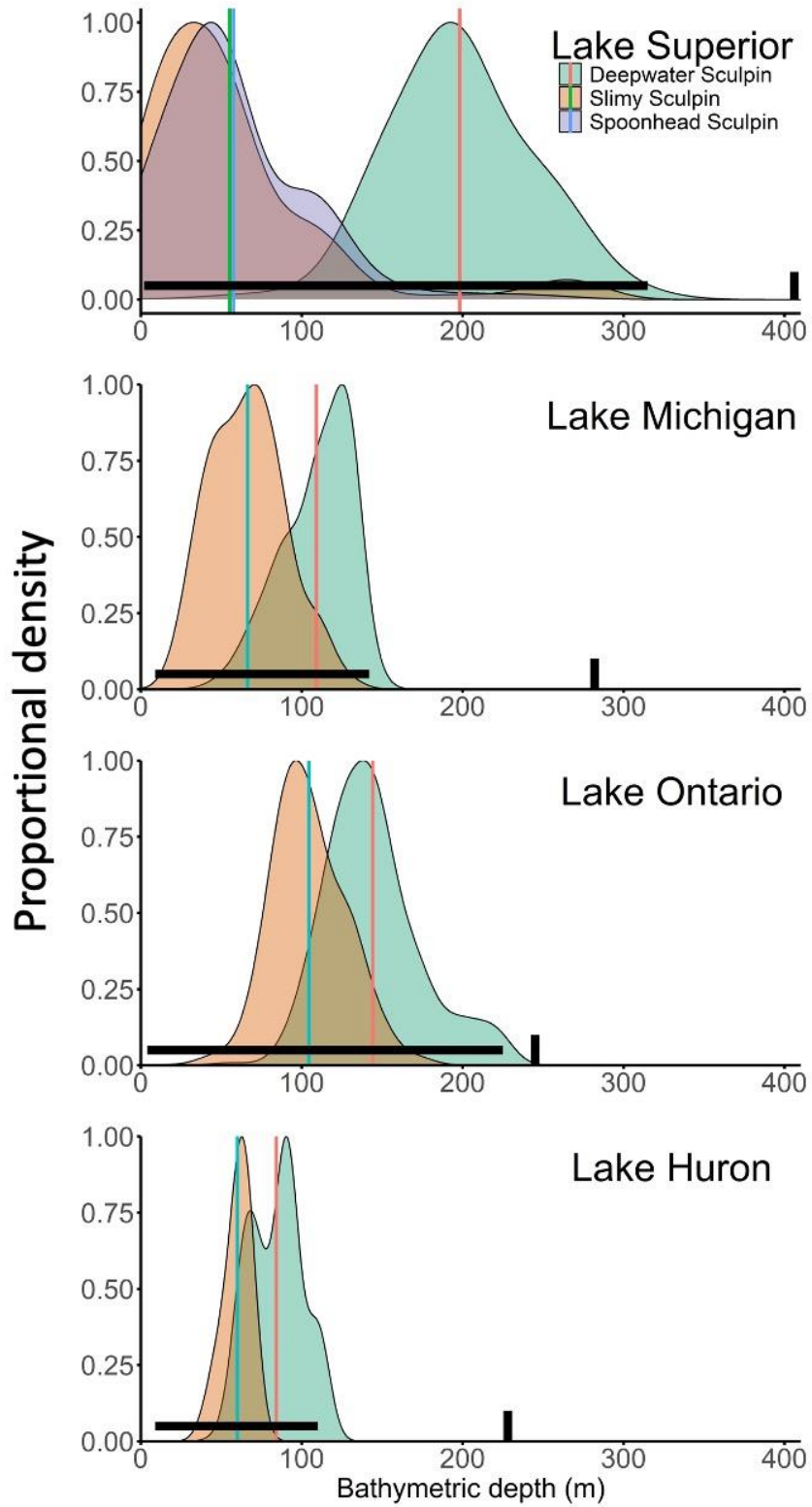
1446   **Figure 3**

1447

1448   **Figure 4**

1449

1450   **Figure 5**

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