

EVALUATION OF CHANGES IN SCULPIN POPULATIONS IN THE GREAT LAKES
ASSOCIATED WITH SHIFTS IN BENTHIC SPECIES COMPOSITION

By

Shea Lynn Volkel

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife—Masters of Science

2019

ABSTRACT

EVALUATION OF CHANGES IN SCULPIN POPULATIONS IN THE GREAT LAKES ASSOCIATED WITH SHIFTS IN BENTHIC SPECIES COMPOSITION

By

Shea Lynn Volkel

In the Great Lakes, slimy sculpins (*Cottus cognatus*) and deepwater sculpins (*Myoxocephalus thompsonii*) were historically abundant native deepwater fishes that served as important prey items for native piscivores (e.g., lake trout, *Salvelinus namaycush*, and burbot, *Lota lota*). However, both of these species have been declining in abundance and biomass recent decades according to USGS trawl surveys. The timing of these declines in sculpin biomass and abundance coincides with several ecological disturbances that have occurred throughout the Great Lakes, including the invasions of dreissenid mussels (zebra, *Dreissena polymorpha*; quagga, *D. bugensis*) and the aggressive round goby (*Neogobius melanostomus*), along with the collapse of *Diporeia* (formerly one of the most important prey items for these sculpin species). In this dissertation, we provide a comprehensive review of the state of knowledge and investigate the effect of these ecological disturbances on slimy and deepwater sculpins in the Great Lakes. We predicted that these ecological disturbances have negatively affected both slimy and deepwater sculpin populations, particularly slimy sculpins, which we could observe through changes in their spatial (depth) distribution patterns (e.g., shifting deeper to avoid round goby) and body condition (e.g., lower body condition associated with ecological disturbance). Our results indicate that slimy sculpins may be more vulnerable to these ecological disturbances than deepwater sculpins, but data limitations prevent us from offering conclusive causal mechanisms for sculpin spatial and body condition patterns. Both our review and analyses implicate that we need to gain a better understanding of sculpins in order to restore these species in this system.

Copyright by
SHEA LYNN VOLKEL
2019

ACKNOWLEDGEMENTS

I would like to express my gratitude to my amazing advisor, Dr. Kelly Robinson, as she has been immensely supportive and instrumental in the development of both my research and my career. It has been a pleasure an honor to be her first graduate student, and I wish her the best with future students. I would also like to extend my thanks to all of my collaborators at the USGS (Dr. Bo Bunnell, Dr. Darryl Hondorp, Dr. Brian Weidel, Dr. Ed Roseman, Dr. Stephen Riley, Dr. Mark Vinson) and the University of Vermont (Dr. Ellen Marsden) for providing an impressive amount of data and valuable input at various times during my degree. I must also thank Bo Bunnell for his service as an ad hoc member my committee. Additionally, I would like to thank my official committee members, Dr. Brian Roth and Dr. Mike Jones, for also providing me feedback on my project. I would also like to thank several of my colleagues within the Quantitative Fisheries Center family for their guidance and assistance. In particular, I would like to thank Dr. Jim Bence and Jean Adams for their guidance with quantitative skills, and I would like to thank several of my peers for aiding me in data collection. Finally, I would like to acknowledge the Great Lakes Fishery Commission and MSU for providing financial support, and the Fisheries and Wildlife Department as a whole for supporting my professional development. Go Spartans!

TABLE OF CONTENTS

LIST OF TABLES.....	vi
LIST OF FIGURES.....	ix
CHAPTER 1. SLIMY SCULPINS AND DEEPWATER SCULPINS IN THE GREAT LAKES: A SYNTHESIS.....	1
Introduction	1
Geographic Distribution, Habitat, and Depth Distribution	2
Life History	4
Ecology and Trophic Interactions	6
Population Dynamics and Ecosystem Changes	7
Conclusion	11
REFERENCES.....	13
CHAPTER 2. SLIMY SCULPIN AND ROUND GOBY SPATIAL OVERLAP IN THE GREAT LAKES FOLLOWING ROUND GOBY INVASION.....	23
Abstract	23
Introduction	24
Methods	26
<i>Trawl Surveys</i>	26
<i>Species Depth Distribution</i>	29
<i>Spatiotemporal (Depth) Overlap Between Species</i>	32
Results	34
<i>Species Depth Distribution</i>	34
<i>Spatiotemporal (Depth) Overlap Between Species</i>	40
Discussion	45
REFERENCES.....	50
CHAPTER 3. SLIMY AND DEEPWATER SCULPIN BODY CONDITION IN THE GREAT LAKES AND LAKE CHAMPLAIN.....	56
Abstract	56
Introduction	57
Methods	59
<i>Trawl Surveys</i>	59
<i>Body Condition</i>	62
Results	64
<i>Long-term Sculpin Body Condition</i>	64
<i>Current Sculpin Body Condition Among Lakes</i>	66
Discussion	68
REFERENCES.....	73

LIST OF TABLES

Table 1.1. Timeline summary of most recent (i.e.,1990s and 2000s) ecosystem changes in the Great Lakes. Years (or year ranges) indicate the onset (and end) of these changes. *For Lake Superior *Diporeia* still persist and dreissenid mussels and round goby are still relatively rare. Also, deepwater sculpin have been recovering in Lake Ontario in recent years.....9

Table 2.1. Time periods, depth ranges, and transects that were consistently sampled (and thus analyzed) from lakes Huron, Michigan, and Ontario.....27

Table 2.2. Mean depth (for entire times series of each species in each lake), R^2 values, and summary of fixed covariates used in models to estimate annual lake-wide mean depth of capture of slimy sculpins, deepwater sculpins, and round gobies for lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017). Models for lakes Huron and Michigan related annual port-specific mean depths of capture to year (fixed), port (random), Julian day (random), and the port and Julian day interaction (random). Models for Lake Ontario related annual port- and season-specific mean depths of capture to year (fixed), port (random), Julian day (random), season of the year (spring, summer, fall; fixed), trawl type (random), and the port and Julian Day interaction (random). Asterisks by p values indicate covariates that were statistically significant. Degrees of freedom for each model varied based on amount of years and seasons that were available for each species in each lake.....35

Table 2.3. Summary of best-fit and other supported models for mean depth of capture of round goby, slimy sculpins, and deepwater sculpins for lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017), considering constant, linear, and changepoint model specifications (where applicable). In cases where change point models were considered, the best fit was selected using AIC_c , and the change point(s) of the best model is (are) given along with the Akaike weight. The number of other models with substantial support ($\Delta AIC_c \leq 2$) along with the year ranges of changepoints are also listed. In cases where no changepoint models were considered, ANOVA was used to determine if the linear regression model fit better than the null model. In all cases below, R^2 (except when the null model was the best-fit model) and the slopes of each line segment (where applicable) are given. Asterisks indicate slopes that were statistically significant. Negative slopes indicate a trend toward shallower water, and positive slopes a trend toward deeper water.....38

Table 2.4. Summary of paired t-test comparisons of seasonal mean depth of capture (last three columns) in Lake Ontario (1978–2017). For each paired t-test comparison of mean depth of capture between seasons of each species, the values listed (from left to right) are the estimated average depth difference (in meters) between the two seasons, the degrees of freedom, the t-statistic, and the Bonferroni-adjusted p-value. Asterisks indicate statistically significant seasonal depth differences.....39

Table 2.5. Mean GIC (for entire times series of each species combination in each lake), R^2 values, and summary of fixed covariates used in models Summary of covariates used to estimate

annual lake-wide depth overlap (GIC) between slimy sculpins and round gobies, and between slimy sculpins and deepwater sculpins lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017). Models for lakes Huron and Michigan related annual port-specific GIC to year, port, Julian day, and the port and Julian day interaction, except for slimy sculpin and round goby depth overlap in Lake Huron where port effects were excluded due to limited data. Models for Lake Ontario related annual port- and season-specific GIC to year, port, Julian day, season of the year (spring, summer, fall), trawl type, and the port and Julian Day interaction. Slope coefficients are only listed for Julian day as this was the only covariate not treated as a factor. Asterisks by p values indicate covariates that were statistically significant. For depth overlap between slimy sculpin and round goby in Lake Huron, the F statistic is listed instead since it was a fixed effect model.....41

Table 2.6. Summary of best-fit and other supported models for depth overlap (GIC) between slimy sculpins and round gobies, and slimy sculpins and deepwater sculpins for lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017), considering constant, linear, and changepoint model specifications (where applicable). In cases where change point models were considered, the best fit was selected using AIC_c, and the change point(s) of the best model is (are) given, along with the Akaike weight. The number of other models with substantial support ($\Delta AIC_c \leq 2$) along with the year ranges of changepoints are also listed. In cases where no changepoint models were considered, ANOVA was used to determine if the linear regression model fit better than the null model. In all cases below, R² (except when the null model was the best-fit model) and the slopes of each line segment (where applicable) are given. Asterisks indicate slopes that were statistically significant. Positive slopes indicate an increase in depth overlap between species, and negative slopes indicate a decrease in depth overlap between species. *For Lake Michigan, there was significant autocorrelation in overlap with between slimy sculpins and deepwater sculpins, and the best fit model was the AR-1 null model.....42

Table 2.7. Summary of paired t-test comparisons of seasonal mean depth of capture (last three columns) in Lake Ontario (2002–2017). For each paired t-test comparison of GIC between slimy sculpins and gobies between seasons, the values listed (from left to right) are the estimated average depth difference (in meters) between the two seasons, the degrees of freedom, the t-statistic, and the Bonferroni-adjusted p-value. Asterisks indicate statistically significant seasonal depth differences. *Paired t-test were not performed for comparing depth overlap between slimy sculpins and deepwater sculpins because season was not a statistically significant predictor (p = 0.263, Table 7) for slimy sculpin and deepwater sculpin depth overlap in Lake Ontario.....44

Table 3.1. Data used for sculpin body condition analyses for each lake.....60

Table 3.2. Logarithmic length-weight relationship models ($\log W_i = \log a + b \log L_i$) tested for long-term analyses of Lake Huron (deepwater sculpin, 1979, 1980, 2002, 2017–2018) and Lake Ontario (slimy sculpin, 1978–1982, 1984–2000, 2005–2018), as well as current (2015–2018 only) logarithmic length-weight relationships for slimy sculpin among lakes Champlain (2015–2018), Michigan (2016–2018), Ontario (2015–2018), and Superior (2017), and deepwater sculpin among lakes Huron (2017–2018), Michigan (2016–2018), Ontario (2015–2018), and

Superior (2017). Models are listed in order from best to worst fit based on AICc. In all models listed (where applicable), year is a fixed effect, and port and lake are random effects. As indicated in parentheses, each covariate had either slope, intercept, or both slope and intercept variation. *Mixed models that failed to converge.....65

LIST OF FIGURES

Figure 2.1. Port locations included in analyses for Lake Michigan (A), Lake Huron (B), and Lake Ontario (C).....28

Figure 2.2. Top row: Annual mean depth of capture in meters and best-fit linear models for round gobies (cross symbols and black uneven dashed lines), slimy sculpins (closed circles and black solid lines), and deepwater sculpins (closed diamonds and black even dashed lines) for each lake (Huron, Michigan, and Ontario) between 1973–2017. Note that vertical axes are inverted (200–0 m) to display trends in terms of bathymetric distribution. Bottom row: Annual mean GIC and best-fit linear models between slimy sculpins and round gobies (cross symbols and black uneven dashed lines), and slimy sculpins and deepwater sculpins (closed diamonds and black even dashed lines) for each lake. Grey vertical lines in all graphs for various ecological changes that occurred in each lake, including A) zebra mussel invasion, B) quagga mussel invasion, C) round goby invasion, and D) *Diporeia* collapse. *Overlap for between sculpin species in Lake Michigan is based on the null model with AR-1 correlation.....37

Figure 3.1. Maps with trawl sites for lakes A) Michigan, B) Huron, C) Ontario, D) Superior, and E) Champlain.....61

Figure 3.2. Mean current slimy sculpin and deepwater sculpin body condition (i.e., relative condition factor, K_n ; 2015–2018) and 95% confidence interval among more disturbed and less disturbed lakes. For slimy sculpin body condition, less disturbed lakes included lakes Champlain and Superior, and more disturbed lakes included lakes Michigan and Ontario. For deepwater sculpin body condition, less disturbed lakes included only Lake Superior, and more disturbed lakes included lakes Huron, Michigan, and Ontario. *Note different lakes included in each graph and different vertical axis scales.....67

CHAPTER 1. SLIMY SCULPINS AND DEEPWATER SCULPINS IN THE GREAT LAKES: A SYNTHESIS

Introduction

Sculpins (cottids) are a highly diverse family of fishes that reside in both freshwater and marine ecosystems and exhibit a vast array of life histories (Kinziger et al. 2005, Adams and Schmetterling 2007). Sculpins are ecologically important food web intermediates (Fratt et al. 1997, Madenjian et al. 1998, Sierszen et al. 2003, O'Brien et al. 2009, Jacobs et al. 2010), abundant prey resources for several vertebrate taxa (Beauchamp 1990, Poe et al. 1991, Birzaks et al. 1998, Hodgens et al. 2004, Madenjian et al. 2005a, Koczaja et al. 2005), and bioindicators of ecosystem health (Maret and MacCoy 2002, Brinkman and Woodling 2005,). In the Great Lakes, four native cottid species occur in benthic habitats (Selgeby 1988, Zimmerman and Krueger 2009): mottled sculpins (*Cottus bairdi*), slimy sculpins (*C. cognatus*), spoonhead sculpins (*C. ricei*), and deepwater sculpins (*Myoxocephalus thompsonii*). Inshore, mottled sculpins have been declining in abundance in Lake Michigan since the late 1990s (Lauer et al. 2004). Offshore, slimy, spoonhead, and deepwater sculpins were historically abundant in the Great Lakes (Bronte et al. 2003, Owens et al. 2003, Bunnell et al. 2006, Roseman and Riley 2009). However, spoonhead sculpins have been extirpated from lakes Huron, Erie, and Ontario (Zimmerman and Krueger 2009), and catch of both slimy and deepwater sculpin in annual trawl surveys has generally declined throughout the Great Lakes since the 1990s (Bunnell et al. 2017, Riley et al. 2017, Vinson et al. 2017).

In light of these declines in sculpin abundance in the Great Lakes, a Great Lakes Fishery Commission (GLFC) Sculpin Workshop was held in June 2017 Ann Arbor to revisit several hypotheses made by Zimmerman and Krueger (2009) in relation to the re-establishment of sculpins in the Laurentian Great Lakes (Volkel and Robinson 2017). During this workshop,

several future areas of research were highlighted as important to aiding in sculpin restoration efforts including genetics, dispersal, early-life history, spawning, interspecific interactions between sculpins and non-native species, age, growth, mortality, and diet (Volkel and Robinson 2017). The purpose of this review is to provide an overview of the current state of knowledge on sculpins in the Great Lakes with regard to their habitat and spatial distribution, life history, and ecology, as well as to provide insight ecological factors (including interspecific interactions) that may be driving the recent declines in in sculpin abundance. This review primarily focuses on slimy and deepwater sculpins as both of these sculpin species are important prey for native predators such (lake trout, *Salvelinus namaycush*, and burbot, *Lota lota*, Owens and Bergstedt 1994, Madenjian et al. 2002, Van Oosten and Deason 1938), and both species are particularly relevant to the GLFC's theme of re-establishing native deepwater fishes.

Geographic Distribution, Habitat, and Depth Distribution

In cold North American freshwater systems, slimy sculpins are widely distributed in lakes and streams, whereas deepwater sculpins are limited to glacial lakes in the northern United States and Canada (Scott and Crossman 1998, Sheldon et al. 2008, Arciszewski et al. 2015). Both slimy and deepwater sculpins are found throughout the Great Lakes, except in Lake Erie, where no viable deepwater sculpin population has been identified because most of Lake Erie is too eutrophic and shallow for deepwater sculpins (Roseman et al. 1998, Lantry et al. 2007). Both sculpin species are adapted for benthic cold-water habitats (Arciszewski et al. 2015) and occur on both soft and rocky substrates (Janssen et al. 2005, Arciszewski et al. 2015). Stable isotope analysis suggests that slimy sculpins have small home ranges (e.g., in Lake Superior, Harvey and Kitchell 2000). However, a Lake Champlain isolation by distance (IBD) study revealed that slimy sculpins are genetically panmictic (i.e., gene flow across a broad geographical range,

Euclide et al. 2017), which indicates that slimy sculpin habitat range might not be as restricted as otherwise suggested. Slimy sculpins prefer low concentrations of dissolved organic carbon, high concentrations of calcium, and relatively neutral pH levels (i.e., 6.8–8.4, Van Vliet 1964, Matuszek et al. 1990), and likely prefer, but do not necessarily require high dissolved oxygen concentrations (Cott et al. 2008, Arciszewski et al. 2015). Conversely, much less is known about deepwater sculpin water chemistry preferences, but they do require high concentrations of dissolved oxygen (COSEWIC 2006).

Depth distribution of sculpins in the Great Lakes seems to differ among species and various life stages, which may, in part, be related to sculpin prey preferences (Owens and Weber 1995, Kraft and Kitchell 1986, Hondorp et al. 2011) and ontogenetic shifts (Geffen and Nash 1992). Adult deepwater sculpins occur in deeper water than adult slimy sculpins in the Great Lakes (Owens and Weber 1995, Kraft and Kitchell 1986, Hondorp et al. 2011). The depth segregation between slimy and deepwater sculpins seems to reflect sculpin prey preferences, or prey preferences reflect depth preferences, as deepwater sculpin prefer opossum shrimp (*Mysis diluviana*) prevalent at deeper depths, whereas slimy sculpins favor *Diporeia* spp. located in shallower depths (Owens and Weber 1995, Kraft and Kitchell 1986, Hondorp et al. 2011). Depth-partitioning across adults of these sculpin species does not appear to be related to water temperature as both species have similar water temperature preferences (Arciszewski et al. 2015). Adult slimy sculpins can survive in water temperatures up to 30°C (Van Vliet 1964), but are most concentrated at colder water temperatures in the Great Lakes (e.g., 4 – 6°C in Lake Michigan, Wells 1968) at depths between 50–90 m (Zimmerman and Krueger 2009). Adult deepwater sculpins tend to occur in water temperatures less than 8°C at depths greater than 70 m in the Great Lakes (Deason 1939, Selgeby 1988, Zimmerman and Krueger 2009). Across life

stages of sculpins, ontogenetic niche shifts may play a role in sculpin depth distribution.

Juveniles are concentrated at shallower depths than adults for both species (i.e., juvenile slimy sculpin at < 60 m in Lake Ontario, Brandt 1986a; juvenile deepwater sculpin 50–90 m in Lake Ontario, Brandt 1986b, 55–75 m in Lake Michigan, Geffen and Nash 1992). Early life stages of slimy sculpins are assumed to be benthic based on collection of slimy sculpin larvae and possibly eggs (though eggs were not identified to the species) from shallow benthic habitats (1.5–15 m) in Lake Michigan (Madenjian and Jude 1985). In southeastern Lake Michigan, deepwater sculpin eggs are benthic and located offshore (Geffen and Nash 1992). Conversely, deepwater sculpin larvae are pelagic and distributed throughout the water column, though larvae are more developed inshore than offshore (Geffen and Nash 1992). Deepwater sculpin larvae prefer temperatures less than 11°C (Mansfield et al. 1983).

Life History

Beyond depth distribution of various sculpin life stages, little is known about the life-history of sculpins in the Great Lakes. For all life stages and both sexes, understanding of sculpin life history and long-term dynamics is hindered by limited sampling at greater depths (i.e., deepwater sculpins tend to be more abundant at greater depths than surveyed by trawls, O'Brien et al. 2009, Bunnell et al. 2017, Weidel et al. 2017), on rocky substrates (where sculpins likely spawn, Balon 1975, Mohr 1984, Keeler and Cunjak 2007, Majeski and Cochran 2009), as well as at night (when slimy sculpins may be more actively foraging, Brandt 1986a, Selegby 1988, Holeck et al. 2008) and year-round. Understanding of juvenile and adult life stages is also limited by difficulties in reliably aging deepwater sculpins (i.e., close spacing of otolith increments, Roseman 2014) and lack of long-term age data for both sculpin species. Additionally, there have been challenges with correctly identifying sculpin species (Kinziger et

al. 2005, though Arciszewski et al. 2015 summarize some distinctions between slimy sculpins, spoonhead sculpins, and deepwater sculpins) and determining sex externally (though Arciszewski et al. 2010 indicate that external sexing of mature slimy sculpin is possible).

The location and timing of sculpin spawning in the Great Lakes is unclear. Deepwater, slimy, and spoonhead sculpins are assumed to spawn offshore on rocky substrate in the Great Lakes (Balon 1975, Goodyear et al. 1982, Mansfield et al. 1983, Mohr 1984, Keeler and Cunjak 2007, Majeski and Cochran 2009). Deepwater sculpins have egg clusters in open indentations (Westin 1970, Crowder 1980), and slimy sculpin eggs tend to be stuck on the underside of rocks and ledges (Crowder 1980). For deepwater sculpins, male and female spawning occurs at approximately ages 2 and 3, respectively (Black and Lankester 1981). Males of both species guard eggs (McKenzie and Keenleyside 1970, Scott and Crossman 1973, Crowder 1980, Bunnell et al. 2006), but only slimy sculpin males guard larvae (McKenzie and Keenleyside 1970, Scott and Crossman 1973, Bunnell et al. 2006). Slimy and deepwater sculpin spawning could potentially occur year-round based on several reports indicating spawning for deepwater sculpins in all seasons (Scott and Crossman 1973, Wojcik et al. 1986; Selgeby 1988, Zimmerman and Krueger 2009) and anecdotal evidence of slimy sculpins carrying eggs throughout the year (Zimmerman and Krueger 2009). However, spawning timing and depth of sculpins likely varies across species and lakes (and perhaps, location within lakes), based on temperature preferences of each species (e.g., slimy sculpin spawn at 6–10°C, Arciszewski et al. 2015) and different latitudinal and bathymetric temperature patterns and substrate availability in each lake. Slimy sculpin spawning has been reported to occur in spring–early summer in lakes Michigan (45–65m, peak egg hatching mid-June, Madenjian et al. 2008) and Superior (Selgeby 1988). Deepwater sculpin spawning in Lake Michigan has been reported between November and May

(Mansfield et al. 1983), and eggs hatch at temperatures $< 5^{\circ}\text{C}$ primarily in March, but also in August and November (Geffen and Nash 1992). In Lake Superior, deepwater sculpin spawning has been reported in midwinter (Selgeby 1988).

As sculpins develop into juvenile and adult life stages, they become adapted for offshore benthic lifestyles (Brandt 1986a, Geffen and Nash 1992). Deepwater sculpin larvae in Lake Michigan shift from offshore to inshore and metamorphose at 20 mm length by July, followed by juvenile settlement by September at depths >50 m (Geffen and Nash 1992). Slimy sculpins exhibit similar ontogenetic patterns of shifting to deeper water as they mature (Brandt 1986a). The lifespan of sculpins in the Great Lakes reaches at least 5–7 years (Selgeby 1988), and based on trawl survey data, sculpin total length may reach up to approximately 150 mm and 200 mm for slimy sculpins and deepwater sculpins, respectively (M. Vinson and D. Hondorp, USGS, unpublished data), but these might not be the maximum ages and lengths overall in the lakes.

Ecology and Trophic Interactions

Trophic dynamics of sculpins also vary across life stages and species. It is important to consider the complex food web interactions between sculpins and both native and non-native species to understand the dynamics of sculpin populations in the Great Lakes. As trophic intermediates (Fratt et al. 1997, Madenjian et al. 1998, Sierszen et al. 2003, O'Brien et al. 2009, Jacobs et al. 2010), slimy and deepwater sculpin juveniles and adults are consumed by other species, including native juvenile lake trout and adult burbot (Owens and Bergstedt 1994, Madenjian et al. 2002, Van Oosten and Deason 1938). Non-native alewife (*Alosa pseudoharengus*) consume deepwater sculpin pelagic larvae (Crowder 1980, Janssen 1978, Lantry et al. 2007, Madenjian et al. 2008). Sculpins may also be cannibalistic of younger life stages and piscivorous of smaller fish species (Arciszewski et al. 2015). Deepwater sculpin

larvae feed on calanoid copepods, and juvenile deepwater sculpin consume mysids and chironomids (Roseman 2014). Adult slimy sculpins exhibit a greater preference for both *Diporeia* and chironomids, whereas adult deepwater sculpins exhibit a greater preference for mysids (Owens and Weber 1995, Kraft and Kitchell 1986, Hondorp et al. 2011). In addition to prey availability, prey size may be another factor driving prey selectivity of sculpins, as deepwater sculpins consume larger prey than slimy sculpins (Hondorp et al. 2011). However, both slimy and deepwater sculpins will feed on both *Mysis* and *Diporeia*, along with other benthic invertebrate species (e.g., chironomids) and fish eggs (e.g., lake trout, Kraft and Kitchell 1986, Marsden and Tobi 2014, Owens and Weber 1995, Selgeby 1988, Wojcik et al. 1986).

Population Dynamics and Ecosystem Changes

Fluctuations in the abundance of sculpin populations in the Great Lakes have been influenced by a complex array of ecological and environmental processes and disturbances over time. One of the earliest disturbances was the introduction of non-native alewife, which first appeared in Lake Ontario in the mid-1800s and spread into the rest of the Great Lakes within a century (Smith 1970). Declines in deepwater sculpin abundance in Lake Ontario beginning in the early 1900s and later in lakes Huron and Michigan between the 1960s and 1980s were attributed to adult alewife predation on pelagic larvae, as well as adult burbot predation on juveniles and adults (Madenjian et al. 2005a). Declines in deepwater sculpins abundance in Lake Ontario, in particular, were so sharp that they were considered extirpated by the late 1900s (COSEWIC, 2006, Weidel et al. 2016a). In contrast, slimy sculpin did not experience declines in abundance in the Great Lakes concurrent with alewife invasion arguably because benthic slimy sculpin larvae are not vulnerable to alewife predation (Crowder 1980, Janssen 1978, Lantry et al. 2007, Madenjian et al. 2008). Patterns in slimy sculpin abundance in Lake Michigan were attributed

instead to lake trout predation (Madenjian et al. 2005a). Deepwater sculpins reappeared in bottom trawl catches in 1996 in Lake Ontario, and more recent surveys indicate that deepwater sculpin may actually be recovering in this lake (Weidel et al. 2016a). The reappearance of deepwater sculpins was linked to salmonine management efforts (sea lamprey control and salmonine stocking) leading to a reduction in alewife populations (Madenjian et al. 2002, Bunnell et al. 2014). However, increased predation pressure by lake trout as a result of intense stocking efforts was linked to declines of slimy sculpins in lakes Ontario, Huron, and Michigan (1970s and 1980s), along with declines in both sculpin species in Lake Superior from 1978-1999 (Eck and Wells 1987, Owens and Bergstedt 1994, Bronte et al. 2003). Later emphasis of lake trout stocking offshore rather than nearshore may have reduced predation pressure on slimy sculpins (Lake Trout Working Group 2014, Madenjian et al. 2015).

Aside from the recent recovery of deepwater sculpins in Lake Ontario, both sculpin species have been declining in abundance and biomass in the Great Lakes since the 1990s and 2000s (Table 1.1, Bunnell et al. 2017, Riley et al. 2017, Weidel et al. 2017). For deepwater sculpins in Lake Michigan, these declines may actually be because deepwater sculpins have moved to deeper water not sampled by trawl surveys (Madenjian and Bunnell 2008). However, based on timing and ecology, the most recent declines in sculpin abundance and biomass in the Great Lakes could be associated with *Diporeia* collapse, along with invasions of dreissenid mussels (zebra, *Dreissena polymorpha*; quagga, *D. bugensis*) and round goby (*Neogobius melanostomus*, Table 1.1). Prior to their collapse, *Diporeia* were the dominant component of benthic invertebrate offshore biomass (>70%) and sculpin diets (estimated between 90–100%, Cook and Johnson 1974, Nalepa 1989, Selgeby 1988, Wells 1980, Wojcik et al. 1986). Between

Table 1.1 Timeline summary of most recent (i.e., 1990s and 2000s) ecosystem changes in the Great Lakes. Years (or year ranges) indicate the onset (and end) of these changes. *For Lake Superior *Diporeia* still persist and dreissenid mussels and round goby are still relatively rare. Also, deepwater sculpin have been recovering in Lake Ontario in recent years.

	Lake Huron	Lake Michigan	Lake Ontario	Lake Superior
Slimy sculpin abundance decline	1997, absent or scarce in the most recent trawl surveys (2014–2016)	2005	1990	1995 nearshore, 2012 offshore
Deepwater sculpin abundance decline	1995	1997	N/A*	1995 nearshore, 2012 offshore
<i>Diporeia</i> collapse	2000–2007	1994–2005	1993–2003	NA*
Zebra mussel invasion	1991	1987	1989	1989*
Quagga mussel invasion	1997	1997	1990	2005*
Round goby invasion	1997	1993	1998	1995*

the 1990s and 2000s, *Diporeia* declined by over 90% in lakes Huron, Michigan, and Ontario (Nalepa et al. 2007, Nalepa et al. 2009, Watkins et al. 2007). Only *Diporeia* in Lake Superior persist without a consistent declining pattern (Barbiero et al. 2011). As a result, sculpins have shifted their diets to rely more on alternative prey sources (French et al. 2010, Hondorp et al. 2005, Owens and Dittman 2003, Walsh et al. 2008), and the increased reliance of sculpins on alternative prey has been linked to reduced energy densities observed in deepwater sculpins (e.g., lakes Huron and Michigan, Hondorp et al. 2005, Pothoven et al. 2011).

The introduction of dreissenid mussels in the Great Lakes during the 1980s and 1990s (first zebra mussels inshore superseded by quagga mussels inshore and offshore, Bunnell 2009, Nalepa 2010, Wilson et al. 2006) may have both direct and indirect effects on the benthic

community, including sculpins. As a direct negative effect on sculpins, mussel colonization of soft sediments can inhibit slimy sculpin foraging (Beeky et al. 2004). Indirectly, dreissenid mussel invasions have been proposed as the cause of the collapse of *Diporeia* in the Great Lakes (Table 1.1, Bunnell et al. 2014, Dermott 2001, Dermott and Kerec 1997, Madenjian et al. 2015, Nalepa et al. 2010), either as a result of competition between mussels and *Diporeia* for phytoplankton or exposing *Diporeia* to toxic pseudofeces or pathogens (Watkins et al. 2007). Additionally, mussels have been linked to a suite of environmental and ecological changes in the Great Lakes, including increased water clarity and reduction in primary production (Bunnell et al. 2014, Vanderploeg et al. 2010, 2012). Lake Michigan ranks highest in peak mussel density, exceeding 16,000 g/m² (Nalepa et al. 2009). Lakes Ontario and Huron have peak mussel density levels at approximately 50% and 90% less than that observed in Lake Michigan, respectively (Bunnell et al. 2014, Cha et al. 2011). Meanwhile, low levels of calcium has prevented mussels from becoming particularly abundant in Lake Superior (Madenjian et al. 2015), which may partially explain the persistence of *Diporeia* in this lake (Bunnell et al. 2014).

Another invasive species, round goby, arrived in the 1990s and, facilitated by availability of dreissenid mussel prey, spread throughout the Great Lakes (Table 1.1, Jude et al. 1995). In Lake Ontario, round goby have surpassed the abundance of native deepwater sculpins to become the most prevalent benthic prey fish in this system (Weidel et al. 2016a, b). As was observed with other invaders, only Lake Superior has been relatively resistant to perturbation, as round goby abundance has not expanded in this lake (Bunnell et al. 2014). This highly aggressive and highly fecund benthic invader has been observed to outcompete native benthic species (e.g., mottled sculpins) for food and habitat resources (Dubs and Corkum 1996, Jude and DeBoe 1996, Charlebois et al. 1997, French and Jude 2001, Janssen and Jude 2001, Jude 2001, Ray and

Corkum 2001, Lauer et al. 2004, Balshine et al. 2005). Bergstrom and Mensinger (2009) also found evidence for interspecific competition between round goby and sculpins in experimental trials in which spoonhead sculpins lost weight in the presence of round goby. In this same study, slimy sculpins did not lose weight in the presence of round goby, but round goby gained more weight in trials than all native species tested (Bergstrom and Mensinger 2009). Although round goby feed on dreissenid mussels, Walsh and others (2007) indicated that gobies in Lake Ontario have incorporated *Mysis* into their diet more at deeper depths, which could pose a threat to sculpins in the Great Lakes during offshore migration of gobies in autumn through early spring (Miller 1986, Schaeffer et al. 2005, Walsh et al. 2007), especially in areas with limited prey availability for sculpin species.

Conclusion

Compared to apex predators in the Great Lakes, sculpins have been neglected with regard to research and management (Adams and Schmetterling 2007, Muir et al. 2012). Such efforts may have been hindered by difficulties with distinguishing different sculpin species, the ability to age them, as well as limited sampling efforts (Adams and Schmetterling 2007, Kinziger et al. 2007, Roseman 2014, Sheldon et al. 2008). This reviews offers some insight into several areas of sculpin biology and ecology in the Great Lakes, but many of the areas of research discussed during the GLFC Sculpin Workshop remain to be investigated thoroughly. In particular, sculpin life history, reproduction, and population dynamics/structure (aside from abundance estimates) are not well-understood. Based on the timing of recent declines in the abundance slimy and deepwater sculpins (Table 1.1, Bunnell et al. 2017, Riley et al. 2017, Vinson et al. 2017), we suspect that these declines in sculpins are associated with the invasions of dreissenid mussels and round gobies through various direct and indirect mechanisms related to hindering sculpin

foraging on *Diporeia* in the case of both invaders or aggressive interactions in the case of round gobies. Therefore, in order to restore both slimy and deepwater sculpins in the Great Lakes, it is important that future research aims to address these gaps in knowledge related to sculpin biology and ecology, and to investigate the effect of dreissenid mussels and round gobies on these sculpin species.

REFERENCES

REFERENCES

- Adams, S.B., and Schmetterling, D.A. 2007. Freshwater sculpins: phylogenetics to ecology. *Trans. Am. Fish. Soc.* 136:1736–1741.
- Arciszewski, T., Gray, M.A., Hrenchuk, C., Cott, P.A., Mochnacz, N.J., and Reist, J.D. 2015. Fish life history, diets, and habitat use in the Northwest Territories: freshwater sculpin species. *Can. Manuscr. Rep. Fish. Aquat. Sci.* 3066:vi–41.
- Arciszewski, T., Gray, M.A., Munckittrick, K.R., and Baron, C. 2010. Guidance for the collection and sampling of slimy sculpin (*Cottus cognatus*) in northern Canadian lakes for environmental effects monitoring (EEM). *Can. Tech. Rep. Fish. Aquat. Sci.* 2909:v–21.
- Balon, E.K. 1975. Reproductive guilds of fishes: A proposal and definition. *J. Fish. Res. Bd. Can.* 32:821–864.
- Balshine, S.A., Verma, Chant, V., and Theysmeyer, T. 2005. Competitive interactions between round gobies and logperch. *J. Great Lakes Res.* 31:68–77.
- Barbiero, R.P., Schmude, K., Lesht, B.M., Riseng, C.M., Warren, G.J., and Tuchman, M.L. 2011. Trends in *Diporeia* populations across the Laurentian Great Lakes, 1997–2009. *J. Great Lakes Res.* 37(1):9–17.
- Beauchamp, D.A. 1990. Seasonal and diel food habits of rainbow trout stocked as juveniles in Lake Washington. *Trans. Am. Fish. Soc.* 119:475–482.
- Beekey, M.A., McCabe, D.J., and Marsden, J.E. 2004. Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. *Oecologia* 141:164–170.
- Bergstrom, M.A., and Mensinger, A.F. 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. *Trans. Am. Fish. Soc.* 138:1009–1017.
- Birzaks, J., Ozolins, J., and Omicans, A. 1998. Otter (*Lutra lutra*) diet related to abundance of fish in some Latvia's rivers. Proceedings of the Latvian Academy of Sciences Section B Natural Exact and Applied Sciences 52:7–76.
- Brandt, S.B. 1986a. Ontogenetic shifts in habitat, diet, and diel-feeding periodicity of slimy sculpin in Lake Ontario. *Trans. Am. Fish. Soc.* 115(5):711–715.
- Brandt, S.B. 1986b. Disappearance of the deepwater sculpin (*Myoxocephalus thompsonii*) from Lake Ontario – The keystone predator hypothesis. *J. Great Lakes Res.* 12(1):18–24.
- Brinkman, S., and Woodling, J. 2005. Zinc toxicity to the mottled sculpin (*Cottus bairdi*) in

- high-hardness water: short communication. *Environ. Toxicol. Chem.* 24:1515–1517.
- Bronte, C.R. et al. 2003. Fish community change in Lake Superior, 1970–2003. *Can. J. Fish. Aquat. Sci.* 60:1552–1574.
- Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., and Weidel, B.C. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. *Bioscience* 64(1):26–39.
- Bunnell, D.B., C.P. Madenjian, and Claramunt, R.M. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 63:2434–2446.
- Bunnell, D.B., Madenjian, C.P., Desorcie, T.J., Kostich, M., Armenio, P., and Adams, J. 2017. Status and trends of prey fish populations in Lake Michigan, 2016. U.S. Geological Survey. Ann Arbor, MI.
- Bunnell, D.B., Madenjian, C.P., Holuszko, J.D., Adams, J.V., and French III, J.R.P. 2009. Expansion of *Dreissena* into offshore waters of Lake Michigan and potential impacts on fish populations. *J. Great Lakes Res.* 35:74–80.
- Cha Y., Stow, C.A., Nalepa, T.F., and Reckhow, K.H. 2011. Do invasive mussels restrict offshore phosphorus transport in Lake Huron? *Environ. Sci. Technol.* 45:7226–7231.
- Charlebois, P.M., Marsden, J.E., Goettel, R.G., Wolfe, R.K., Jude, D.J., and Rudnika, S. 1997. The round goby, *Neogobius melanostomus* (Pallus), a review of European and North American literature. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey (76 pp.)
- Cook, D.G., and Johnson, G. 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. *J. Fish. Res. Bd. Can.* 31:763–782.
- Cott, P.A., Sibley, P.K., Gordon, A.M., Bodaly, R.A., Mills, K.H., Somers, W.M., and Fillatre, G.A. 2008. Effects of water withdrawal from ice-covered lakes on oxygen, temperature, and fish. *J. Am. Water Res. Assoc.* 44: 328–342.
- COSEWIC. 2006. COSEWIC assessment and update status report on the deepwater sculpin *Myoxocephalus thompsonii* (Western and Great Lakes-Western St. Lawrence populations) in Canada. Committee on the Status of Endangered Wildlife in Canada.
- Crowder, L.B. 1980. Alewife, rainbow smelt and native fishes in Lake Michigan: competition or predation? *Environ. Biol. Fishes* 5:225–233.
- Deason, H.J. 1939. The distribution of cottid fishes in Lake Michigan. *Pap. Mich. Acad. Sci. Arts*

- Lett.* 24(2):105–115.
- Dermott, R. 2001. Sudden disappearance of the amphipod *Diporeia* from eastern Lake Ontario, 1993–1995. *J. Great Lakes Res.* 27(4):423–433.
- Dermott, R., and Kerec, D. 1997. Changes in the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. *Can. J. Fish. Aquat. Sci.* 54:922–930.
- Dubs, D.O.L., and Corkum, L.D. 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). *J. Great Lakes Res.* 22:838–844.
- Fratt, T.W., Coble, D.W., Copes, F., and Bruswitz, R.E. 1997. Diet of burbot in Green Bay and western Lake Michigan with comparison to other waters. *J. Great Lakes Res.* 23:1–10.
- French III, J.R.P., and Jude, D.J. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *J. Great Lakes Res.* 27:300–311.
- French III, J.R.P., Stickel, R.G., Stockdale, B.A., Black, M.G. 2010. A short-term look at potential changes in Lake Michigan slimy sculpin diets. *J. Great Lakes Res.* 36:376–379.
- Eck, G.W., and 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(2):53–60.
- Euclide, P.T., Flores, N.M., Wargo, M.J., Kilpatrick, C.W., Marsden, J.E. 2017. Lack of population genetic structure of slimy sculpin in a large, fragmented lake. *Ecol. Freshw. Fish.* 2017:1–11.
- Geffen, A.J., and Nash, R.D.M. 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.* 41:101–110.
- Goodyear, C.S., Edsall, T.A., Ormsby Dempsey, D. M., Moss, G. D., and Polanski, P. E. 1982. Atlas of the spawning and nursery areas of Great Lakes fishes. Volume 13. Reproductive characteristics of Great Lakes fishes. U.S. Fish and Wildlife Service, FWS/OBS-82/52. 144 p.
- Gray, M.A. 2003. Assessing non-point source pollution in agricultural regions of the upper St. John River basin using the Slimy Sculpin (*Cottus cognatus*). Thesis (Ph.D.). University of New Brunswick, Fredericton, NB. 167p.
- Harvey, C.J., and Kitchell, J.F. 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.

- Hodgens, L.S., Blumenshine, S.C., and Bednarz, J.C. 2004. Great blue heron predation on stocked rainbow trout in an Arkansas tailwater fishery. *N. Am. J. Fish. Manag.* 24:63-75.
- Hogan, L.S., Marschall, E., Folt, C., and Stein, R.A. 2007. How non-native species in Lake Erie influence trophic transfer of mercury and lead to top predators. *J. Great Lakes Res.* 33:46–61.
- Holeck, K., Watkins, J., Mills, E., Johannsson, O., Millard, S., Richardson, V., and Bowen, K. 2008. Spatial and long-term temporal assessment of Lake Ontario water clarity, nutrients, chlorophyll a, and zooplankton. *Aquat. Ecosyst. Health.* 11(4): 377–391.
- Hondorp, D.W., Pothoven, S.A., and Brandt, S.B. 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.* 37:165–172.
- Hondorp, D.W., Pothoven, S.A., Brandt, S.B. 2005. Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. *Trans. Am. Fish. Soc.* 134:588–601.
- Jacobs, G.R., Madenjian, C.P., Bunnell, D.B., and Holuszko, J.D. 2010. Diet of lake trout and burbot in northern Lake Michigan during spring: evidence of ecological interaction. *J. Great Lakes Res.* 36(2):312–317.
- Janssen, J. 1978. Feeding-behavior repertoire of the alewife, *Alosa pseudoharengus*, and the ciscoes *Coregonus hoyi* and *C. artedii*. *J. Fish. Res. Bd. Can.* 35:249–253.
- Janssen, J., and Jude, D.J. 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.* 27:319–328.
- Janssen, J., Berg, M.B., and Lozano, S.J. 2005. Submerged terra incognita: Lake Michigan's abundant but unknown rocky zones. In *State of Lake Michigan: Ecology, Health and Management*, ed. TA Edsall, M Munawar, pp. 113–39. Ecovis. World Monogr. Ser. Amsterdam: Academic
- Jude, D. J. 2001. Round and tubenose gobies: 10 years with the latest Great Lakes phantom menace. *Dreissena* 11:1–14.
- Jude, D.J and DeBoe, S.F. 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. *Can. J. Fish. Aquat. Sci.* 53(1): 136–141.
- Jude, D.J., Janssen, J., and Crawford, G. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit Rivers. pp. 447–460 *In The Lake Huron ecosystem: ecology, fisheries, and management.* M. Munawar, T. Edsall, and J. Leach, eds. The Netherlands: S.P.B. Academic Publishing.

- Keeler, R.A., and Cunjak, R.A. 2007. Reproductive ecology of slimy sculpin in small New Brunswick streams. *Trans. Am. Fish. Soc.* 136:1762–1768.
- Kinziger, A.P., Wood, R.M., and Neely, D.A. 2005. Molecular systematics of the genus *Cottus* (Scorpaeniformes: Cottidae). *Copeia* 2005:303-311.
- Koczaja, C., McCall, L., Fitch, E., Glorioso, B., Hanna, C., Kyzar, J., Niemiller, M., Spiess, J., Tolley, A., Wyckoff, R., and Mullen, D. 2005. Size-specific habitat segregation and intraspecific interactions in banded sculpin (*Cottus carolinae*). *Southeastern Naturalist* 4:207–218.
- Kraft, C.E., and Kitchell, J.F. 1986. Partitioning of food resources by sculpins in Lake Michigan. *Environ. Biol. Fishes* 16:309–316.
- Lantry, B.F., O’Gorman, R., Walsh, M.G., Casselman, J.M., Hoyle, J.A., Keir, M.J., and Lantry, J.R. 2007. Reappearance of deepwater sculpin in Lake Ontario: resurgence or last gasp of a doomed population? *J. Great Lakes Res.* 33:34–45.
- Lake Trout Working Group, 2014. 2013 Lake Michigan Lake Trout Working Group report. A Report to the Great Lakes Fishery Commission. Lake Michigan Committee, Windsor, Ontario (March 26, 2014).
- Lauer, T.E., Allen, P.J., and McComish, T.S. 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.* 133:185–189.
- Madenjian, C.P., and Bunnell, D.B. 2008. Depth distribution dynamics of the sculpin community in Lake Michigan. *Trans. Am. Fish. Soc.* 137:1346–1357.
- Madenjian, C.P., DeSorcie, T.J., and Stedman, R.M. 1998. Ontogenetic and spatial patterns in diet and growth of lake trout in Lake Michigan. *Trans. Am. Fish. Soc.* 127: 236–252.
- Madenjian, C.P., Hondorp, D.W., Desorcie, T. J., and Holuszko, J. D. 2005a. Sculpin community dynamics in Lake Michigan. *J. Great Lakes Res.* 31:267–276.
- Madenjian, C.P., Hook, T.O., Rutherford, E.S., Mason, D.M., Croley II, T. E., Szalai, E.B., and Bence, J.R. 2005b. Recruitment variability of alewives in Lake Michigan. *Trans. Am. Fish. Soc.* 134:218– 230.
- Madenjian, C.P. et al. 2002. Dynamics of the Lake Michigan food web, 1970-2000. *Can. J. Fish. Aquat. Sci.* 59:736–753.
- Madenjian, C.P., Bunnell, D.B., Desorcie, T.J., Kostich, M.J., Armenio, P.M., Adams, J.V. 2014. Status and trends of prey fish populations in Lake Michigan, 2013. Compiled Reports to the Great Lakes Fishery Commission of the Annual Bottom Trawl and Acoustics Surveys, 2013. Great Lakes Fishery Commission, Ann Arbor, pp. 46–61.

- Madenjian, C.P., Bunnell, D.B., Warner, D.M., Pothoven, S.A., Fahnenstiel, G.L., Nalepa, T.F., Vanderploeg, H.A., Tsehaye, I., Claramunt, R.M., Clark Jr., R.D. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: a synthesis. *J. Great Lakes Res.* 41(3):217–231.
- Majeski, M.J., and Cochran, P.A. 2009. Spawning season and habitat use of slimy sculpin (*Cottus cognatus*) in southeastern Minnesota. *J. Freshw. Ecol.* 24:301–307.
- Mansfield, P.J., Jude, D.J., Brazo, D.C., and Gulvas, J. 1983. Distribution and abundance of larval burbot and deepwater sculpin in Lake Michigan. *Trans. Am. Fish. Soc.* 112:162–172.
- Maret, T.R., and MacCoy, D.E. 2002. Fish assemblages and environmental variables associated with hard-rock mining in the Coeur d'Alene River basin, Idaho. *Trans. Am. Fish. Soc.* 13(1):865–884.
- Marsden, J.E, and Tobi, H. 2014. Sculpin predation on lake trout eggs in interstices: skull compression as a novel foraging mechanism. *Copeia* 4:654–658.
- Matuszek, J.E., Goodier, J., and Wales, D.L. 1990. The occurrence of Cyprinidae and other small fish species in relation to pH in Ontario lakes. *Trans. Am. Fish. Soc.* 119:850–861.
- McKenzie, J.A., and Keenleyside, M.H.A. 1970. Reproductive behavior of ninespine sticklebacks (*Pungitius pungitius* (L.)) in South Bay, Manitoulin Island, Ontario. *Can. J. Zool.* 48:55–61.
- Miller, P.J. 1986. Gobiidae. In *Fishes of the northeast Atlantic and Mediterranean*, eds. P.J.P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen, and E. Tortonese, pp. 1019–1095. UNESCO, Paris.
- Mohr, L.C. 1984. The general ecology of the Slimy Sculpin (*Cottus cognatus*) in Lake 302 of the Experimental Lakes Area, Northwestern Ontario. *Can. Tech. Rep. Fish. Aquat. Sci.* 1227:iv–16.
- Muir, A.M., Bronte, C.R., and Mida Hinderer, J.L. 2012. Fourth Reintroduction of Native Fishes Workshop. Report to the Great Lakes Fishery Commission, Ann Arbor, MI.
- Mychek-Londer, J.G., Bunnell, D.B., Stott, W., Diana, J.S., French, J.R.P., and Chriscinske, M.A. 2013. Using diets to reveal overlap and egg predation among benthivorous fishes in Lake Michigan. *Trans. Am. Fish. Soc.* 142:492–504.
- Nalepa, T. F., 2010. An overview of the spread, distribution, and ecological impacts of the quagga mussel, *Dreissena rostriformis bugensis*, with possible implications to the Colorado River system. Proceedings, Colorado River Basin Science and Resource Management Symposium. Coming Together, Coordination of Science and Restoration Activities for the Colorado River Ecosystem, Scottsdale, AZ, November 18–20, 2008. U.S. Geological Survey Scientific Investigations Report: 2010–5135.

- Nalepa, T.F. 1989. Estimates of macroinvertebrate biomass in Lake Michigan. *J. Great Lakes Res.* 15:437–443.
- Nalepa, T.F., Fanslow, D.L., Lang, G.A. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia spp.* to the invasive mussel *Dreissena rostriformis bugensis*. *Freshw. Biol.* 54:466–479.
- Nalepa T.F., Fanslow, D.L., Pothoven, S.A., Foley III, A.J., and Lang, G.A. 2007. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. *J. Great Lakes Res.* 33:421–436.
- O'Brien, T.P., Roseman, E.F., Kiley, C.S., and Schaeffer, J.S. 2009. Fall diet and bathymetric distribution of deepwater sculpin (*Myoxocephalus thompsonii*) in Lake Huron. *J. Great Lakes Res.* 35:464–472.
- Owens, R.W., and Bergstedt, R.A. 1994. Response of slimy sculpins to predation by juvenile lake trout in southern Lake Ontario. *Trans. Am. Fish. Soc.* 123:28–36.
- Owens, R.W., and Dittman, D.E. 2003. Shifts in the diets of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod *Diporeia*. *Aquat. Ecosyst. Health Manag.* 6:311–323.
- Owens, R.W., and Weber, P.G. 1995. Predation on *Mysis relicta* by slimy sculpins (*Cottus cognatus*) in southern Lake Ontario. *J. Great Lakes Res.* 21:275–283.
- Parker, B.J. 1988. Status of the deepwater sculpin, *Myoxocephalus thompsoni*, in Canada. *Can. Field-Nat.* 102:126–131.
- Poe, T.P., Hansel, H.C., Vigg, S., Palmer, D.E., and Prendergast, L.A. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids on John Day Reservoir, Columbia River, USA. *Trans. Am. Fish. Soc.* 120:405–420.
- Pothoven, S.A., Hondorp, D.W., and Nalepa, T.F. 2011. Declines in deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia spp.* in lakes Huron and Michigan. *Ecol. Freshw. Fish* 20:14–22.
- Ray, W.J., and Corkum, L.D. 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environ. Biol. Fishes* 50:267–273.
- Riley, S.C., Roseman, E.F., Hondorp, D.W., Chriscinske, M.A., Galassini, E., and Smith, M. 2017. Status and trends of the Lake Huron offshore demersal fish community, 1976–2016. U.S. Geological Survey. Ann Arbor, MI.
- Roseman, E.F., 2014. Diet and habitat use by age-0 deepwater sculpins in northern Lake Huron, Michigan and the Detroit River. *J. Great Lakes Res.* 40(2):110–117.

- Roseman, E.F., and Riley, S.C. 2009. Biomass of deepwater demersal forage fishes in Lake Huron, 1994–2007: implications for offshore predators. *Aquat. Ecosyst. Health Manag.* 12:29–36.
- Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada, deepwater sculpin. Fisheries Research Board of Canada. Royale Ontario Museum, Ontario, pp. 842–848.
- Scott, W.B., and Crossman, E.J. 1998. Freshwater Fishes of Canada. Oakville, Canada: Galt House Publications Ltd.
- Schaeffer, J.S., Bowen, A., Thomas, M., French III, J.R.P., and Curtis, G.L. 2005. Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in western Lake Huron, USA. *J. Great Lakes Res.* 31:414–425.
- Sheldon, T.A., Mandrak, N.E., Lovejoy, N.R. 2008. Biogeography of the deepwater sculpin (*Myoxocephalus thompsonii*) a nearctic glacial relict 86. pp. 108–115.
- Selgeby, J.H. 1988. Comparative biology of the sculpins of Lake Superior. *J. Great Lakes Res.* 14:44–51.
- Sierszen, M.E., McDonald, M.E., and Jensen, D.A. 2003. Benthos as the basis for arctic lake food webs. *Aquat. Ecol.* 37:437–445.
- Smith, S.H. 1970. Species interactions of the alewife in the Great Lakes. *Trans. Am. Fish. Soc.* 99:754–765.
- Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., Pothoven, S.A. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *J. Great Lakes Res.* 36(3):50–59.
- Vanderploeg, H.A. et al. 2012. Seasonal zooplankton dynamics in Lake Michigan: Disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *J. Great Lakes Res.* 38:336–352.
- Van Oosten, J., and Deason, H.J. 1938. The food of the lake trout (*Cristovomer namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan. *Trans. Am. Fish. Soc.* 67:155–177.
- Van Vliet, W.H. 1964. An ecological study of *Cottus cognatus* Richardson in Northern Saskatchewan. Thesis (M.A.). University of Saskatchewan, Saskatoon, SK
- Vinson, M., Evrard, L., Gorman, O.T., and Yule, D.L. 2017. Status and trends in the Lake Superior fish community, 2016. U.S. Geological Survey. Ashland, WI
- Volkel, S., and Robinson, K.F. 2017. Sculpin workshop report. Report to the Great Lakes Fishery Commission, Ann Arbor, MI.

- Walsh, M.G., Dittman, D.E., and O’Gorman, R.O. 2007. Occurrence and food habits of the round goby in the profundal zone of Southwestern Lake Ontario. *J. Great Lakes Res.* 33:83–92.
- Watkins, J.M., Dermott, R., Lozano, S.J., Mills, E.L., Rudstam, L.G., Scharold, J.V. 2007. Evidence for remote effects of dreissenid mussels on the amphipod *Diporeia*: analysis of Lake Ontario benthic surveys, 1972–2003. *J. Great Lakes Res.* 33:642–657.
- Wells, L. and McLain, A.L. 1973. Lake Michigan: man’s effects on native fish stocks and other biota. Great Lakes Fishery Commission Tech. Rep. 20.
- Weidel, B.C., Walsh, M.G., Connerton, M.J., Lantry, B.F., Lantry, J.R., Holden, J.P., Yuille, M.J., and Hoyle, J.A. 2016a. Deepwater sculpin status and recovery in Lake Ontario. *J. Great Lakes Res.* 43(5): 854-862.
- Weidel, B.C., Walsh, M.G., Holden, J.P., Connerton, M.J., 2016b. Lake Ontario benthic prey fish assessment, 2015. 2015 Annual Report, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee.
- Wojcik, J.A., Evans, M.S., and Jude, D.J. 1986. Food of deepwater sculpin, *Myoxocephalus thompsoni*, from Southeastern Lake Michigan. *J. Great Lakes Res.* 12:225–231.
- Zimmerman, M.S., and Krueger, C.C. 2009. An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. *N. Am. J. of Fish. Manag.* 29:1352–1371.

CHAPTER 2. SLIMY SCULPIN AND ROUND GOBY SPATIAL OVERLAP IN THE GREAT LAKES FOLLOWING ROUND GOBY INVASION

Abstract

Between the late 1980s and early 2000s, Great Lakes benthic communities have undergone several ecological changes, including collapse of *Diporeia* spp. and invasions of dreissenid mussels (zebra, *Dreissena polymorpha*; quagga, *D. bugensis*) and round goby (*Neogobius melanostomus*). Coincident with these changes, large declines in biomass and abundance of historically dominant demersal prey fishes (slimy sculpins, *Cottus cognatus*; deepwater sculpins *Myoxocephalus thompsonii*) have been observed throughout these systems. We used long-term USGS bottom trawl data to evaluate trends in the depth distribution of sculpins and overlap between round goby and slimy sculpin in lakes Huron, Michigan, and Ontario. We predicted that round gobies have colonized further offshore at both annual and seasonal scales as they have become more widespread, and that slimy sculpin would shift deeper to avoid aggressive round gobies and follow limited prey resources. Additionally, we predicted that slimy sculpins would maintain spatial segregation with deepwater sculpins, effectively squeezing slimy sculpins out of their native habitat range. We found evidence that gobies have shifted to deeper depths annually in lakes Michigan and Huron, and evidence of seasonal migration in round goby to deeper depths in Lake Ontario. We also found evidence of slimy sculpins shifting to deeper depths in recent years concurrent with round goby invasion. Aside from Lake Huron, where depth overlap between slimy sculpins and round gobies is increasing, slimy sculpins are still maintaining depth segregation with gobies. In lakes Huron and Ontario, depth overlap is increasing between slimy and deepwater sculpins in recent years.

Introduction

Historically, slimy sculpins (*Cottus cognatus*) and deepwater sculpins (*Myoxocephalus thompsonii*) were among the most abundant demersal fishes in the Great Lakes (Bronte et al. 2003, Owens et al. 2003, Bunnell et al. 2006, Roseman and Riley 2009). Sculpins are critical trophic intermediates that consume benthic invertebrates (e.g., *Mysis* and *Diporeia*, Wells 1980, Kraft and Kitchell, 1986, Selgeby 1988) and are consumed by native deepwater fishes (e.g., lake trout, *Salvelinus namaycush*; burbot, *Lota lota*, Van Oosten and Deason 1938, Owens and Bergstedt 1994, Madenjian et al. 2002). Both sculpin species have coexisted in the lakes due to spatial segregation (i.e., deepwater sculpins occupy greater depths than slimy sculpins) and prey partitioning (i.e., deepwater sculpins prefer *Mysis* whereas slimy sculpins prefer *Diporeia*, Zimmerman and Krueger 2009, Hondorp et al. 2011). However, the abundance of both sculpin species throughout the Great Lakes has generally declined since the 1990s (Weidel et al. 2016a, Bunnell et al. 2017, Riley et al. 2017, Vinson et al. 2017).

Declines in the abundance of sculpins in the Great Lakes could be attributed to a suite of ecological disturbances that have occurred between the late 1980s and early 2000s. In lakes Huron, Michigan, and Ontario, the invasion and spread of dreissenid mussels (zebra, *Dreissena polymorpha*; quagga, *D. bugensis*) has been linked to the collapse of *Diporeia*, a formerly major component of benthic environments and sculpin diets (Cook and Johnson 1974, Nalepa 1989, Selgeby 1988, Nalepa et al. 2010, Madenjian et al. 2015). The loss of *Diporeia* has led many species, including sculpins, to rely more on alternate prey items, which may potentially result in increased competition for limited food resources (Owens and Dittman 2003, Hondorp et al. 2005, Walsh et al. 2008, French et al. 2010). Competition for resources could be further exacerbated by the invasion of round goby (*Neogobius melanostomus*) in the 1990s (Jude et al. 1995). Round

gobies are highly aggressive and fecund benthivores that have been observed to outcompete several native demersal species (e.g., mottled sculpins, *Cottus bairdii*) for food and habitat (Dubs and Corkum 1996, Jude and DeBoe 1996, Charlebois et al. 1997, French and Jude 2001, Janssen and Jude 2001, Jude 2001, Ray and Corkum 2001, Lauer et al. 2004, Balshine et al. 2005). Although round gobies typically prefer shallower habitats, some studies suggest that round gobies may overwinter, from autumn to as late as early spring, in deeper offshore areas where sculpins occur (Miller 1986, Schaeffer et al. 2005, Walsh et al. 2007). Additionally, Walsh and others (2007) indicated that round gobies in Lake Ontario incorporate *Mysis* into their diet more at greater depths, which could pose a threat to sculpins in the Great Lakes during offshore migration of gobies, especially in areas with low abundance of *Diporeia*. Although there is not a strong amount of dietary overlap between these sculpin species and gobies in Lake Michigan, gobies consuming *Mysis* in the absence of *Diporeia* can threaten sculpins, especially if gobies become more widespread (Mychek-Londer et al. 2013).

Although both slimy and deepwater sculpins are likely to be susceptible to being affected by round goby invasion, slimy sculpins may be at greater risk. Unlike deepwater sculpins that appear to be recovering despite round goby invasion in Lake Ontario (Weidel et al. 2016b), slimy sculpins have been declining in abundance in lakes Huron, Michigan, Ontario, and Superior (Weidel et al. 2016a, Bunnell et al. 2017, Riley et al. 2017, Vinson et al. 2017). Also, as gobies move offshore during the winter (Miller 1986, Schaeffer et al. 2005, Walsh et al. 2007), they would first encounter and interact with slimy sculpins, which occur at shallower depths than deepwater sculpins (Zimmerman and Krueger 2009). Along with the absence of their preferred prey source, slimy sculpin would be particularly vulnerable to interactions with aggressive gobies. Slimy sculpins are important for native apex predators offshore (e.g., lake trout and

burbot, Van Oosten and Deason 1938, Owens and Bergstedt 1994, Madenjian et al. 2002), so slimy sculpin disappearance offshore could make managing these predator species more difficult unless deepwater sculpins recovered to compensate for the loss of slimy sculpins or round gobies became a viable prey substitute for lake trout and burbot.

The purpose of this study was to assess if slimy sculpins are susceptible to overlap with round gobies and deepwater sculpins that could set the stage for competition for limited habitat or prey resources based on annual trends in depth and spatial (depth) overlap between slimy sculpins and these species in lakes Huron, Michigan, and Ontario. More specifically, we hypothesized that 1) round gobies have spread to greater depths annually following their initial invasion, resulting in 2) slimy sculpins shifting to greater depths to avoid habitat/food competition or reduce interactions with aggressive round gobies. Shifts to deeper depths by both gobies and slimy sculpins may result in either maintained depth segregation or increased depth overlap between slimy sculpins and round gobies, and either maintained depth segregation or increased depth overlap between slimy sculpins and deepwater sculpins. If slimy sculpins are unable to successfully avoid round gobies and coexist with deepwater sculpins, slimy sculpins would be “squeezed” out of their habitat range.

Methods

Trawl Surveys

All data were obtained from long-term USGS bottom trawl surveys occurring between the 1970s–2017 for lakes Huron, Michigan, and Ontario (Table 2.1, Figure 2.1). For lakes Huron and Michigan, all trawl surveys occurred during the fall. For Lake Ontario, surveys occurred during spring, summer, and fall. Therefore, seasonal patterns were only considered for Lake Ontario. In Lake Huron, the ports that were surveyed primarily encompassed the western basin

of the lake. For Lake Ontario, surveys occurred on both the Canadian northern and western coasts and United States southern and eastern coasts. However, only 18 of the 37 ports surveyed in Lake Ontario were analyzed because of inconsistent sampling, and these ports primarily encompassed the southern and eastern coasts of the lake. Therefore, most survey data analyzed for lakes Huron and Ontario were obtained from U.S. waters. For Lake Michigan, surveys encompassed the entire perimeter of the lake.

Table 2.1. Time periods, depth ranges, and transects that were consistently sampled (and thus analyzed) from lakes Huron, Michigan, and Ontario.

Lake	Years	Months	Depth Range	Number of Ports	Trawl Types
Huron	1976–1999, 2001–2016	September – November	9 –110 m	6	12-m bottom trawl (1976–1991), 21-m headropes (1992–2007)
Michigan	1973–1997, 1999–2016	September – November	9 –110 m	7	12-m bottom trawl
Ontario	1978–2017	April – November	5 – 150 m	18	39' Otter/Yankee bottom trawl, 39' Roller Trawl, 3 in 1 trawl, 3 in 1 tickler trawl, 30' orange Keir trawl (drop chain foot rope)

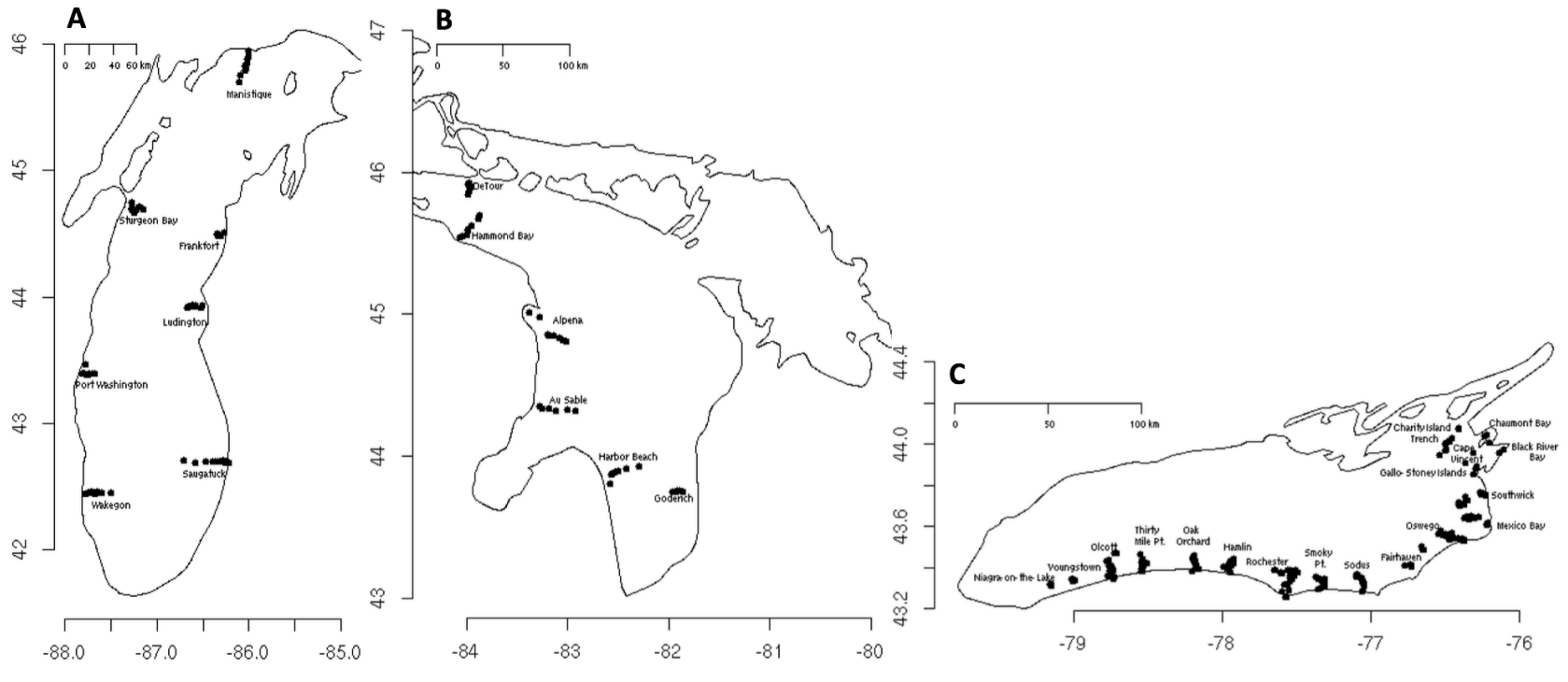


Figure 2.1. Port locations included in analyses for Lake Michigan (A), Lake Huron (B), and Lake Ontario (C).

At each port (Figure 2.1), trawl surveys were performed along transects at several fixed depths spanning from nearshore to offshore, though only depth ranges that were consistently sampled for several years throughout the duration of trawl surveys in each lake were included in data analyses (Table 2.1). This resulted in excluding some deeper depths, where prior studies have suggested that deepwater sculpins may be found in greater abundances than those typically sampled in these trawl surveys (O'Brien et al. 2009, Bunnell et al. 2017, Weidel et al. 2016a). For each survey in each lake, catches at depth for slimy sculpins, deepwater sculpins, and round gobies were converted to catch per effort (CPE, number caught per hectare), which were based on scaled estimates of the trawl area swept for each survey. For Lake Huron, CPE estimates between two different trawl types (Table 2.1) were standardized with a fishing power correction (Adams et al. 2009). Only one trawl type was used for Lake Michigan (Table 2.1), and trawl type for Lake Ontario was not accounted for in CPE estimates, but was later accounted for in the linear model used to estimate mean depth of capture for each species. Bottom water temperature was also collected for each trawl survey, though this was not collected consistently.

Species Depth Distribution

To assess long-term lake-wide trends in the depth distribution of each species within each lake, we calculated annual estimates of mean depth of capture using the methods of Riley and Adams (2010). For lakes Huron and Michigan, mean depth of capture for each species was first calculated for each year (i) and port (j):

Equation 2.1.
$$d_{ij} = \frac{\sum_{ij} C_{ij} D_{ij}}{\sum_{ij} C_{ij}}$$

where mean depth of capture for each year and port (d_{ij} , meters) is a function of catch (C_{ij} , number caught per hectare) at transect depth (D_{ij} , in meters). For each species in each lake (lakes Huron and Michigan), annual lake-wide mean depth of capture was estimated by accounting for port and Julian day of sampling using the following mixed effect linear model:

Equation 2.2.
$$d_{ij} = \mu + Y_i + P_j + T_{ij} + P_j T_{ij} + \varepsilon_{ij}$$

including the overall global mean depth of capture (μ), the fixed year effect of year i (Y_i), the random port effect of port j (P_j), the random Julian day effect for year i and port j (T_{ij} , i.e., accounts for survey date variation and may serve as proxy for environmental effects such as water temperature, clarity, productivity, species migration, etc.), an interaction term between the random effects of Julian day effect and port ($P_j T_{ij}$), and the normally distributed error (ε_{ij} , Riley and Adams 2010).

To account for seasonal effects, estimates of mean depth of capture for each species in Lake Ontario were estimated for each year (i), port (j), and season (k):

Equation 2.3.
$$d_{ijk} = \frac{\sum_{ijk} C_{ijk} D_{ijk}}{\sum_{ijk} C_{ijk}}$$

Therefore, the mixed effect linear model used to estimate annual lake-wide mean depth of capture for each species in Lake Ontario was modified to account for a fixed seasonal effect (i.e., spring, summer, and fall), along with random trawl type effect because no prior fishing power correction has been established to standardize CPE estimates:

Equation 2.4.
$$d_{ijk} = \mu + Y_i + P_j + S_{ik} + U_{ijk} + T_{ijk} + P_j T_{ijk} + \varepsilon_{ijk}$$

where the mean depth of capture for each year (i), port (j), and season (k) is also affected by season in a given year (S_{ik}), along with trawl type used in a given year, port, and season (U_{ijk}). In all lakes, the estimated annual lake-wide mean depth of capture (\widehat{M}_i) for a given lake and species in year i is the sum of the overall global mean depth of capture and the estimated year effect of year i (i.e., $\widehat{M}_i = \widehat{\mu} + \widehat{Y}_i$). Significance of fixed covariates (year and season) was tested using an analysis of variance test (ANOVA). For each species in Lake Ontario, seasonal mean depth of capture was estimated and compared among seasons for each species using paired t-tests with a Bonferroni correction if the season effect was significant.

The annual mean depth of capture estimates (\widehat{M}_i) for each species and lake were fit to four different types of models (Riley and Adams 2010); 1) an intercept-only (null) model, where mean depth of capture remained constant over time with random variation, 2) a simple linear regression model where mean depth of capture varies annually with a linear trend, 3) a segmented linear regression model with a single change point where the annual linear trend before and after the change point is allowed to vary, and 4) a segmented regression model with two changepoints where the annual linear trends before and after both change points may vary. For all changepoint models, at least five years of annual mean depth of capture estimates must be used to estimate the linear trend of each segment. There were not enough years of data for round goby (all lakes) or deepwater sculpin (Lake Ontario) to fit changepoint models. The best fit model for each species in each lake was either selected by using Akaike's Information Criterion (adjusted for sample size, AIC_c ; Burnham and Anderson 2002), or ANOVA if no change point models were tested. For best-fit models that were selected using AIC_c , the Akaike weight was also calculated, indicating the weight of evidence for the best model relative to the other models considered; Burnham and Anderson 2002).

The Durbin-Watson test was used to test for first-order autocorrelation of residuals for all selected models (Bence 1995, Pyper and Peterman 1998, Riley and Adams 2010). In each lake, mean annual bottom water temperature was calculated at 55 m based on the methods of Riley and Adams (2010), where measurements of temperature from the trawl surveys performed at 55m (where available) were averaged for each year. Residuals of each selected model for annual mean depth of capture were tested for a significant correlation with the mean annual bottom water temperature at 55 m in each lake. For both autocorrelation and temperature correlation, a Bonferroni correction was applied to control for multiple comparisons. If any of the best fit models showed significant autocorrelation, they were then compared to the null model with autoregressive (AR1) error structure and the best fit model with an AR1 error structure using AICc. All statistical analyses were performed in R studio.

Spatiotemporal (Depth) Overlap Between Species

We estimated the degree of spatiotemporal overlap between slimy sculpins and gobies, as well as between slimy sculpins and deepwater sculpins in each lake, to assess if slimy sculpins are susceptible to habitat competition with round goby and deepwater sculpins in any of the lakes. In addition to calculating mean depth of capture for each year and port (Equation 2.1), or year, port, and season for Lake Ontario (Equation 2.3), the weighted variance in the depth range of each species around the mean (i.e., inertia, I) was first calculated as follows (Brodeur et al. 2014):

Equation 2.5.

$$I = \frac{\sum_{ij}(D_{ij}-d_{ij})^2 C_{ij}}{\sum_{ij} C_{ij}}$$

where inertia is defined as the mean square distance between a positive catch location and the center of gravity (i.e., mean depth of capture) of the population.

The mean depth of capture (Equation 2.1, or instead Equation 2.3 for Lake Ontario) and inertia (Equation 2.5) for each species were then used to calculate the global index of collocation (GIC):

Equation 6.
$$GIC_{ij} = 1 - \frac{\Delta d_{ij}^2}{\Delta d_{ij}^2 + I_1 + I_2}$$

where GIC_{ij} estimates the proportion of spatial overlap between two species in each year and port by comparing the difference in distance (i.e., depth) between the mean depths of capture of two species and their respective inertias (Bez and Rivoirard 2000, Woillez et al. 2009, Brodeur et al. 2014). The value of GIC ranges between 0 (complete spatial segregation) and 1 (complete spatial overlap, Brodeur et al. 2014).

Annual lake-wide GIC between species for each lake was estimated using a similar linear model to Equation 2.2 (Riley and Adams 2010) to account for port effects, Julian day effects, and random variation (i.e., $GIC_{ij} = \mu + Y_i + P_j + T_{ij} + P_j T_{ij} + \varepsilon_{ij}$), or the modified version of Equation 2.2 for Lake Ontario that also accounts for seasonal and trawl effects (i.e., $GIC_{ijk} = \mu + Y_i + P_j + S_{ik} + U_{ijk} + T_{ijk} + P_j T_{ijk} + \varepsilon_{ijk}$). The exception to using these equations was for assessing slimy sculpin and round goby overlap in Lake Huron, where port effects were excluded from the model due to the limited amount of port locations where both slimy sculpins and gobies were both caught. For Lake Ontario, seasonal GIC trends between species were compared using paired t-tests with a Bonferroni correction when seasonal effects were significant. For depth overlap between slimy sculpins and round gobies, intercept-only and simple linear regression models were fit to assess long-term trends, but no changepoint models

were assessed because there were a small number of years of data for round gobies. For depth overlap between slimy sculpins and deepwater sculpins, intercept-only, simple linear regression models, and both single and two changepoint models (where there were enough data) were fit. Again, the best fit models for in each case for each lake were selected either by using AIC_c (Akaike weight calculated for these best-fit models), or ANOVA if no change point models were tested. As with mean depth of capture, residuals of selected models were tested for first-order autocorrelation and correlation with mean bottom temperature at 55 m, with Bonferroni adjustment applied to control for multiple comparisons. Any best fit models that showed significant autocorrelation were compared to the null model with AR1 error structure and the best fit model with an AR1 error structure using AIC_c .

Results

Species Depth Distribution

Across all three lakes for the entire time series, the mean depth of capture ranged from 28.7–57.5 m for round gobies, 52.4–81.1 m for slimy sculpins, and 80.6–127.3 m for deepwater sculpins (Table 2.2). The variability explained by the models used to produce annual estimates of lake-wide mean depth of capture by accounting for effects of year, port, and day of year (and season for Lake Ontario) ranged from 34% to 100%. For all lakes and species, the year effect on mean depth of capture was statistically significant ($p < 0.05$), except for with slimy sculpins in Lake Huron and deepwater sculpins in Lake Ontario. In Lake Ontario, the seasonal effect ($p < 0.001$) was statistically significant for all three species.

Table 2.2. Mean depth (for entire times series of each species in each lake), R² values, and summary of fixed covariates used in models to estimate annual lake-wide mean depth of capture of slimy sculpins, deepwater sculpins, and round gobies for lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017). Models for lakes Huron and Michigan related annual port-specific mean depths of capture to year (fixed), port (random), Julian day (random), and the port and Julian day interaction (random). Models for Lake Ontario related annual port- and season-specific mean depths of capture to year (fixed), port (random), Julian day (random), season of the year (spring, summer, fall; fixed), trawl type (random), and the port and Julian Day interaction (random). Asterisks by p values indicate covariates that were statistically significant. Degrees of freedom for each model varied based on amount of years and seasons that were available for each species in each lake.

Lake/Species	Mean Depth (m)	R ²	Covariate	df	Chi-square	p
Huron, Round Goby	41.86	0.58	year	18	37.04	0.005*
Huron, Slimy Sculpin	52.44	0.34	year	33	32.24	0.505
Huron, Deepwater Sculpin	80.57	0.81	year	39	85.37	<0.001*
Michigan, Round Goby	28.67	0.84	year	13	24.88	0.024*
Michigan, Slimy Sculpin	67.06	0.53	year	42	93.02	<0.001*
Michigan, Deepwater Sculpin	96.44	0.52	year	42	61.98	0.024*
Ontario, Round Goby	57.49	0.89	year	15	41.34	<0.001*
			season	2	427.07	<0.001*
Ontario, Slimy Sculpin	81.05	0.73	year	39	379.70	<0.001*
			season	2	193.65	<0.001*
Ontario, Deepwater Sculpin	127.27	1.00	year	14	19.27	0.155
			season	2	53.70	<0.001*

For lakes Huron and Michigan, the best-fit models indicate that round goby have shifted deeper annually ($p = 0.005$ and $p = 0.043$, respectively, Figure 2.2, Table 2.3). There was no evidence of an annual trend in round goby mean depth of capture in Lake Ontario ($p = 0.606$, Figure 2.2, Table 2.3). In all lakes, slimy sculpin mean depth of capture trended deeper in recent years (Figure 2.2, Table 2.3). In Lake Huron, slimy sculpin mean depth of capture initially shifted deeper annually (1976–2001, $p = 0.032$), then shifted shallower (2001–2005, $p < 0.001$), and shifted deeper again recently (2005–2016, $p < 0.001$). In Lake Michigan, slimy sculpin mean depth of capture initially shifted shallower annually (1973–1983, $p < 0.001$), then deeper at a significant rate prior to 1989 (1983–1989, $p = 0.021$), then deeper at a not significant rate afterward (1989–2016, $p = 0.441$). In Lake Ontario, slimy sculpin mean depth of capture has trended deeper throughout the entire survey period from 1978–2017 ($p < 0.001$), with the steepest trends occurring after 2006. There is no evidence that deepwater sculpins have shifted deeper in recent years in any of the lakes, and instead appear to be migrating to shallower depths (Figure 2.2, Table 2.3). In Lake Huron, deepwater sculpin mean depth of capture trended significantly shallower from 1976–2016 ($p < 0.001$). In Lake Michigan, deepwater sculpin mean depth of capture initially trended shallower (1973–1984, $p = 0.001$), then deeper (1984–2002, $p < 0.001$), and then shallower (2002–2016, $p < 0.001$). There was no evidence of a significant annual trend in deepwater sculpin mean depth of capture in Lake Ontario ($p = 0.255$). Residuals for mean depth of capture did not show significant autocorrelation for any species. However, round goby mean depth of capture significantly correlated with annual mean bottom water temperature at 55 m correlations for any species.

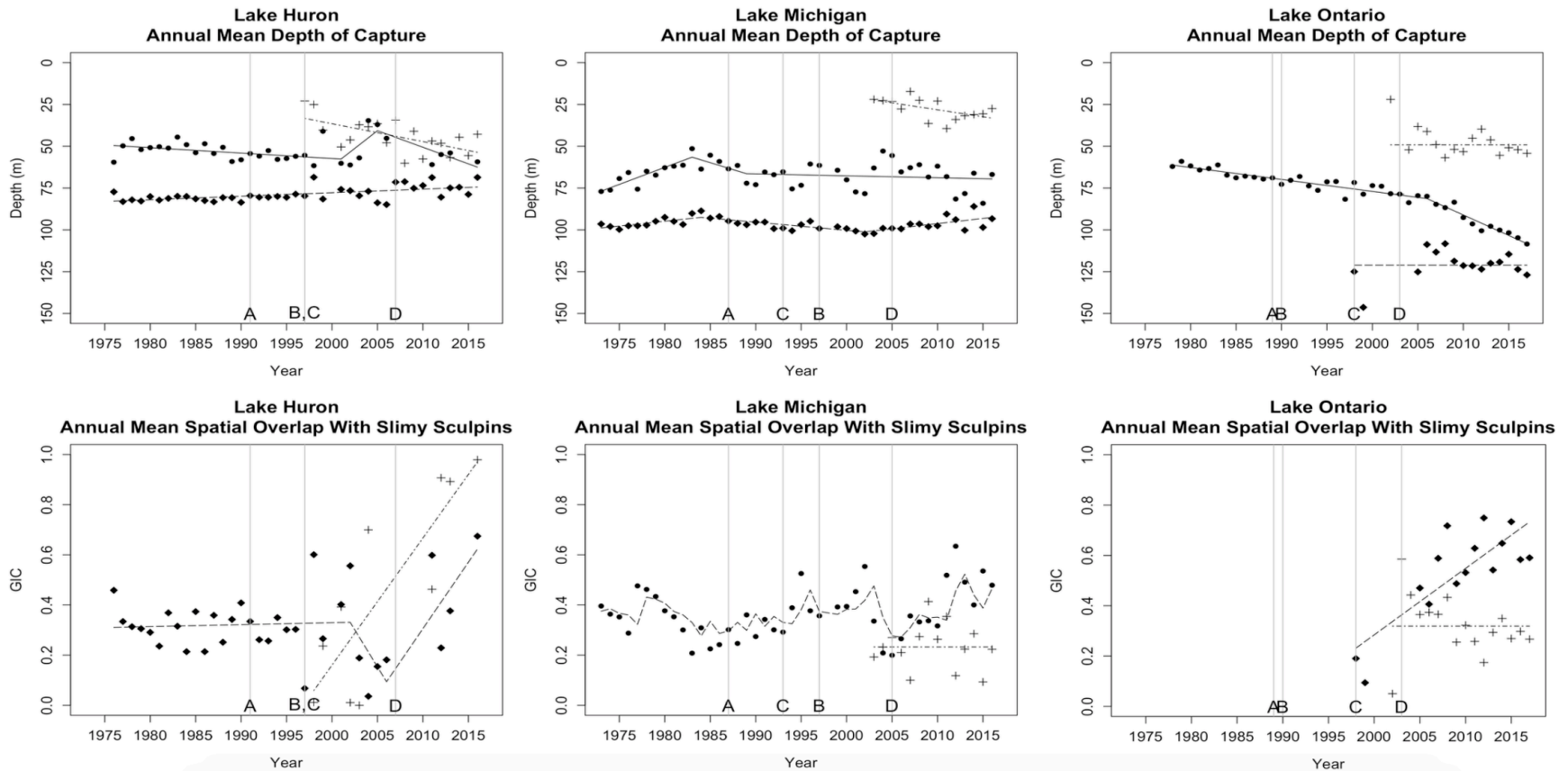


Figure 2.2. Top row: Annual mean depth of capture in meters and best-fit linear models for round gobies (cross symbols and black uneven dashed lines), slimy sculpins (closed circles and black solid lines), and deepwater sculpins (closed diamonds and black even dashed lines) for each lake (Huron, Michigan, and Ontario) between 1973–2017. Note that vertical axes are inverted (200–0 m) to display trends in terms of bathymetric distribution. Bottom row: Annual mean GIC and best-fit linear models between slimy sculpins and round gobies (cross symbols and black uneven dashed lines), and slimy sculpins and deepwater sculpins (closed diamonds and black even dashed lines) for each lake. Grey vertical lines in all graphs for various ecological changes that occurred in each lake, including A) zebra mussel invasion, B) quagga mussel invasion, C) round goby invasion, and D) *Diporeia* collapse. *Overlap for between sculpin species in Lake Michigan is based on the null model with AR-1 correlation.

Table 2.3. Summary of best-fit and other supported models for mean depth of capture of round goby, slimy sculpins, and deepwater sculpins for lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017), considering constant, linear, and changepoint model specifications (where applicable). In cases where change point models were considered, the best fit was selected using AIC_c, and the change point(s) of the best model is (are) given along with the Akaike weight. The number of other models with substantial support ($\Delta AIC_c \leq 2$) along with the year ranges of changepoints are also listed. In cases where no changepoint models were considered, ANOVA was used to determine if the linear regression model fit better than the null model. In all cases below, R² (except when the null model was the best-fit model) and the slopes of each line segment (where applicable) are given. Asterisks indicate slopes that were statistically significant. Negative slopes indicate a trend toward shallower water, and positive slopes a trend toward deeper water.

Lake	Species	Change point(s)	Akaike weight	R ²	Slopes			Other models with support	
					First	Second	Third	No.	Range of change points
Huron	round goby	N/A	N/A	0.38	1.07*			N/A	N/A
	slimy sculpin	2001, 2005	0.39	0.39	0.32*	-4.24*	1.98*	0	N/A
	deepwater sculpin	N/A	0.01	0.34	-0.21*			31	1980–1999, 2001–2006, 2009–2010, 2012
Michigan	round goby	N/A	N/A	0.30	0.83*			N/A	N/A
	slimy sculpin	1983, 1989	0.02	0.29	0.29*	1.65*	0.11	40	1979–1994, 2006–2010
	deepwater sculpin	1984, 2002	0.08	0.49	-0.58*	0.48*	-0.62*	8	1983–1985, 2000–2004
Ontario	round goby	N/A	N/A	N/A	0			N/A	N/A
	slimy sculpin	2006	0.03	0.96	0.72*	2.45*		19	1984–1990, 2005–2008, 2011–2013
	deepwater sculpin	N/A	N/A	N/A	0			N/A	N/A

In Lake Ontario, the 95% confidence intervals for round goby mean depth of capture were 59.64–95.24m in the spring, 6.78–43.33m in the summer, and 30.21–59.91m in the fall. The 95% confidence intervals for slimy sculpin mean depth of capture in Lake Ontario were 74.46–94.66m in the spring, 59.39–79.49m in the summer, and 70.02–90.57m in the fall. The 95% confidence intervals for deepwater sculpin mean depth of capture in Lake Ontario were 107.83–148.33m in the spring, 87.41–128.34 m in the summer, and 109.77–144.93m in the fall. In Lake Ontario, all three species occurred deeper during the fall and spring than in the summer, though the only significant differences in mean depth of capture were between spring and summer for all three species ($p < 0.001$, Table 2.4) and fall and summer for slimy sculpins ($p < 0.001$).

Table 2.4. Summary of paired t-test comparisons of seasonal mean depth of capture (last three columns) in Lake Ontario (1978–2017). For each paired t-test comparison of mean depth of capture between seasons of each species, the values listed (from left to right) are the estimated average depth difference (in meters) between the two seasons, the degrees of freedom, the t-statistic, and the Bonferroni-adjusted p-value. Asterisks indicate statistically significant seasonal depth differences.

Species	Spring vs Summer				Summer vs Fall				Fall vs Spring			
	Avg. Diff. (m)	df	t	p	Avg. Diff. (m)	df	t	p	Avg. Diff. (m)	df	t	p
Round Goby	52.38	270.74	20.286	<0.001*	-20.00	0.28	-3.786	1.000	32.38	0.26	6.287	1.000
Slimy Sculpin	15.12	347	13.696	<0.001*	-10.86	368	-6.003	<0.001*	4.26	276	2.395	0.052
Deepwater Sculpin	20.20	130.1	7.187	<0.001*	-19.48	17.1	-1.874	0.235	0.73	16.2	0.071	1.000

Spatiotemporal (Depth) Overlap Between Species

Across the lakes for the entire time series, the mean GIC ranged from 0.25–0.51 between slimy sculpins and round gobies, and from 0.31–0.62 between slimy sculpins and deepwater sculpins (Table 2.5). The variability explained by the models from which annual lakewide GIC values were estimated by accounting for effects of year, port, and day of year (and season for Lake Ontario) ranged from 24% to 87%. The effect of year on depth overlap between species was statistically significant in most cases ($p < 0.05$), except for depth overlap between slimy sculpin and gobies in Lake Huron ($p = 0.079$) and in Lake Michigan ($p = 0.510$). In Lake Ontario, the season effect was significant for slimy sculpin and round goby depth overlap ($p < 0.001$).

Since the invasion of round gobies, depth overlap between slimy sculpins and round gobies has significantly increased in Lake Huron ($p = 0.003$, Figure 2.2), but we found no evidence that depth overlap between slimy sculpins and round gobies has significantly changed in lakes Michigan and Ontario ($p > 0.32$, Figure 2.2, Table 2.6). There was no significant autocorrelation in residuals for depth overlap between slimy sculpins and gobies in any lake. However, residuals for GIC between slimy sculpins and gobies in Lake Ontario were weakly correlated with mean bottom water temperature at 55 m ($R^2 = 0.34$, $p = 0.017$).

Depth overlap between slimy sculpins and deepwater sculpins has either not changed or increased in recent years (Figure 2.2, Table 2.6). In Lake Huron, depth overlap between slimy sculpins and deepwater sculpins initially increased, though not significantly (1976–2002, $p = 0.796$), then decreased (2002–2006, $p = 0.025$), and increased again (2006–2016, $p < 0.001$). In Lake Michigan, the best fit model for depth overlap between slimy sculpins and deepwater sculpins had significant autocorrelation ($DW = 1.16$, $p < 0.001$). The best-fit model incorporating

Table 2.5. Mean GIC (for entire times series of each species combination in each lake), R^2 values, and summary of fixed covariates used in models Summary of covariates used to estimate annual lake-wide depth overlap (GIC) between slimy sculpins and round gobies, and between slimy sculpins and deepwater sculpins lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017). Models for lakes Huron and Michigan related annual port-specific GIC to year, port, Julian day, and the port and Julian day interaction, except for slimy sculpin and round goby depth overlap in Lake Huron where port effects were excluded due to limited data. Models for Lake Ontario related annual port- and season-specific GIC to year, port, Julian day, season of the year (spring, summer, fall), trawl type, and the port and Julian Day interaction. Slope coefficients are only listed for Julian day as this was the only covariate not treated as a factor. Asterisks by p values indicate covariates that were statistically significant. For depth overlap between slimy sculpin and round goby in Lake Huron, the F-statistic is listed instead since it was a fixed effect model.

Lake/Species	Mean GIC	R^2	Covariate	df	Chi-sq	p
Huron Slimy Sculpin and Round Goby	0.51	0.87	year	9	F = 3.77	0.079
Huron Slimy Sculpin and Deepwater Sculpin	0.31	0.78	year	33	48.03	0.044*
Michigan Slimy Sculpin and Round Goby	0.25	0.28	year	13	12.22	0.510
Michigan Slimy Sculpin and Deepwater Sculpin	0.37	0.59	year	42	86.73	<0.001*
Ontario Slimy Sculpin and Round Goby	0.31	0.85	year	15	42.12	<0.001*
			season	2	240.18	<0.001*
Ontario Slimy Sculpin and Deepwater Sculpin	0.62	0.24	year	14	26.93	0.020*
			season	2	1.83	0.400

Table 2.6. Summary of best-fit and other supported models for depth overlap (GIC) between slimy sculpins and round gobies, and slimy sculpins and deepwater sculpins for lakes Huron (1976–1999, 2001–2016), Michigan (1973–1997, 1999–2016), and Ontario (1978–2017), considering constant, linear, and changepoint model specifications (where applicable). In cases where change point models were considered, the best fit was selected using AIC_c, and the change point(s) of the best model is (are) given, along with the Akaike weight. The number of other models with substantial support ($\Delta AIC_c \leq 2$) along with the year ranges of changepoints are also listed. In cases where no changepoint models were considered, ANOVA was used to determine if the linear regression model fit better than the null model. In all cases below, R² (except when the null model was the best-fit model) and the slopes of each line segment (where applicable) are given. Asterisks indicate slopes that were statistically significant. Positive slopes indicate an increase in depth overlap between species, and negative slopes indicate a decrease in depth overlap between species. *For Lake Michigan, there was significant autocorrelation in overlap with between slimy sculpins and deepwater sculpins, and the best fit model was the AR-1 null model.

Lake	Species	Change point(s)	Akaike weight	R ²	Slopes			Other models with support	
					First	Second	Third	No.	Range of change points
Huron	slimy sculpin and round goby	N/A	N/A	0.70	0.05*			N/A	N/A
	slimy sculpin and deepwater sculpin	2002, 2006	0.10	0.34	0.0008	-0.06*	0.05*	2	2001, 2005–2006
Michigan	slimy sculpin and round goby	N/A	N/A	N/A	0			N/A	N/A
	slimy sculpin and deepwater sculpin	N/A	0.16	N/A*	0			1*	2008, 2012
Ontario	slimy sculpin and round goby	N/A	N/A	N/A	0			N/A	
	slimy sculpin and deepwater sculpin	N/A	N/A	0.65	0.03*			N/A	

AR1 error structure was the null model, indicating that depth overlap between slimy sculpins and deepwater sculpin had no significant pattern over time. Since the reappearance of deepwater sculpins in trawls in Lake Ontario, spatial overlap between slimy sculpins and deepwater sculpins has increased ($p < 0.001$). Aside from Lake Michigan, there was no significant autocorrelation in residuals for spatial overlap between slimy sculpins and deepwater sculpins. Residuals in GIC between slimy sculpins and deepwater sculpins were not correlated with mean bottom water temperature at 55 m in any of the lakes.

For Lake Ontario, 95% confidence intervals of slimy sculpin depth overlap with gobies ranged from 0.31–0.85 in the spring, -0.15–0.34 in the summer, and 0.11–0.39 in the fall. Slimy sculpins generally had the most depth overlap with gobies during the spring, though paired t-tests revealed that only the significant difference in slimy sculpins and goby depth overlap was between spring and summer ($p < 0.001$, Table 2.7). There was no significant seasonal variation in depth overlap between sculpin species ($p = 0.400$), with depth overlap between species ranging from 0–0.91.

Table 2.7. Summary of paired t-test comparisons of seasonal mean depth of capture (last three columns) in Lake Ontario (2002–2017). For each paired t-test comparison of GIC between slimy sculpins and gobies between seasons, the values listed (from left to right) are the estimated average depth difference (in meters) between the two seasons, the degrees of freedom, the t-statistic, and the Bonferroni-adjusted p-value. Asterisks indicate statistically significant seasonal depth differences. *Paired t-test were not performed for comparing depth overlap between slimy sculpins and deepwater sculpins because season was not a statistically significant predictor ($p = 0.263$, Table 7) for slimy sculpin and deepwater sculpin depth overlap in Lake Ontario.

Species	Spring vs Summer				Summer vs Fall				Fall vs Spring			
	Avg. Diff.	df	t	p	Avg. Diff.	df	t	p	Avg. Diff.	df	t	p
Slimy Sculpin and Round Goby	0.46	243.86	15.225	<0.001*	-0.13	2.19	-1.490	0.793	0.33	2.22	3.822	0.158

Discussion

The proliferation of round gobies in the Great Lakes has been associated with declines in abundance of native sculpins, including mottled sculpins in southern Lake Michigan (Janssen and Jude 2001) and juvenile slimy sculpins in Lake Ontario (Weidel et al 2016a). Additionally, laboratory studies of interactions between gobies and sculpins (i.e., mottled sculpins and spoonhead sculpins, *Cottus ricei*) indicate that aggressive round gobies may displace sculpins from their habitat and outcompete sculpins for food resources, or even consume sculpin eggs (Dubs and Corkum 1996, Bergstrom and Mensinger 2009, Hirsch et al. 2016). Seasonal offshore migration of round gobies in the Great Lakes would allow for round gobies to potentially displace slimy and deepwater sculpins from their habitat, and in light of *Diporeia* collapse, monopolize limited prey resources (Owens and Dittman 2003, Hondorp et al. 2005, Walsh et al. 2008, French et al. 2010). In offshore waters Lake Huron (> 50 m), gobies tend to rely more on *Mysis* and other native invertebrates rather than dreissenid mussels (Schaeffer et al. 2005), which may explain the recent scarcity of slimy sculpins in Lake Huron in relation to gobies shifting deeper. Consistent with other studies (Schaeffer et al. 2005, Walsh et al. 2007), we observed seasonal offshore migration of gobies in Lake Ontario in fall and spring, with depths typically ranging from 40–90 m during this period, and also found evidence of round gobies shifting to deeper depths since their initial invasion in lakes Huron and Michigan (Figure 2.2, Table 2.3). Although there was no evidence of an annual trend in mean depth of capture of round gobies in Lake Ontario (Figure 2.2, Table 2.3), there was a considerable amount of variability in their bathymetric distribution (ranging from 5 – 142 m), with gobies nearly spanning the entire depth range analyzed in the lake. The observed variability in round goby depth distribution in Lake

Ontario may, in part, be a representation of sampling throughout the year rather than just the fall, as was the case with the other lakes.

Slimy sculpins appear to have also shifted deeper in all three lakes (though not significantly in Lake Michigan), though we found no evidence of a change in overlap between slimy sculpins and gobies (Figure 2.2, Table 2.6). The lack of an increase in depth overlap between round gobies and slimy sculpins could be due to slimy sculpins maintaining depth segregation with round gobies to avoid interactions with this aggressive competitor. However, our analysis does not suggest that slimy sculpin distribution is directly, or at least exclusively, affected by round goby competition for food and habitat in all the lakes, as shifts of slimy sculpins to deeper depths in lakes Michigan and Ontario actually precede round goby invasion in these lakes. Additionally, slimy sculpins have become absent or scarce in the most recent trawl surveys (2014–2016) in Lake Huron (Riley et al. 2017), which could skew annual depth estimates due to small sample sizes and exaggerate the increase in and degree of depth overlap between slimy sculpins and round gobies. Of course, it is also plausible that the recent scarcity of slimy sculpins in Lake Huron is related to round gobies colonizing deeper, and it appears that slimy sculpins in Lake Huron began shifting deeper coincident with round gobies invading slimy sculpin depth habitat. (Figure 2.2). Similarly, in Lake Ontario the most recent and rapid increase in mean depth of capture of slimy sculpins seems to coincide with round goby appearance in trawl surveys.

Conversely to slimy sculpins, we found no evidence that deepwater sculpins are shifting to deeper depths to maintain spatial segregation with slimy sculpins or avoid gobies. In fact, deepwater sculpins appear to be shifting to shallower depths on average in lakes Huron and Michigan, and possibly in Lake Ontario based on their recent reappearance in trawl surveys

(Figure 2.2, Table 2.3). Also, depth overlap between deepwater and slimy sculpins more recently appears to be greater than it has historically been in trawl surveys in lakes Huron and Ontario (Figure 2.2, Table 2.6). However, greater densities of deepwater sculpins caught in offshore trawls beyond depths typically sampled in surveys imply that the population dynamics of deepwater sculpins are not adequately represented by the trawl data (O'Brien et al. 2009, Bunnell et al. 2017, Weidel et al. 2016a). Therefore, the degree of depth overlap between slimy sculpins and deepwater sculpins may also be overestimated. Even so, the shift of slimy sculpins to deeper depths and the consequent increase in spatial overlap between sculpin species could eventually lead to interspecific competition for habitat and food resources, especially considering that diet partitioning may become more difficult to maintain given the lack of *Diporeia*. Food competition between slimy and deepwater sculpins would be likely to occur in offshore waters of Lake Michigan, where both sculpin species have substantial diet overlap with regard to *Mysis* (Bunnell et al. 2015). If so, slimy sculpins would likely have the greater disadvantage as they tend to rely more heavily on *Diporeia* than deepwater sculpins (Hondorp et al. 2011), and according to our results, slimy sculpins may have more frequent encounters than deepwater sculpins with aggressive round gobies.

As previously mentioned, trends in depth habitat usage of sculpins are probably not influenced exclusively by round gobies, and may also be influenced by other ecological or environmental factors. Bunnell and others (2014) suggest that both bottom-up controls (in all three lakes) and top-down controls (in Lake Michigan), may influence fish population dynamics. Dreissenid mussels have been linked to declines in phytoplankton primary productivity (Vanderploeg et al. 2010, 2012), *Diporeia* collapse (Vanderploeg et al. 2002, Watkins et al. 2007), round goby expansion (Jude et al. 1995), and increased water clarity (Vanderploeg et al.

2012). All of these changes may affect the availability and distribution of alternate prey sources for sculpins (e.g., mysids and chironomids) in various ways, and sculpins might be migrating to areas where *Diporeia* remain or alternate prey species (e.g., *Mysis*) are more abundant. In Lake Michigan, trends of slimy sculpins shifting deeper would align with higher densities of *Mysis* offshore (Pothoven et al. 2004).

It is also plausible that predation affects sculpin depth distribution. In Lake Michigan, slimy sculpin abundances have been inversely related to juvenile lake trout predation, whereas deepwater sculpin abundances have been linked to alewife predation on deepwater sculpin pelagic larvae and burbot predation on juvenile and adult deepwater sculpins (Madenjian et al. 2005). Lake trout predation remains a plausible influence on slimy sculpin abundance and depth distribution patterns, as salmonine biomass and natural reproduction has increased as a result of effective stocking programs and sea lamprey control (Bunnell et al. 2014), and catches of sculpins in trawls can be affected by salmonine (stocking) location (Lake Trout Working Group 2014, Madenjian et al. 2015). However, lower abundances of burbot (in lake Michigan) and alewife (in all three lakes) in recent years do not support the hypothesis that burbot or alewife predation are driving the recent sculpin abundance declines (Bunnell et al. 2017). Either independent of or in conjunction with interspecific interactions, variability depth distribution patterns of slimy and deepwater sculpins could simply relate to the declining abundance of both these species throughout the lakes, and depth distribution patterns may be a result of these species being restricted to only their preferred habitat. As for deepwater sculpin occurring in shallower depths in recent years, this could relate to deepwater sculpin expanding their depth range as they have recently reappeared in trawl surveys.

Aside from complex ecological and physical processes confounding our interpretation of results, limitations of the trawl data must also be considered. As a general concern for any species captured in these surveys, catchability for different trawl designs was not always known, which may have led to biased CPE estimates. On a species-specific level, trawl surveys did not sufficiently sample deepwater sculpin depth habitat (O'Brien et al. 2009, Bunnell et al. 2017, Weidel et al. 2016a), nor did they reach areas with rocky substrates, which may be more ideal habitat for both gobies and sculpins (Janssen et al. 2005). Concerning the hypotheses of this study, the lack of consistent data collection on other aforementioned factors (i.e., *Mysis/Diporeia* availability, dreissenid mussel, alewife, and predator abundance/distribution, water clarity, etc.) that may affect sculpin depth distribution at these sites prevented us from analyzing a comprehensive set of covariates. Having such data would have allowed us to parse out which ecosystem changes were actually relevant, especially considering the close timing of many potentially relevant ecosystem changes in the lakes (Figure 2).

Despite the ecological and data complexities, the depth distribution patterns assessed in this study show that gobies are indeed colonizing offshore (seasonally and/or annually), allowing for increased potential for interaction between gobies and (slimy) sculpins in the Great Lakes. However, the implications of these sculpin-goby interactions remain unclear, and should be further investigated in behavioral studies in both laboratory experiments and field observations. Recent assessments indicate that the abundance and biomass and preyfishes in the Great Lakes has declined (Bunnell et al. 2017, Riley et al. 2017), which could have cascading effects for higher trophic levels.

REFERENCES

REFERENCES

- Adams, J.V., Riley, S.C., and Adlerstein, S.A. 2009. Development of fishing power corrections for 12-m Yankee and 21-m wing trawls used in the USGS Lake Huron fall bottom trawl survey. Great Lakes Fish Comm Tech Rep No 68. Ann Arbor, MI
- Balshine, S., Verma, A., Chant, V., and Theysmeyer, T. 2005. Competitive interactions between round gobies and logperch. *J. Great Lakes Res.* 31:68–77.
- Bence, J.R. 1995. Analysis of short time series: correcting for autocorrelation. *Ecology* 76:628–639.
- Bergstrom, M.A., and Mensinger, A.F. 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. *Trans. Am. Fish. Soc.* 138:1009–1017.
- Bez, N., and Rivoirard, J. 2000. Indices of collocation between populations. *In*, Checkley DM, Hunter JR, Motos L, van der Lingen CL eds. Report of a Workshop on the Use of Continuous Underway Fish Egg Sampler (CUFES) for Mapping Spawning Habitat of Pelagic Fish. GLOBEC Report 14, GLOBEC International, Plymouth, p 48–52.
- Brodeur, R.D., Barceló, C., Robinson, K.L., Daly, E.A., and Ruzicka, J.J. 2014. Spatial overlap between forage fishes and the large medusa *Chrysaora fuscescens* in the northern California Current region. *Mar. Ecol. Prog. Ser.* 510:167–181.
- Bronte, C.R. et al. 2003. Fish community change in Lake Superior, 1970– 2003. *Can. J. Fish. Aquat. Sci.* 60:1552–1574.
- Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., and Weidel, B.C. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. *Bioscience* 64(1):26–39.
- Bunnell, D.B., Davis, B.M., Chriscinske, M.A., Keeler, K.M., and Mychek-Londer, J. G. 2015. Diet shifts by planktivorous and benthivorous fishes in northern Lake Michigan in response to ecosystem changes. *J. Great Lakes Res.* 41(3):161–171.
- Bunnell, D.B., Madenjian, C.P., and Claramunt, R.M. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 63:2434–2446.
- Bunnell, D.B., Madenjian, C.P., Desorcie, T.J., Kostich, M., Armenio, P., and Adams, J. 2017. Status and trends of prey fish populations in Lake Michigan, 2016. U.S. Geological Survey.

Ann Arbor, MI.

- Burnham, K. P., and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Charlebois, P.M., Marsden, J.E., Goettel, R.G., Wolfe, R.K., Jude, D.J., Rudnika, S. 1997. The round goby, *Neogobius melanostomus* (Pallus), a review of European and North American literature. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey (76 pp.)
- Cook, D.G., Johnson, G., 1974. Benthic macroinvertebrates of the St. Lawrence Great Lakes. *J. Fish. Res. Bd. Can.* 31:763–782.
- Dubs, D.O.L., and Corkum, L.D. 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). *J. Great Lakes Res.* 22:838–844.
- French III, J.R.P., and Jude, D.J. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *J. Great Lakes Res.* 27:300–311.
- French III, J.R.P., Stickel, R.G., Stockdale, B.A., and Black, M.G. 2010. A short-term look at potential changes in Lake Michigan slimy sculpin diets. *J. Great Lakes Res.* 36:376–379.
- Hirsch, P.E., N’Guyen, A., Adrian-Kalchhauser, I., and Burkhardt-Holm, P. 2016. What do we really know about the impacts of one of the 100 worst invaders in Europe? A reality check. *Ambio* 45:267–279.
- Hondorp, D.W., Pothoven, S.A., and Brandt, S.B., 2005. Influence of Diporeia density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. *Trans. Am. Fish. Soc.* 134:588–601.
- Hondorp, D.W., Pothoven, S.A., and Brandt, S.B. 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.* 37:165–172.
- Janssen J., Berg, M.B., and Lozano S.J. 2005. Submerged terra incognita: Lake Michigan’s abundant but unknown rocky zones. In *State of Lake Michigan: Ecology, Health and Management*, ed. TA Edsall, M Munawar, pp. 113–39. Ecovis. World Monogr. Ser. Amsterdam: Academic
- Janssen, J., and Jude, D.J. 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.* 27:319–328.
- Jude, D. J. 2001. Round and tubenose gobies: 10 years with the latest Great Lakes phantom menace. *Dreissena* 11:1-14.

- Jude, D.J. and DeBoe, S.F. 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. *Can. J. Fish. Aquat. Sci.* 53(1): 136–141.
- Jude, D.J., Janssen, J., and Crawford, G. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit Rivers. pp. 447–460 *In* The Lake Huron ecosystem: ecology, fisheries, and management. M. Munawar, T. Edsall, and J. Leach, *eds.* The Netherlands: S.P.B. Academic Publishing.
- Kraft, C.E., and Kitchell, J.F. 1986. Partitioning of food resources by sculpins in Lake Michigan. *Environ. Biol. Fishes* 16:309–316.
- Lake Trout Working Group, 2014. 2013 Lake Michigan Lake Trout Working Group report. A Report to the Great Lakes Fishery Commission. Lake Michigan Committee, Windsor, Ontario (March 26, 2014).
- Lauer, T.E., Allen, P.J., and McComish, T.S. 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.* 133:185–189.
- Madenjian, C.P., Bunnell, D.B., Warner, D.M., Pothoven, S.A., Fahnenstiel, G.L., Nalepa, T.F., Vanderploeg, H.A., Tsehaye, I., Claramunt, R.M., and Clark Jr., R.D. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: a synthesis. *J. Great Lakes Res.* 41(3):217–231.
- Madenjian, C.P. et al. 2002. Dynamics of the Lake Michigan food web, 1970-2000. *Can. J. Fish. Aquat. Sci.* 59:736–753.
- Madenjian, C.P., Hondorp, D.W., Desorcie, T.J., and Holuszko, J.D. 2005. Sculpin community dynamics in Lake Michigan. *J. Great Lakes Res.* 31:267–276.
- Miller, P.J. 1986. Gobiidae. *In* Fishes of the northeast Atlantic and Mediterranean, eds. P.J.P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen, and E. Tor-tonese, pp. 1019–1095. UNESCO, Paris.
- Mychek-Londer, J.G., Bunnell, D.B., Stott, W., Diana, J.S., French, J.R.P., and Chriscinske, M.A. 2013. Using diets to reveal overlap and egg predation among benthivorous fishes in Lake Michigan. *Trans. Am. Fish. Soc.* 142:492–504.
- Nalepa T.F. 1989. Estimates of macroinvertebrate biomass in Lake Michigan. *J. Great Lakes Res.* 15:437–443.
- Nalepa, T.F., Fanslow, D.L., and Pothoven, S.A. 2010. Recent changes in density, biomass, recruitment, size structure, and nutritional state of Dreissena populations in Southern Lake Michigan. *J. Great Lakes Res.* 36:5–19.

- O'Brien, T.P., Roseman, E.F., Kiley, C.S., and Schaeffer, J.S. 2009. Fall diet and bathymetric distribution of deepwater sculpin (*Myoxocephalus thompsonii*) in Lake Huron. *J. Great Lakes Res.* 35:464–472.
- Owens, R.W., and Bergstedt, R.A. 1994. Response of slimy sculpins to predation by juvenile lake trout in southern Lake Ontario. *Trans. Am. Fish. Soc.* 123:28–36.
- Owens, R.W., and Dittman, D.E. 2003. Shifts in the diets of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod *Diporeia*. *Aquat. Ecosyst. Health Manag.* 6:311–323.
- Owens, R. W., O’Gorman, R., Eckert, T.H., Lantry, B.F., 2003. The offshore fish community in southern Lake Ontario. In: M. Munawar (Ed.), *State of Lake Ontario (SOLO): Past, Present, and Future*. Ecovision World Monograph Series. Aquatic Ecosystem Health and Management Society.
- Pothoven, S.A., Fahnenstiel, G.L., Vanderploeg, H.A. 2004. Spatial distribution, biomass, and population dynamics of *Mysis relicta* in Lake Michigan. *Hydrobiologia* 522: 291–299.
- Pyper, B.J., and Peterman, R.M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* 55:2127–2140.
- Ray, W.J., and Corkum, L.D. 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environ. Biol. Fishes* 50:267–273.
- Riley, S.C., and Adams, J.V. 2010. Long-term trends in habitat use of offshore demersal fishes in Western Lake Huron suggest large-scale ecosystem change. *Trans. Am. Fish. Soc.* 139:1322–1334.
- Riley, S.C., Roseman, E.F., Hondorp, D.W., Chriscinske, M.A., Galassini, E., and Smith, M. 2017. Status and trends of the Lake Huron offshore demersal fish community, 1976–2016. U.S. Geological Survey. Ann Arbor, MI.
- Roseman, E.F., and Riley, S.C. 2009. Biomass of deepwater demersal forage fishes in Lake Huron, 1994–2007: implications for offshore predators. *Aquat. Ecosyst. Health Manag.* 12:29–36.
- Selgeby, J.H. 1988. Comparative biology of the sculpins of Lake Superior. *J. Great Lakes Res.* 14:44–51.
- Schaeffer, J. S., Bowen, A., Thomas, M., French III, J.R.P., and Curtis, G.L. 2005. Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in western Lake Huron, USA. *J. Great Lakes Res.* 31:414–425.
- Walsh, M.G., Dittman, D.E., and O’Gorman, R.O. 2007. Occurrence and food habits of the round goby in the profundal zone of Southwestern Lake Ontario. *J. Great Lakes Res.*

33:83–92.

- Walsh, M.G., O’Gorman, R., Strang, T., Edwards, W.H., and Rudstam, L.G. 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 Manag.* 11:368–376.
- Watkins, J.M., Dermott, R., Lozano, S.J., Mills, E.L., Rudstam, L.G., Scharold, J.V. 2007. Evidence for remote effects of dreissenid mussels on the amphipod *Diporeia*: analysis of Lake Ontario benthic surveys, 1972–2003. *J. Great Lakes Res.* 33:642–657.
- Weidel, B.C., Walsh, M.G., Holden, J.P., Connerton, M.J., 2016a. Lake Ontario benthic prey fish assessment, 2015. 2015 Annual Report, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee.
- Weidel, B.C., Walsh, M.G., Connerton, M.J., Lantry, B.F., Lantry, J.R., Holden, J.P., Yuille, M.J., and Hoyle, J.A.. 2016b. Deepwater sculpin status and recovery in Lake Ontario. *J. Great Lakes Res.* 43(5): 854-862.
- Wells, L. and McLain, A.L. 1973. Lake Michigan: man’s effects on native fish stocks and other biota. Great Lakes Fishery Commission Tech. Rep. 20.
- Wuillez M., Rivoirard, J., and Petitgas, P. 2009. Notes on survey based spatial indicators for monitoring fish populations. *Aquatic Living Resources* 22: 155–164.
- Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., Pothoven, S.A. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *J. Great Lakes Res.* 36(3):50–59.
- Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 59:1209–1228.
- Vanderploeg, H.A. et al. 2012. Seasonal zooplankton dynamics in Lake Michigan: Disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *J. Great Lakes Res.* 38:336–352.
- Van Oosten, J., and Deason, H.J. 1938. The food of the lake trout (*Cristovomer namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan. *Trans. Am. Fish. Soc.* 67:155–177.
- Vinson, M., Evrard, L., Gorman, O.T., and Yule, D.L. 2017. Status and trends in the Lake Superior fish community, 2016. U.S. Geological Survey. Ashland, WI
- Zimmerman, M.S., and Krueger, C.C. 2009. An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. *N. Am. J. Fish. Manag.* 29:1352–1371.

CHAPTER 3. SLIMY AND DEEPWATER SCULPIN BODY CONDITION IN THE GREAT LAKES AND LAKE CHAMPLAIN

Abstract

In the Great Lakes, slimy and deepwater sculpins declined in abundance in recent decades. Concurrent with these declines in sculpin abundance, several ecological disturbances have occurred, including the invasion of dreissenid mussels and round gobies, and the disappearance of *Diporeia*. We used trawl data from the USGS to assess long-term changes in sculpin body condition in lakes Huron (deepwater sculpin) and Ontario (slimy sculpin), and we predicted that sculpin body condition has declined after the invasion of dreissenid mussels and subsequent ecological disturbances. We also used trawl data from both the USGS and University of Vermont to compare current sculpin body condition among lakes Huron, Michigan, Ontario, Superior, and Champlain, and we predicted that sculpin body condition would be greater in lakes where dreissenid mussels (and other ecological disturbances) are not as prevalent (i.e., Lake Champlain and Lake Superior). We did not find significant evidence of a long-term decline in body condition for either deepwater sculpin body condition in Lake Huron and slimy sculpin body condition in Lake Ontario following dreissenid mussel invasion. As predicted, current body condition of slimy sculpins was significantly greater in less disturbed lakes than the more disturbed lakes. Deepwater sculpin body condition was not significantly different among Superior and the more disturbed lakes. Although sculpin body condition may be affected by these ecological disturbances to some degree, we did not find evidence of a significant long-term effect of these ecological disturbances on sculpin body condition, or conclusive evidence that these ecological disturbances strongly affect sculpin body condition. Our results suggest that other factors (e.g., life history, prey dynamics, environmental variables) play a greater role in determining sculpin body condition.

Introduction

Slimy sculpins (*Cottus cognatus*) and deepwater sculpins (*Myoxocephalus thompsonii*) are ecologically important in the Great Lakes because they historically have been the most prevalent native benthic species (Bronte et al. 2003, Owens et al. 2003, Bunnell et al. 2006, Roseman and Riley 2009), they serve as prey for native predators (e.g., juvenile lake trout, *Salvelinus namaycush*; burbot, *Lota lota*; Van Oosten and Deason 1938, Owens and Bergstedt 1994, Madenjian et al. 2002), and they are trophic intermediates between benthic and pelagic environments (Fratt et al. 1997, Madenjian et al. 1998). However, based on USGS trawl survey estimates, both of these sculpin species have declined in abundance in the Great Lakes since the late 1980s (Weidel et al. 2016a, Bunnell et al. 2017, Riley et al. 2017, Vinson et al. 2017), except for a resurgence of deepwater sculpin in recent years in Lake Ontario (Weidel et al. 2016b). Declines in sculpin abundance in recent years appear to be concurrent with several ecological disturbances, including the invasion of non-native species from the Ponto-Caspian region (i.e., zebra mussels, *Dreissena polymorpha*; quagga mussels, *D. bugensis*; round gobies, *Neogobius melanostomus*), as well as shifts in prey composition and availability (i.e., *Diporeia* spp. collapse). Slimy and deepwater sculpins have historically coexisted in part because of depth and prey partitioning in that slimy sculpins occur shallower than deepwater sculpins, and slimy sculpins prefer *Diporeia* over *Mysis relicta* while deepwater sculpins prefer *Mysis* over *Diporeia* (Hondorp et al. 2011). The invasion of the dreissenid mussels has been linked to the collapse of *Diporeia* (Nalepa et al. 2009, 2010), and therefore may indirectly make foraging more difficult for sculpins, as both sculpin species rely more on *Mysis* (Owens and Dittman 2003, Pothoven et al. 2011, Madenjian et al. 2015). However, *Mysis* production has also been declining in Lake Michigan (Pothoven and Bunnell 2016), which would make it even more difficult for slimy and

deepwater sculpins to meet their dietary needs since *Mysis* is their second most important prey source (Selgeby 1988).

In addition to the invasion of dreissenid mussels and prey declines, the invasion of round gobies may also affect slimy and deepwater sculpins in the Great Lakes. Previous studies indicate that round gobies are an aggressive species capable of outcompeting other sculpin species for food and habitat (e.g., spoonhead sculpin, *Cottus ricei*, Bergstrom and Mensinger 2009; mottled sculpin, *Cottus bairdii*, Dubs and Corkum 1996, Jude and DeBoe 1996, Charlebois et al. 1997, French and Jude 2001, Janssen and Jude 2001, Jude 2001, Ray and Corkum 2001, Lauer et al. 2004, Balshine et al. 2005). Round gobies overwinter offshore in the Great Lakes where slimy sculpin and deepwater sculpin may reside (Miller 1986, Schaeffer et al. 2005, Walsh et al. 2007), and round gobies have been found to consume *Mysis* in offshore waters in lakes Huron and Michigan (Schaeffer et al. 2005, Mychek-Londer et al. 2013). Both the occurrence of aggressive gobies and the consumption of *Mysis* by gobies and sculpins may allow for more interactions and potentially competition (for food or habitat) between round goby and these sculpin species.

The objective of this study was to assess if slimy sculpin and deepwater sculpin body condition has declined in relation to these ecological disturbances. We predicted that sculpin body condition has declined after dreissenid mussel invasion (i.e., the first of these ecological disturbances) in the Great Lakes. Among all lakes in this study, we also predicted that current sculpin body condition would generally be lower in lakes where these ecological disturbances have occurred earlier in time and have been of greater magnitude (e.g., greater abundance of invasive species). We defined lakes Superior and Champlain as “less disturbed” by these ecological changes than lakes Huron, Michigan, and Ontario. We defined Lake Superior as “less

disturbed” because dreissenid mussels and gobies have not yet become abundant, and *Diporeia* still persist in this lake (Barbiero et al. 2011, Bunnell et al. 2014). Lake Champlain was defined as less disturbed because although it has also been invaded by zebra mussels (Herbst et al. 2017), it has not been invaded by either quagga mussels or round gobies.

Methods

Trawl Surveys

For lakes Huron, Michigan, Ontario, and Superior, the USGS performed bottom trawl surveys between the 1970s and 2017 (Table 3.1, Figure 3.1). Bottom trawl surveys were also performed by University of Vermont for Lake Champlain between 2015–2017 (Table 3.1, Figure 3.1). Surveys were performed at various times of year depending on the lake, with surveys broadly occurring between April and November. Most trawl surveys occurred in fall in lakes Huron, Michigan, and Ontario, whereas trawl surveys primarily occurred in the spring and summer in lakes Superior and Champlain. In all lakes except for Lake Superior, trawl surveys were carried out by performing transects at fixed depth contours. In Lake Superior, trawls were instead performed at a series of long-term stations at various nearshore and offshore locations throughout the lake. Other sampling protocols that varied among the lakes were the depth range sampled (Table 3.1) and gear types for trawls.

Table 3.1. Data used for sculpin body condition analyses for each lake.

Lake	Years	Months	Number of Ports	Depths sampled (m)
Champlain Slimy sculpin	2015–2017	Apr.–Jul., Oct.	15	34–64
Huron Deepwater sculpin	1979,1980, 2002, 2017–2018	Oct.–Nov.	5	37–110
Michigan Slimy sculpin	2016–2018	Sept.	7	18–128
Deepwater sculpin	2016–2018	Aug.–Oct.	7	46–128
Ontario Slimy sculpin	1978–1982, 1984–2000 2005–2018	Aug.–Nov.	27	15–175
Deepwater sculpin	2015–2018	Apr.–Nov.	3	35–225
Superior Slimy sculpin	2017	May–Jul.	22	11–270
Deepwater sculpin	2017	May–Jul.	22	3.9–271

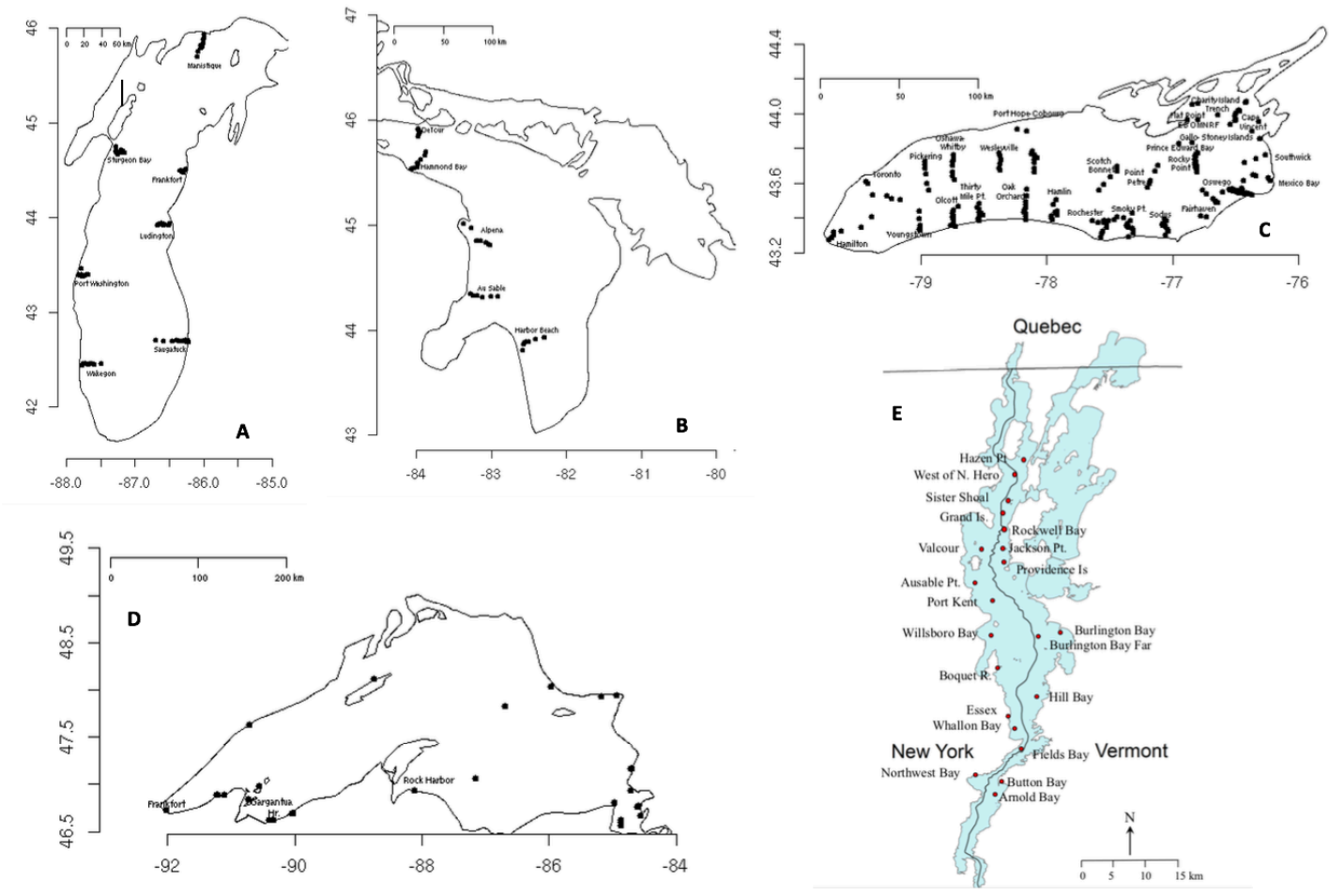


Figure 3.1. Maps with trawl sites for lakes A) Michigan, B) Huron, C) Ontario, D) Superior, and E) Champlain.

Body Condition

Both slimy and deepwater sculpin were measured individually for total length (TL, mm) and wet weight (g) in lakes Michigan, Ontario, and Superior. Data for slimy sculpins were insufficient in Lake Huron, so analyses were restricted to deepwater sculpins in this lake. Lake Champlain does not have deepwater sculpins, so only slimy sculpin TL and wet weight were measured for this lake. Most sculpin specimens were not measured immediately after collection and were instead frozen and later measured in the laboratory. Long-term analyses were only performed for deepwater sculpin in Lake Huron and slimy sculpin in Lake Ontario, due to lack of length and weight data prior to dreissenid mussel invasion for any sculpin populations in other lakes. Long-term analyses were restricted to only fall data. Current sculpin body condition analyses included only length-weight data from 2015–2018 for each species in each lake. For all analyses of body condition for each species and lake, we first determined the best-fit allometric growth relationship, with some of these relationships including fixed (year) and random (port) covariates. We used the log-length log-weight relationship for allometric growth

Equation 3.1.
$$\log W_i = \log a + b \log L_i$$

where W_i is wet weight of each sculpin, L_i is the total length of each fish, and a and b are coefficients estimated by regression analysis. In addition to Equation 3.1, we tested modified versions of this equation in both the long-term and current sculpin body condition analyses. In the long-term analyses for each species and lake (deepwater sculpin, Lake Huron; slimy sculpin, Lake Ontario), modified versions of Equation 3.1 included either a fixed year covariate (as the length-weight relationship may have temporal variation), a random port covariate (as individual

observations within ports may not be independent of each other), or both a fixed year and random port covariate. For each covariate included, the slope and/or intercept was allowed to vary. Modified versions of Equation 3.1 for current sculpin body condition analyses included either a random lake or a hierarchical random port within lake effect (to allow the length-weight relationship to differ among lakes, and to account for lack of independence of individual observations). For both long-term and current sculpin body condition analyses, the best logarithmic length-weight model was selected using Akaike's information criterion with the small sample size correction (AIC_c ; Burnham and Anderson 2002).

For each analysis, the best-fit allometric model was then used to estimate relative condition factor (K_n). Relative condition factor was calculated for each individual sculpin (Le Cren 1951)

Equation 3.2.
$$K_n = \frac{W}{W_i}$$

as the proportion of an individual sculpins observed wet weight (g) relative to its back-transformed (with bias correction $\frac{\sigma^2}{2}$) predicted weight (W_i) based on the best fit length-weight model (based on Equation 3.1 or a modified form of Equation 3.1). In the long-term sculpin body condition analyses, we compared relative condition factor before and after dreissenid mussel invasion for deepwater sculpins in Lake Huron (before 1979–1994, after 1995–2018) and slimy sculpins in Lake Ontario (before 1978–1988, after 1989–2018) with an analysis of variance (ANOVA). In current sculpin body condition analyses for each species, we compared relative condition factor among less disturbed and more disturbed lakes using ANOVA as well. For slimy sculpin body condition, lakes Superior and Champlain (less disturbed lakes) were compared to lakes Michigan and Ontario (more disturbed lakes). For deepwater sculpin body

condition, Lake Superior (less disturbed lake) was compared to lakes Huron, Michigan, and Ontario (more disturbed lakes). All analyses were performed in R studio.

Results

Long-term Sculpin Body Condition

In Lake Huron, the best fit logarithmic length-weight model for deepwater sculpin included a fixed year effect with varying slope and intercept and a random effect of port with varying slope and intercept (Table 3.2). No other models were within the confidence set of models ($\Delta AIC_c \leq 2$ from the best fit model), and these other models all had low Akaike weights (< 0.01). Deepwater sculpin body condition was lower after zebra mussel invasion ($K_n = 1.00 \pm 0.01$) than before zebra mussel invasion ($K_n = 1.02 \pm 0.01$), but the difference was not statistically significant ($p = 0.07$, $df = 1$, $F = 3.26$).

In Lake Ontario, the best fit logarithmic length-weight model for slimy sculpin body condition included a fixed year effect with varying slope and intercept. No other models were within the confidence set of models, and these other models all had low Akaike weights (Akaike weight < 0.01). Slimy sculpin body condition was lower after zebra mussel invasion ($K_n = 1.01 \pm 0.01$) than before zebra mussel invasion ($K_n = 1.01 \pm 0.01$), but the difference was not statistically significant ($p = 0.30$, $df = 1$, $F = 1.08$).

Table 3.2. Logarithmic length-weight relationship models ($\log W_i = \log a + b \log L_i$) tested for long-term analyses of Lake Huron (deepwater sculpin, 1979,1980, 2002, 2017–2018) and Lake Ontario (slimy sculpin, 1978–1982, 1984–2000, 2005–2018), as well as current (2015–2018 only) logarithmic length-weight relationships for slimy sculpin among lakes Champlain (2015–2018), Michigan (2016–2018), Ontario (2015–2018), and Superior (2017), and deepwater sculpin among lakes Huron (2017–2018), Michigan (2016–2018), Ontario (2015–2018), and Superior (2017). Models are listed in order from best to worst fit based on AICc. In all models listed (where applicable), year is a fixed effect, and port and lake are random effects. As indicated in parentheses, each covariate had either slope, intercept, or both slope and intercept variation. *Mixed models that failed to converge were not included.

Lake/ Species	Additional covariates	$\Delta AICc$	Log-likelihood	Akaike Weight
Huron Deepwater Sculpin	Year (slope and intercept), Port (slope and intercept)	0.00	3505.59	1.00
	Year (slope and intercept), Port (slope)	39.21	3483.97	0.00
	Year (slope and intercept), Port (intercept)	42.84	3482.16	0.00
	Year (slope), Port (slope and intercept)	52.65	3475.24	0.00
	Year (slope and intercept)	52.95	3476.10	0.00
	Year (intercept), Port (slope and intercept)	70.71	3465.20	0.00
	Year (intercept), Port (intercept)	82.29	3458.41	0.00
	Year (slope), Port (slope)	100.17	3449.46	0.00
	Year (slope), Port (intercept)	103.04	3448.03	0.00
	Year (intercept)	115.11	3440.99	0.00
	Year (slope)	132.00	3432.55	0.00
	Year (intercept), Port (slope)	145.47	3425.81	0.00
	Port (slope and intercept)	763.62	3114.73	0.00
	Port (intercept)	869.93	3060.57	0.00
	Port (slope)	932.33	3028.36	0.00
None	1145.15	2921.96	0.00	
Ontario Slimy Sculpin	Year (slope and intercept)	0.00	12261.25	1.00
	Year (slope and intercept), Port (slope and intercept)	416.00	12056.30	0.00
	Year (slope and intercept), Port (slope)	459.25	12032.64	0.00
	Year (slope and intercept), Port (intercept)	461.03	12031.75	0.00
	Year (slope)	556.64	11947.53	0.00
	Year (intercept)	559.66	11946.02	0.00
	Year (intercept), Port (slope and intercept)	835.18	11810.28	0.00
	Year (slope), Port (slope and intercept)	859.20	11799.27	0.00
	Year (intercept), Port (intercept)	865.65	11794.03	0.00
	Year (intercept), Port (slope)	890.47	11780.62	0.00
	Year (slope), Port (slope)	903.93	11774.89	0.00
	Year (slope), Port (intercept)	909.14	11772.28	0.00
	Port (intercept)	1713.07	11335.16	0.00
	None	1723.39	11329.00	0.00
	Port (slope)	1733.69	11323.85	0.00

Table 3.2 (cont'd)

Current (among lakes)	Port within Lake (slope and intercept)	0.00	1951.44	1.00
	Lake (slope)	45.54	1926.66	0.00
	Port within Lake (slope)	223.50	1837.68	0.00
Slimy Sculpin	Port within Lake (intercept)	239.05	1830.92	0.00
	Lake (intercept)	258.24	1821.32	0.00
	None	9851.99	-2976.56	0.00
Current (among lakes)	Port within Lake (intercept)	0.00	2686.78	1.00
	Port within Lake (slope)	482.94	2444.31	0.00
	Lake (slope)	484.98	2443.29	0.00
Deepwater Sculpin	Lake (intercept)	500.40	2436.58	0.00
	None	694.06	2338.75	0.00

Current Sculpin Body Condition Among Lakes

The best fit logarithmic length-weight model for current (2015–2018) slimy sculpin included a random hierarchical port within lake effect with varying slope and intercept. No other models were within the confidence set of models, and these other models all had low Akaike weights (<0.01). The ANOVA test revealed that less disturbed lakes (Champlain and Superior) had significantly higher condition than the more disturbed lakes (Michigan, and Ontario, Figure 3.2, $p < 0.01$, $df = 1$, $F = 10.53$).

The best fit logarithmic length-weight model for current (2015–2018) deepwater sculpin included a random hierarchical port within lake effect with varying intercept. No other models were within the confidence set of models, and these other models all had low Akaike weights (<0.01). The ANOVA test did not revealed a significant difference in deepwater sculpin body among the less disturbed lake (Lake Superior) and the more disturbed lakes (Huron, Michigan, and Ontario, Figure 3.2, $p = 0.50$, $df = 1$, $F = 0.46$).

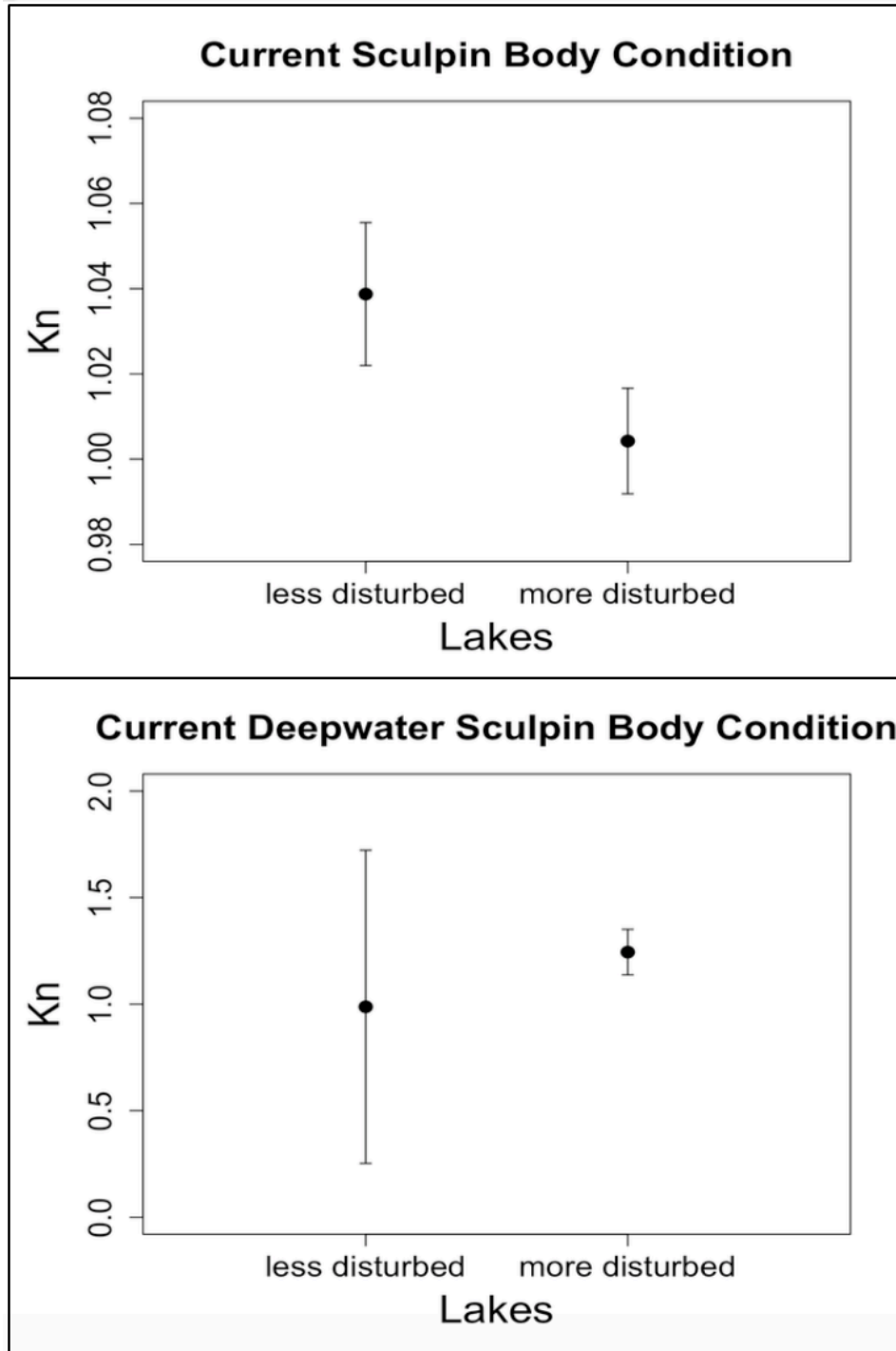


Figure 3.2. Mean current slimy sculpin and deepwater sculpin body condition (i.e., relative condition factor, K_n ; 2015–2018) and 95% confidence interval among more disturbed and less disturbed lakes. For slimy sculpin body condition, less disturbed lakes included lakes Champlain and Superior, and more disturbed lakes included lakes Michigan and Ontario. For deepwater sculpin body condition, less disturbed lakes included only Lake Superior, and more disturbed lakes included lakes Huron, Michigan, and Ontario. *Note different lakes included in each graph and different vertical axis scales.

Discussion

In the Great Lakes, dreissenid mussels have been linked to declines in primary productivity (Vanderploeg et al. 2010, 2012), *Diporeia* collapse (Vanderploeg et al. 2012, Watkins et al. 2007), goby expansion (Jude et al. 1995), and increased water clarity (Vanderploeg et al. 2012). Declines in body condition and growth of lake whitefish (*Coregonus clupeaformis*), another important native species in the Great Lakes, have been linked to dreissenid mussel invasion and *Diporeia* collapse (Herbst et al. 2017). We found no statistically significant difference in sculpin body condition after dreissenid mussel invasion, our results indicate a pattern of sculpin body condition decreasing slightly after dreissenid mussel invasion in lakes Huron (deepwater sculpin) and Ontario (slimy sculpin). Although sculpin body condition declines were not significant for the sculpin populations in the lakes that we were able to test, this may not be that case for all sculpin populations in the Great Lakes. For instance, slimy sculpins likely fare worse than deepwater sculpins in relation to the recent ecological disturbances initiated by dreissenid mussels, as slimy sculpins rely more on *Diporeia* than deepwater sculpins and slimy sculpins occur at shallower depth, which would make slimy sculpins more vulnerable than deepwater sculpins to decline in *Diporeia* and interactions with aggressive round gobies that migrate offshore (Miller 1986, Schaeffer et al. 2005, Walsh et al. 2007, Hondorp et al. 2011). The scarcity of slimy sculpins in recent trawl surveys in Lake Huron may also reflect a decline in body condition as a result of these ecological disturbances (Riley et al. 2017), or at least a negative effect of these ecological disturbances. However, the scarcity of slimy sculpins could also relate to lake trout predation on sculpins, as more natural reproduction of lake trout has been occurring in Lake Huron (Riley et al. 2007). In Lake Ontario, Weidel and others (2016b) proposed that deepwater sculpin body condition has not declined because prey

has not yet become a limiting factor this species, and our results suggest that this may also be the case for slimy sculpins in this lake. The lack of length-weight data before and after dreissenid mussel invasion for other Great Lakes sculpin populations did not allow us to determine if long-term sculpin body condition patterns differ among species.

Within lakes for each sculpin population, the lack of a significant overall temporal difference in sculpin body condition could also be a result of spatial variation in sculpin body condition patterns within lakes as prey availability may vary in different areas of the lake. In both lakes Huron and Michigan, deepwater sculpins have lower energy density in the absence of *Diporeia* (Pothoven et al. 2011). In Lake Huron, *Diporeia* first disappeared in the southeast shores, though *Diporeia* had become sparser throughout the lake by 2007 (Barbiero et al. 2011). In Lake Michigan, *Diporeia* became absent along the eastern shore prior to the western shore (Barbiero et al. 2011). Within these lakes, sculpin body condition may be lower in these locations where *Diporeia* first disappeared than in locations where *Diporeia* are still present or have disappeared later. Similarly, depth patterns in sculpin body condition may also be related to prey availability as *Diporeia* initially declined in shallower depths (< 90 m) in lakes Huron, Michigan, and Ontario (Barbiero et al. 2011). Sculpin body condition depth trends may also relate to the life history of sculpins as mature individuals tend to occur deeper than juveniles of both of these species (Brandt 1986, Geffen and Nash 1992).

Despite insufficient evidence on the long-term scale that slimy sculpins are more vulnerable to the recent ecological disturbances than deepwater sculpins, we found that current slimy sculpin body condition patterns among lakes aligns more closely than deepwater sculpin body condition patterns with ecological disturbances. We found that slimy sculpin populations in less disturbed lakes have higher body condition than more disturbed lakes. These results are

consistent with a similar study of lake whitefish, where lake whitefish from Lake Champlain had higher body condition than lakes Huron, Michigan, and Ontario (Herbst et al. 2017). For deepwater sculpins, variation in body condition among lakes did not apparently coincide with ecological disturbance. Lake Superior deepwater sculpin body condition did not significantly differ from the other lakes due to high variability in deepwater sculpin body condition. Therefore, the variability in sculpin condition among lakes (particularly for deepwater sculpins), may not be directly or exclusively related to these ecological disturbances. The variability in sculpin condition among lakes could also relate to differences in primary productivity, availability of other prey items, and temperature (Bunnell et al. 2014). For instance, Lake Superior is colder than the other Great Lakes (Bunnell et al. 2014), which could potentially lead to Lake Superior sculpin to grow at a slower rate. Having information on these other factors would potentially allow for more resolution in parsing out which factors influence sculpin body condition, but most of these data are not collected during trawl surveys.

Another factor that may contribute to variation in current sculpin body condition among lakes may relate to the timing of sampling sculpins in each lake. Most sculpin populations were measured for length and weight primarily in the fall (lakes Huron, Michigan, and Ontario), but some populations were only or also sampled during the spring and summer (lakes Champlain and Superior). Sculpin body condition may vary seasonally in relation to either ecological or environmental shifts, perhaps in relation to seasonal fluctuation in prey availability (Vanderploeg et al. 2012) or offshore overwintering of round gobies (Miller 1986, Schaeffer et al. 2005, Walsh et al. 2007). The difference observed in slimy sculpin body condition among less disturbed and more disturbed lakes may instead be seasonal factors rather than in relation to ecological disturbance. Additionally, sculpin body condition may vary seasonally due to the maturity and

reproductive status of sculpins. Lake Ontario deepwater sculpin spawning occurs between November and May (Mansfield et al. 1983), during a time when length and weight was not typically measured for either slimy or deepwater sculpins in Lake Ontario. Of course, other sources indicate that sculpin spawning occurs throughout the year (Scott and Crossman 1973, Wojcik et al. 1986, Selgeby 1988, Zimmerman and Krueger 2009). To better understand seasonal patterns in sculpin body condition and life history, it would be necessary for sampling and data collection to occur throughout the year. Additional variation in sculpin body condition among lakes related to sampling may be related to using different gear and sampling at different depths and times of year, which can result in collecting different life stages of sculpins and bias comparisons of sculpin body condition across lakes. Aside from collecting more data throughout the year, having a more standardized protocol across these lakes in sampling regime would improve our inferences.

In addition to not parsing out specific causes for sculpin body condition, this study does not provide an absolute metric of sculpin condition. The metric we used for sculpin body condition (K_n) only provides a relative comparison of body condition over time or among lakes based on averages rather than a clear distinction between sculpins in good or poor condition (Zale et al. 2012). Similar to any other condition metric based on body mass, values of K_n may be misleading if K_n is not strongly related to body composition, growth, or other indicators of fish health (Zale et al. 2012). For instance, if these sculpin species replace lipids with water when they are nutritionally stressed, heavy fish with a high K_n may not necessarily be in good condition. Despite the methodological constraints and the limited scope of this study, we did not find much evidence to support our prediction that ecological disturbances such as dreissenid mussel and round goby invasion and *Diporeia* collapse may negatively influence sculpin body

condition, except possibly for slimy sculpins on a short-term scale. It remains unclear how ecological and environmental factors affect sculpin body condition, especially on a long-term scale. In general, more years and seasons of data where length and weight are recorded, and more consistent collection of potential predictors (e.g., temperature, prey, etc.) would aid in better understanding sculpin ecology and improve sculpin restoration efforts.

REFERENCES

REFERENCES

- Anderson, R. O., and Gutreuter, S.J. 1983. Length, weight, and associated structural indices. In L.A. Nielsen and D.L. Johnson, (eds.), *Fisheries Techniques*, pp . 283–300. Am. Fish. Soc.
- Balshine, S., Verma, A., Chant, V., and Theysmeyer, T. 2005. Competitive interactions between round gobies and logperch. *J. Great Lakes Res.* 31:68–77.
- Barbiero R.P., Schmude, K., Lesht, B.M., Riseng, C.M., Warren, G.J., Tuchman, M.L. 2011. Trends in Diporeia populations across the Laurentian Great Lakes, 1997–2009. *J. Great Lakes Res.* 37(1):9–17.
- Bergstrom, M.A., and Mensinger, A.F. 2009. Interspecific resource competition between the invasive round goby and three native species: logperch, slimy sculpin, and spoonhead sculpin. *Trans. Am. Fish. Soc.* 138:1009–1017.
- Brandt, S.B. 1986. Ontogenetic shifts in habitat, diet, and diel-feeding periodicity of slimy sculpin in Lake Ontario. *Trans. Am. Fish. Soc.* 115(5):711–715.
- Bronte, C.R. et al. 2003. Fish community change in Lake Superior, 1970– 2003. *Can. J. Fish. Aquat. Sci.* 60:1552–1574.
- Bunnell, D.B., Barbiero, R.P., Ludsin, S.A., Madenjian, C.P., Warren, G.J., Dolan, D.M., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Walsh, M.G., Warner, D.M., and Weidel, B.C., 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. *Bioscience* 64(1):26–39.
- Bunnell, D.B., Madenjian, C.P., and Claramunt, R.M. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 63:2434–2446.
- Bunnell, D.B., Madenjian, C.P., Desorcie, T.J., Kostich, M., Armenio, P., and Adams, J. 2017. Status and trends of prey fish populations in Lake Michigan, 2016. U.S. Geological Survey. Ann Arbor, MI.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Charlebois, P.M., Marsden, J.E., Goettel, R.G., Wolfe, R.K., Jude, D.J., and Rudnika, S. 1997. The round goby, *Neogobius melanostomus* (Pallus), a review of European and North American literature. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey (76 pp.)

- Dubs, D.O.L., and Corkum, L.D. 1996. Behavioral interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). *J. Great Lakes Res.* 22:838–844.
- Fratt, T.W., Coble, D.W., Copes, F., and Bruswitz, R.E. 1997. Diet of burbot in Green Bay and western Lake Michigan with comparison to other waters. *J. Great Lakes Res.* 23: 1–10.
- French III, J.R.P., and Jude, D.J. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *J. Great Lakes Res.* 27:300–311.
- Geffen, A.J., and Nash, R.D.M. 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.* 41:101–110.
- Herbst, S.J., Marsden, E., and Lantry, B.F. 2013. Lake whitefish diet, condition, and energy density in Lake Champlain and the lower four Great Lakes following dreissenid invasions. *Trans. Am. Fish. Soc.* 142(2):388–398.
- Hirsch, P.E., N’Guyen, A., Adrian-Kalchhauser, I., Burkhardt-Holm, P. 2016. What do we really know about the impacts of one of the 100 worst invaders in Europe? A reality check. *Ambio* 45:267–279.
- Hondorp, D.W., Pothoven, S.A., and Brandt, S.B. 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.* 37:165–172.
- Janssen, J., and Jude, D.J. 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.* 27:319–328.
- Jude, D. J. 2001. Round and tubenose gobies: 10 years with the latest Great Lakes phantom menace. *Dreissena* 11:1-14.
- Jude, D.J and DeBoe, S.F. 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. *Can. J. Fish. Aquat. Sci.* 53(1):136–141.
- Jude, D.J., Janssen, J., and Crawford, G. 1995. Ecology, distribution, and impact of the newly introduced round and tubenose gobies on the biota of the St. Clair and Detroit Rivers. pp. 447–460 *In* The Lake Huron ecosystem: ecology, fisheries, and management. M. Munawar, T. Edsall, and J. Leach, eds. The Netherlands: S.P.B. Academic Publishing.
- La Cren, E.D. 195. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch *Perca fluviatilis*. *J. Animal Ecology* 20:201–219.

- Lauer, T.E., Allen, P.J., and McComish, T.S. 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.* 133:185–189.
- Madenjian, C.P., Bunnell, D.B., Warner, D.M., Pothoven, S.A., Fahnenstiel, G.L., Nalepa, T.F., Vanderploeg, H.A., Tsehaye, I., Claramunt, R.M., and Clark Jr., R.D. 2015. Changes in the Lake Michigan food web following dreissenid mussel invasions: a synthesis. *J. Great Lakes Res.* 41(3):217–231.
- Madenjian, C.P., DeSorcie, T.J., and Stedman, R.M. 1998. Ontogenic and spatial patterns in diet and growth of lake trout in Lake Michigan. *Trans. Am. Fish. Soc.* 127: 236–252.
- Madenjian, C.P. et al. 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Can. J. Fish. Aquat. Sci.* 59:736–753.
- Mansfield, P. J., Jude, D. J., Brazo, D. C., and Gulvas, J. 1983. Distribution and abundance of larval burbot and deepwater sculpin in Lake Michigan. *Trans. Am. Fish. Soc.* 112:162–172.
- Miller, P.J. 1986. Gobiidae. In *Fishes of the northeast Atlantic and Mediterranean*, eds. P.J.P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen, and E. Tortonese, pp. 1019–1095. UNESCO, Paris.
- Nalepa, T. F. 2010. An overview of the spread, distribution, and ecological impacts of the quagga mussel, *Dreissena rostriformis bugensis*, with possible implications to the Colorado River system. Proceedings, Colorado River Basin Science and Resource Management Symposium. Coming Together, Coordination of Science and Restoration Activities for the Colorado River Ecosystem, Scottsdale, AZ, November 18–20, 2008. U.S. Geological Survey Scientific Investigations Report: 2010–5135.
- Nalepa, T.F., Fanslow, D.L., Lang, G.A. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia spp.* to the invasive mussel *Dreissena rostriformis bugensis*. *Freshw. Biol.* 54:466–479.
- Owens, R.W., and Bergstedt, R.A. 1994. Response of slimy sculpins to predation by juvenile lake trout in southern Lake Ontario. *Trans. Am. Fish. Soc.* 123:28–36.
- Owens, R.W., and D.E. Dittman. 2003. Shifts in the diets of slimy sculpin (*Cottus cognatus*) and lake whitefish (*Coregonus clupeaformis*) in Lake Ontario following the collapse of the burrowing amphipod *Diporeia*. *Aquat. Ecosyst. Health Manag.* 6:311–323.
- Owens, R.W., O’Gorman, R., Eckert, T.H., Lantry, B.F., 2003. The offshore fish community in southern Lake Ontario. In: M. Munawar (Ed.), *State of Lake Ontario (SOLO): Past, Present, and Future*. Ecovision World Monograph Series. Aquatic Ecosystem Health and Management Society.
- Pothoven, S. A., and Bunnell, D.B. (2016) A shift in bloater consumption in Lake

- Michigan between 1993 and 2011 and its effects on *Diporeia* and *Mysis* prey, *Trans. Am. Fish. Soc.* 145:1, 59-68.
- Pothoven, S.A., Hondorp, D.W., and Nalepa, T.F. 2011. Declines in deepwater sculpin *Myoxocephalus thompsonii* energy density associated with the disappearance of *Diporeia* spp. in lakes Huron and Michigan. *Ecol. Freshw. Fish* 20:14–22.
- Ray, W.J., and Corkum, L.D. 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environ. Biol. Fishes* 50:267–273.
- Riley, S.C., He, J., Johnson, J.E., O'Brien, T.P., and Schaeffer, J.S. 2007. Evidence of widespread natural reproduction by lake trout *Salvelinus namaycush* in the Michigan waters of Lake Huron. *J. Great Lakes Res.* 33:917–921.
- Riley, S.C., Roseman, E.F., Hondorp, D.W., Chriscinske, M.A., Galassini, E., and Smith, M. 2017. Status and trends of the Lake Huron offshore demersal fish community, 1976-2016. U.S. Geological Survey. Ann Arbor, MI.
- Roseman, E.F., and Riley, S.C. 2009. Biomass of deepwater demersal forage fishes in Lake Huron, 1994–2007: implications for offshore predators. *Aquat. Ecosyst. Health Manag.* 12:29–36.
- Scott, W.B., Crossman, E.J. 1973. Freshwater fishes of Canada, deepwater sculpin. Fisheries Research Board of Canada. Royale Ontario Museum, Ontario, pp. 842–848.
- Selgeby, J.H. 1988. Comparative biology of the sculpins of Lake Superior. *J. Great Lakes Res.* 14:44–51.
- Schaeffer, J.S., Bowen, A., Thomas, M., French III, J.R.P., and Curtis, G. L. 2005. Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in western Lake Huron, USA. *J. Great Lakes Res.* 31:414–425.
- Walsh, M.G., Dittman, D.E., and O’Gorman, R.O. 2007. Occurrence and food habits of the round goby in the profundal zone of Southwestern Lake Ontario. *J. Great Lakes Res.* 33:83–92.
- Watkins, J.M., Dermott, R., Lozano, S.J., Mills, E.L., Rudstam, L.G., Scharold, J.V. 2007. Evidence for remote effects of dreissenid mussels on the amphipod *Diporeia*: analysis of Lake Ontario benthic surveys, 1972–2003. *J. Great Lakes Res.* 33:642–657.
- Weidel, B.C., Walsh, M.G., Holden, J.P., Connerton, M.J., 2016a. Lake Ontario benthic prey fish assessment, 2015. 2015 Annual Report, Bureau of Fisheries Lake Ontario Unit and St. Lawrence River Unit to the Great Lakes Fishery Commission's Lake Ontario Committee.
- Weidel, B.C., Walsh, M.G., Connerton, M.J., Lantry, B.F., Lantry, J.R., Holden, J.P., Yuille, M.J., and Hoyle, J.A. 2016b. Deepwater sculpin status and recovery in Lake Ontario. *J.*

Great Lakes Res. 43(5): 854-862.

Wojcik, J.A., Evans, M.S., and Jude, D.J. 1986. Food of deepwater sculpin, *Myoxocephalus thompsoni*, from Southeastern Lake Michigan. *J. Great Lakes Res.* 12:225–231.

Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., Pothoven, S.A. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *J. Great Lakes Res.* 36(3):50–59.

Vanderploeg, H.A. et al. 2012. Seasonal zooplankton dynamics in Lake Michigan: Disentangling impacts of resource limitation, ecosystem engineering, and predation during a critical ecosystem transition. *J. Great Lakes Res.* 38:336–352.

Van Oosten, J., and Deason, H.J. 1938. The food of the lake trout (*Cristovomer namaycush*) and of the lawyer (*Lota maculosa*) of Lake Michigan. *Trans. Am. Fish. Soc.* 67: 155-177.

Vinson, M., Evrard, L., Gorman, O.T., and Yule, D.L. 2017. Status and trends in the Lake Superior fish community, 2016. U.S. Geological Survey. Ashland, WI

Zale, A.V., Parrish, D.L., and Sutton, T.M., editors. 2012. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Zimmerman, M.S., and Krueger, C.C. 2009. An ecosystem perspective on re-establishing native deepwater fishes in the Laurentian Great Lakes. *N. Am. J. Fish.Manag.* 29:1352–1371.