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Broad shifts in the resource use of a commercially harvested fish following the invasion of dreissenid mussels

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Abstract. Dreissenid mussels, including the zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostiformus bugensis*) mussel, are invasive species known for their capacity to act as ecosystem engineers. They have caused significant changes in the many freshwater systems they have invaded by increasing water clarity, reducing primary productivity, and altering zooplankton and benthic invertebrate assemblages. What is less clear is how their ecosystem engineering effects manifest up the food web to impact higher trophic levels, including fish. Here, we use a biological tracer (stable isotopes of carbon and nitrogen) to analyze long-term and broad-scale trends in the resource use of benthivorous lake whitefish (*Coregonus clupeaformis*) in the Laurentian Great Lakes, where dreissenid mussels have become established in each lake except Lake Superior. We measured stable isotope ratios from archived material (fish scale samples) collected over several decades by multiple agencies and from 14 locations around the Great Lakes. In the majority of locations, the δ^{13}C of lake whitefish increased following the establishment of dreissenid mussels. Trends in δ^{15}N were less clear, but significant breakpoints in the time series occurred within 5 yr of dreissenid establishment in several locations, followed by declines in δ^{15}N. In contrast, isotopic signatures in Lake Superior locations did not show these trends. Our results provide evidence that lake whitefish shifted toward greater reliance on nearshore benthic production, supporting the theory that fundamental energy pathways are changed when dreissenid mussels become established. Importantly, these effects were noted across multiple, large, and complex ecosystems spanning a broad geographic area. Our study underscores the potential for aquatic invasive species to alter key ecosystem services as demonstrated here through their impacts on energy pathways supporting a commercially harvested fish species.

Key words: aquatic invasive species; benthic-pelagic coupling; benthification; Coregonidae; mid-depth sink; nearshore phosphorus shunt; regime shift.

INTRODUCTION

Nonnative species comprise a significant proportion of the biota in numerous ecosystems globally, even in remote habitats (Ricciardi 2007). Species invasions are expected to increase further with climate change (Pagnucco et al. 2015) and the increasing globalization of trade (Hulme 2009). There are well-documented examples of invasive species causing significant impacts to biodiversity, ecosystem functioning, human health, and economies (reviewed in Pimentel et al. 2005, Cameron et al. 2016, Gallardo et al. 2016). Species invasions are thus among the most serious threats to ecosystem services (Dudgeon et al. 2006); that is, the benefits that human societies derive from functioning ecosystems (Costanza et al. 1997).

Some invasive species, including dreissenid mussels, can act as ecosystem engineers, affecting the availability of resources to other species by altering their abiotic or biotic physical habitat (Jones et al. 1994). The impacts of ecosystem engineers can occur over broad spatial scales and at multiple trophic levels, but their effects can be difficult to quantify (Jones et al. 1997). Dreissenid mussels, including the zebra (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostiformis bugensis*), are thought to cause a redirection of energy flow within invaded ecosystems, shifting energy from pelagic-profundal pathways to benthic-littoral pathways (Higgins and Vander Zanden 2010). Variations on this theory have been referred to as the nearshore phosphorus shunt model (Hecky et al. 2004), and the mid-depth sink model (Vanderploeg et al. 2010). Dreissenid mussels form dense aggregations on multiple substrate types and by releasing feces and pseudo-feces, they enhance nutrient release, alter microbial communities, and promote benthic algal blooms (Lavrentyev et al. 2000, Nogaro and Steinman 2014, Armenio et al. 2016). As filter

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feeders, dreissenid mussels reduce concentrations of suspended particles, resulting in increased light penetration into the water column (Geisler et al. 2016) and promoting growth of toxic cyanobacteria and filamentous green algae (Sarnelle et al. 2005, Armenio et al. 2016). Across the numerous freshwater systems they have invaded, dreissenid mussels are associated with declines in phytoplankton and zooplankton biomass and increases in benthic algal, macrophyte, bacteria, and zoobenthic biomass (Higgins and Vander Zanden 2010).

The extent to which dreissenid mussels impact higher trophic levels remains uncertain, including whether their effects impair key ecosystem services related to fish production. This is true in the Laurentian Great Lakes where the role of dreissenid mussels in ecosystem changes are still debated (Bunnell et al. 2014, He et al. 2014, Riley and Dunlop 2016) even though dreissenid mussels have been present since the 1980s and have become established in large numbers in each lake except Lake Superior (Appendix S1). A few studies are emerging showing the potential linkages between dreissenid mussels, shifting energy pathways, and responses in fish populations (Rennie et al. 2009, 2013, Turschak et al. 2014). However, while valuable, these studies are limited in temporal scale (lacking data from years prior to dreissenid establishment) or in geographical scope (focusing on single lakes or smaller locations within a lake). There is a need to understand the response of valuable fish species to the establishment of dreissenid mussels more broadly, especially considering that zebra mussels have invaded freshwater ecosystems worldwide and that quagga mussels have recently surpassed zebra mussels in their abundance, are spreading into deeper habitats in many lakes, and continue to colonize new systems (Bunnell et al. 2009, Karatayev et al. 2015, Marescaux et al. 2016). Zebra mussels remain listed among the top 100 of the world's worst invasive species (IUCN/SSC 2016), and quagga mussels have been identified as the invasive species that poses the greatest risk to biodiversity (Roy et al. 2014).

Here, we investigate the association between dreissenid mussel establishment and resource use in a keystone benthivorous fish in the Great Lakes, the lake whitefish (*Coregonus clupeaformis*). Lake whitefish support one of the most economically important commercial fisheries within the Great Lakes (Brenden et al. 2013) and have undergone substantial changes in abundance and reductions in growth in numerous locations over the past one to two decades (Fera et al. 2015). Lake whitefish are also broadly distributed within North America, inhabiting the benthic, cold-water habitats of numerous lakes (Scott and Crossman 1973) and supporting indigenous, commercial, and recreational fisheries. Ecologically, lake whitefish play a unique role in lake food webs as they are a relatively large, benthivorous fish that often include high proportions of offshore invertebrates in their diet. Lake whitefish present an ideal model organism for investigating dreissenid-mediated effects on fish because they feed in the benthic zone where the first signs of any impacts might be more detectable. Previous research in an isolated embayment in Lake Huron found that following the establishment of dreissenid mussels, lake whitefish changed diets from one dependent on a variety of offshore prey items including *Diporeia* spp., to one dominated by dreissenids found in nearshore areas (Rennie et al. 2009). The objective of our study is to examine the consistency of these results across all five Laurentian Great Lakes. Agency netting data indicates that a greater reliance on nearshore resources may not be universal because lake whitefish were being captured at greater depths in some areas following dreissenid mussel establishment (Rennie et al. 2015).

To determine temporal patterns of lake whitefish resource use, we measured stable isotope ratios (carbon $\delta^{13}C$ and nitrogen $\delta^{15}N$) from archived fish scale samples collected and stored over several decades for populations in each of the Great Lakes. Stable isotopes of carbon and nitrogen are widely employed biological tracers that provide information on trophic ecology and spatial feeding patterns (Vander Zanden and Rasmussen 1999), and scale samples provide a valuable source of information for historical analyses that would otherwise not be possible (Perga and Gerdeaux 2003). We contrasted $\delta^{13}C$ and $\delta^{15}N$ in years before and after dreissenid mussel establishment and between locations with and without established populations of dreissenid mussels. By contrasting long-term patterns in both established and non-established sites, we could examine how an invasive species has affected the resource dynamics of a broadly distributed, ecologically and commercially important fish species.

METHODS

We measured the stable isotope ratios for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in fish scale samples. These isotopes in scale material are predictably representative of tissue $\delta^{13}C$ and $\delta^{15}N$ in coregonids (Perga and Gerdeaux 2003, Rennie et al. 2009) and other fishes (Kelly et al. 2006, Fincel and Vandehey 2012). $\delta^{13}C$ of organisms in the aquatic food web is depth dependent and increases from offshore to nearshore habitats (Vander Zanden and Rasmussen 1999, Rennie et al. 2009, Cummings and Schindler 2013; Appendix S2). $\delta^{15}N$ is used to evaluate the trophic level of organisms in the food web, typically undergoing an enrichment of 3.4‰ between prey and consumer (Minagawa and Wada 1984, Cabana and Rasmussen 1994). $\delta^{15}N$ in the food web also varies with depth, declining from offshore to nearshore as ^{15}N becomes depleted (Vander Zanden and Rasmussen 1999, Rennie et al. 2009; Appendix S2). Thus, changes in $\delta^{13}C$ or $\delta^{15}N$ of an organism indicate a change in the food source, either in terms of where in the environment the consumer is feeding or in the trophic level of the consumer (Vander Zanden and Rasmussen 1999, Rennie et al. 2009).

Lake whitefish scales were obtained from agency index netting programs and agency commercial fish monitoring programs for 14 locations within the Great Lakes, including 11 locations where dreissenids have become established and three locations in Lake Superior where dreissenids have not had widespread establishment (Fig. 1; Appendix S1). These scales, retrieved from agency offices between 2010 and 2013, were also used to measure growth rates (Fera et al. 2015). For Lake Erie, we pooled scale samples from partnership assessment and commercial gill netting programs originating from agency offices in Wheatley, Ontario, Canada and Dunkirk, New York, USA due to gaps in years collected and limited samples for the lake.

The methods to prepare samples and analyze stable isotope ratios from lake whitefish scales were the same as those in Rennie et al. (2009). δ^{13}C and δ^{15}N of six individual 5-yr-old fish selected from each year of collection were analyzed, a sample size shown to have statistical power for detecting significant isotopic changes associated with dreissenid mussel establishment for this species (Rennie et al. 2009). Age 5 fish were targeted because of sample availability and to reduce possible confounding effects of size on isotopic values through consistency in the life stage of fish evaluated (Hesslein et al. 1993, Rennie et al. 2009). At age 5, lake whitefish typically consume a large proportion of benthic prey items (Pothoven and Nalepa 2006, Nalepa et al. 2009*b*, Pothoven and Madenjian 2013). Three scales were used for each randomly chosen fish from each year. The scales were soaked for 24 h in deionized water, and then cleaned by hand to remove dead tissues and contaminants. After cleaning, scales were dried and the first two age rings were removed using a punch to avoid contribution of diet during early life stages to isotope ratios. Isotopic signatures measured for each fish thus represented an integrated assessment of that fish's diet over a 3-yr period from ages 2 to 5. The samples were then weighed and sent to Isotope Tracer Technologies (Waterloo, Ontario, Canada), which provided estimates of δ^{13}C and δ^{15}N for each individual fish. The isotope analysis was carried out on a Finnigan Mat DeltaPlus Isotope Ratio Mass Spectrometer (IRMS) with ConFlo III Interface (Bremen, Germany) coupled with a CE instruments EA 1110 CHN (Italy). Data is corrected and normalized using three international standards, IAEA-N1, IAEA-N2, IAEA-C6, and four calibrated internal standards, that bracket the samples. Standards are run at the beginning, middle and end of every run. The results are evaluated and corrected against standards run with the samples, and then reported against the international reference material. The isotope laboratory reported analytical error of C and N determinations at 0.2‰ and 0.3‰, respectively. The analytical precision of isotope ratios were confirmed by running duplicate analysis for 80 randomly selected samples pooled across all populations (paired t test; δ^{13}C, $t_{80} = -0.327$, $P = 0.745$; δ^{15}N, $t_{80} = -0.066$, $P = 0.948$).

Statistical analyses

Following Fera et al. (2015) and Rennie et al. (2015), a dreissenid mussel establishment year was assigned for each location where we obtained scale samples (Appendix S1). Prior to statistical analyses, δ^{13}C was corrected to account for the Seuss effect, i.e., the decrease in δ^{13}C that occurred as a result of anthropogenic activity (Verburg 2007) and variables were transformed to satisfy assumptions of normality (Appendix S3). All statistical analyses were performed within each location as in Fera et al. (2015) to account for differences in time series lengths, invasion

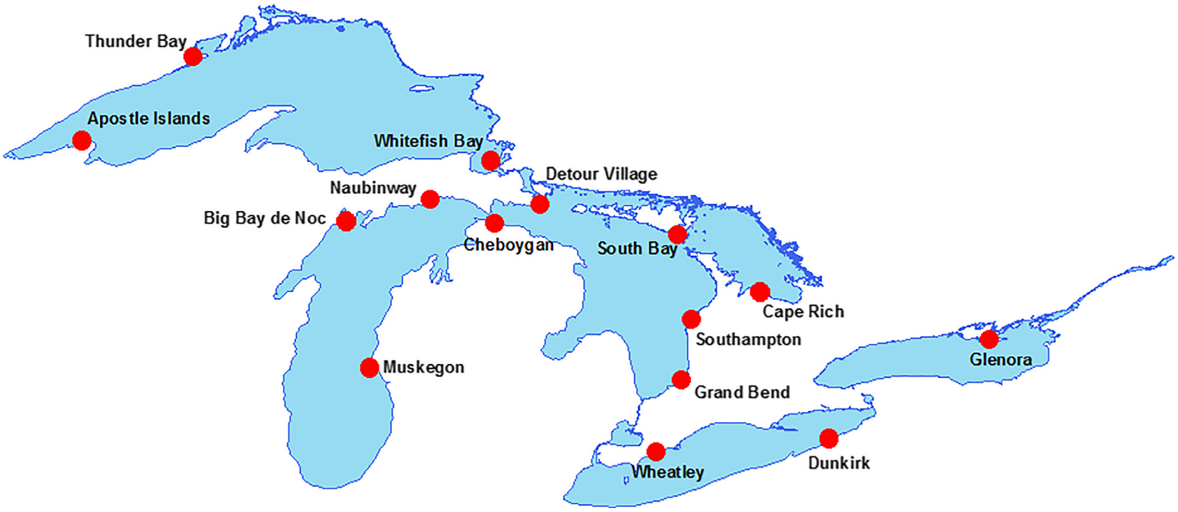

Fig. 1. Map of the Laurentian Great Lakes indicating the origin of lake whitefish scales sampled and used for isotope analysis. Scales were obtained from three locations in Lake Superior (Thunder Bay, Whitefish Bay, and the Apostle Islands), three locations in Lake Michigan (Naubinway, Big Bay de Noc, and Muskegon), six locations in Lake Huron (DeTour Village, Cheboygan, South Bay, Cape Rich, Southampton, and Grand Bend), two locations in Lake Erie (Wheatley and Dunkirk), and one location in Lake Ontario (Glenora).

establishment histories, and data sources. We used two statistical approaches to evaluate the association between stable isotope ratios and dreissenid mussel establishment. In the first approach, we evaluated and compared two linear mixed-effects models using the *lme4* package in R v. 0.999999-2 (Bates et al. 2015):

lmer(Stable Isotope Ratio~Dreissenid Status
+ (1|Dreissenid Status/Year Class))
lmer(Stable Isotope Ratio~1|Year Class).

This model comparison tested the effect of dreissenid mussel establishment while controlling for random year-to-year variation within each dreissenid status category (similar to the approach taken in Rennie et al. 2009). Dreissenid status is a categorical variable describing whether dreissenids are established or not in that year, with year class nested within dreissenid status in model 1. We compared the fit of the two models using a likelihood ratio test. For Lake Superior locations where dreissenids have not had widespread establishment, least squares linear regressions were conducted to examine trends through time in isotopic ratios.

In the second approach, we performed segmented least squares linear regression (i.e., “breakpoint analysis”) to evaluate temporal trends in stable isotope ratios. This was done to identify whether there were breakpoints in the slopes of δ^{13}C or δ^{15}N through time, and whether breakpoints coincided with the specific dreissenid establishment year of each location. We used the R package *segmented* version 0.2-9.4 (Muggeo 2008) and a Davies test (Davies 1987) to detect changes in the slopes of the regressions. Our motivation for choosing the two approaches were that (1) we wanted to identify the role of dreissenids as a categorical explanatory factor; and (2) we wanted to capture temporal trends that might take place that are not well-detected by a categorical approach (see also Appendix S3).

RESULTS

Two out of three Lake Superior locations showed no obvious trends in stable isotope ratios over time (Figs. 2 and 3). Regression analyses found no linear trends through time in δ^{13}C for Thunder Bay ($R^2 = 0.01$, $F_{1,225} = 2.28$, $P = 0.13$) and Whitefish Bay ($R^2 = 0.06$, $F_{1,119} = 7.23$, $P = 0.08$), but a significant decrease in δ^{13}C was observed in the Apostle Islands ($R^2 = 0.43$, $F_{1,63} = 48.1$, $P < 0.001$). For all three Lake Superior locations, there were no temporal trends with strong explanatory power for δ^{15}N (Whitefish Bay, $R^2 = 0.004$, $F_{1,119} = 0.47$, $P = 0.50$; Thunder Bay, $R^2 = 0.07$, $F_{1,225} = 17.41$, $P < 0.001$; Apostle Islands, $R^2 = 0.002$, $F_{1,63} = 0.14$, $P = 0.71$).

In contrast, prominent changes over time in δ^{13}C were apparent in all other lakes, which often coincided with

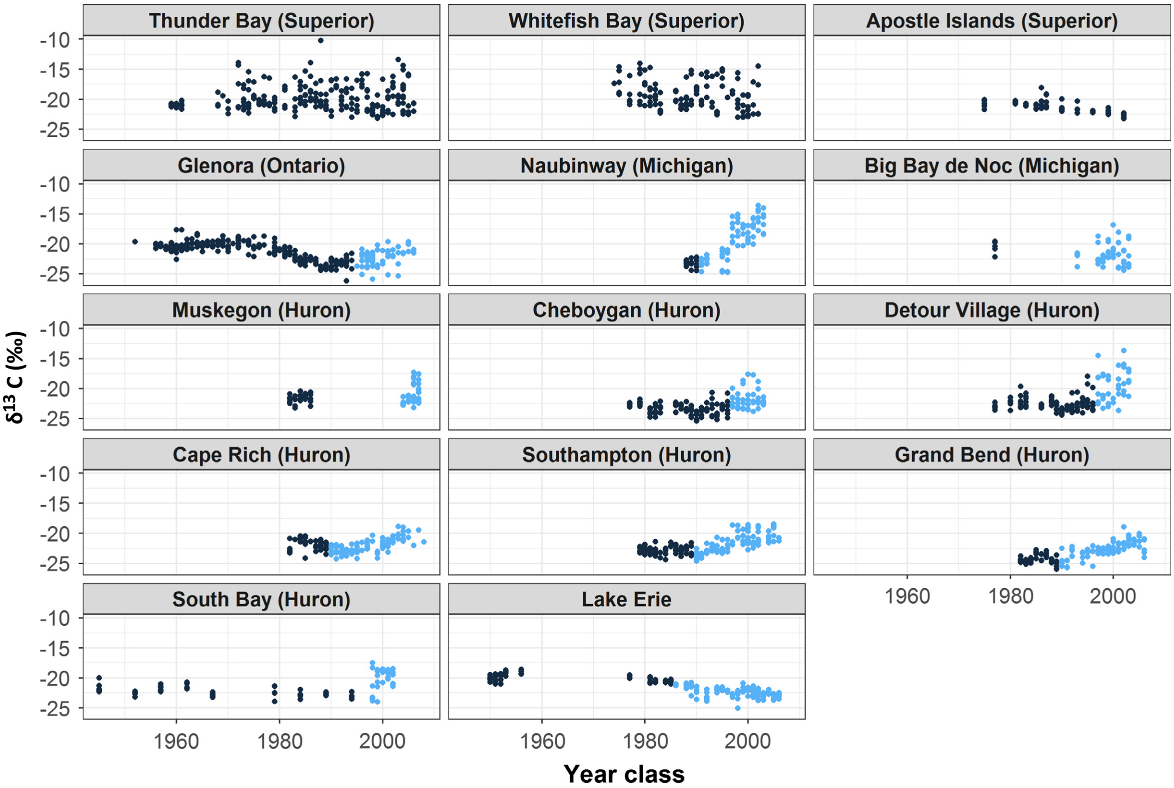

FIG. 2. δ^{13}C measured from lake whitefish scale samples. Values are Suess-corrected according to Verburg (2007). δ^{13}C values are shown by year class to which the individual fish was born. Years prior to dreissenid mussel establishment (black) and post dreissenid mussel establishment (blue) are contrasted.

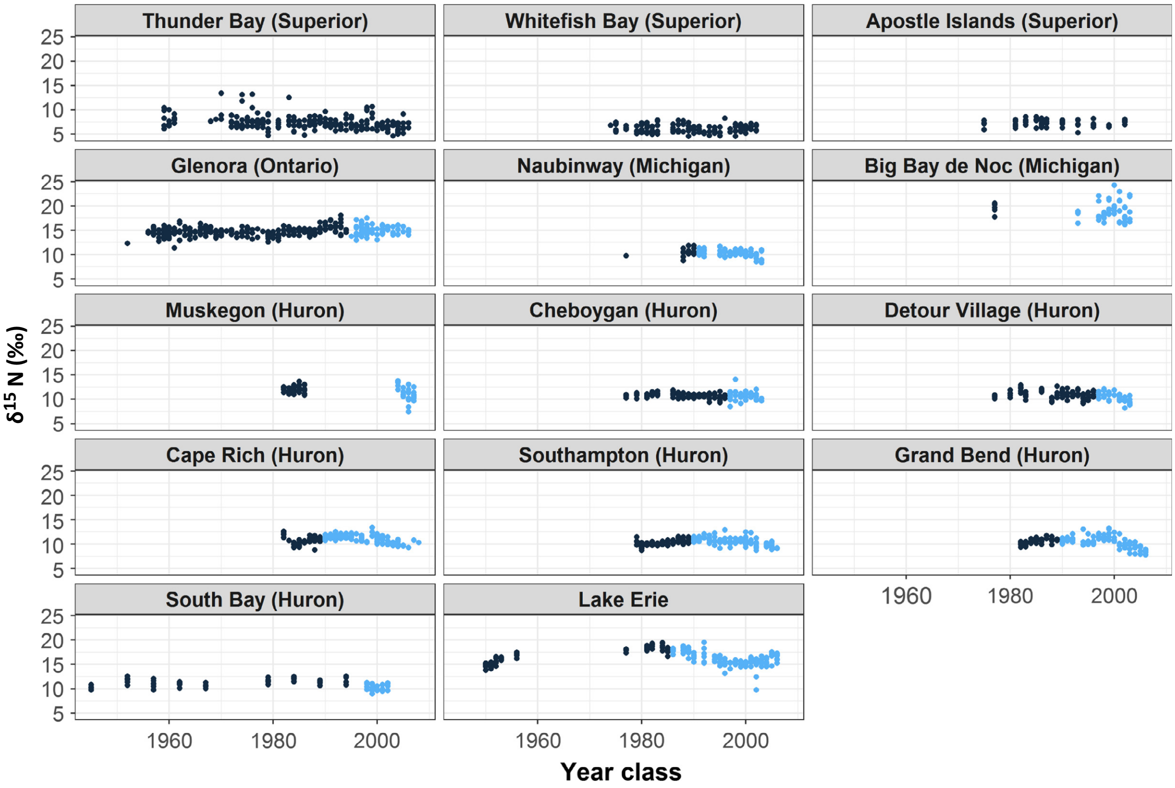

FIG. 3. δ^{15}N measured from lake whitefish scale samples. δ^{15}N values are shown by year class to which the individual fish was born. Years prior to dreissenid mussel establishment (black) and post dreissenid mussel establishment (blue) are contrasted.

the location-specific timeline of dreissenid establishment (Fig. 2). Results of log-likelihood tests indicate a significant effect of dreissenids on δ^{13}C in seven out of 11 locations tested, with six of the seven locations demonstrating a significant increase in δ^{13}C (Table 1) and therefore an increased reliance on nearshore production (Vander Zanden and Rasmussen 1999, Rennie et al. 2009, Appendix S2). In all locations except Glenora, there was an increase in variation of δ^{13}C between pre- and post-dreissenid time periods (Table 1).

Changes in δ^{15}N were not as obvious or consistent as with δ^{13}C (Fig. 3). In Lake Huron, δ^{15}N increased slightly but significantly in Southampton and decreased slightly but significantly in South Bay (Table 1). Among all other locations with established dreissenid mussels, no significant changes in δ^{15}N were observed when comparing pre- to post-establishment years. Variation in δ^{15}N increased, decreased, or remained the same between pre- and post-dreissenid time periods (Table 1).

In the segmented regression analyses, no significant breakpoints in δ^{13}C were detected for Thunder Bay and Whitefish Bay in Lake Superior. Temporal gaps in the data for the Apostle Islands (Lake Superior), Dunkirk (Lake Erie), Wheatley (Lake Erie), Muskegon (Lake Huron), and Big Bay de Noc (Lake Michigan) prevented the application of meaningful breakpoint regression analysis. All other locations with established dreissenid mussels and sufficient samples sizes to run breakpoint models had statistically significant breakpoints in δ^{13}C; two breakpoints were detected for Glenora (Lake Ontario) and one breakpoint was detected for all others (Table 2). The breakpoint years differed more substantially from the establishment year for Detour Village (Lake Huron; 8 yr prior to establishment), Cheboygan (Lake Huron; 9 yr prior), and the first breakpoint in Glenora (Lake Ontario; 14 yr prior). For all other locations, including the second breakpoint in Glenora, breakpoints were more similar to the establishment year (between 1 and 4 yr). Generally, slopes in δ^{13}C tended to be negative or close to zero prior to breakpoints, and then positive (and steeper) following breakpoints. In all cases (except the pre-dreissenid breakpoint at Glenora), slopes of δ^{13}C increased dramatically after breakpoints (Table 2, Fig. 4), indicating increased reliance on nearshore resources.

For δ^{15}N, fewer locations had significant breakpoints (Table 2). In Lake Superior, there were no significant breakpoints observed for Thunder Bay or Whitefish Bay. No breakpoints were detected in δ^{15}N for Glenora and Cheboygan. Six other locations showed significant breakpoints that were within 0–5 yr of dreissenid mussel establishment, and in each case declined dramatically after the breakpoint (Table 2, Fig. 5), consistent with an increased reliance on nearshore resources. Generally, slopes in δ^{15}N tended to be positive or close to zero prior

Table 1. Linear mixed-effects model results for stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) measured from lake whitefish scale samples.

			Before dreissenid mussel establishment		After dreissenid mussel establishment	
Location	Chi-square	*P*	Mean	SD	Mean	SD
$\delta^{13}C$						
Glenora	4.74	0.09	−21.22	1.53	−22.23	1.31
Wheatley/Dunkirk	39.2	<0.0001*	−20.00	0.68	−22.31	0.77
Naubinway	7.62	0.02*	−23.26	0.59	−19.27	3.16
Big Bay de Noc	4.1	0.13	−20.39	0.99	−21.71	1.73
Muskegon	2.0	0.37	−21.71	0.65	−20.88	1.75
Cheboygan	23.7	<0.0001*	−23.40	0.94	−21.75	1.57
Detour Village	27.2	<0.0001*	−22.59	1.14	−19.58	2.51
Cape Rich	0.17	0.91	−21.86	0.93	−22.08	1.16
Southampton	8.5	0.01*	−22.82	0.63	−21.94	1.59
Grand Bend	10.23	0.006*	−24.27	0.73	−22.71	1.39
South Bay	17.14	0.0002*	−22.33	0.77	−20.10	1.75
$\delta^{15}N$						
Glenora	0	1	14.74	0.92	14.99	0.92
Wheatley/Dunkirk	3.71	0.16	16.99	1.59	16.02	1.35
Naubinway	0	1	10.50	0.75	10.26	0.73
Big Bay de Noc	2.17	0.34	19.61	1.07	18.92	1.88
Muskegon	1.7	0.43	12.01	0.74	11.24	1.44
Cheboygan	0	1	10.76	0.50	10.67	0.93
Detour Village	2.0	0.37	11.00	0.80	10.47	0.92
Cape Rich	0	0.99	10.75	0.86	11.10	0.79
Southampton	9.0	0.01*	10.29	0.58	10.54	0.85
Grand Bend	0.04	0.98	10.58	0.56	10.42	1.22
South Bay	9.0	0.011*	11.21	0.71	10.24	0.69

*$P < 0.05$ for likelihood ratio tests between models with and without dreissenid mussels.

Table 2. Segmented regression results for stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) measured from lake whitefish scale samples.

Location	Establishment	Segmented at	Confidence interval	Slope 1	Slope 2	Intercept†	Davies test *P*
$\delta^{13}C$							
Glenora	1993	1977	1975–1979	0.02	−0.37	−67.6	<0.001
		1989	1988–1990	0.48‡		−67.6	<0.001
Southampton	1993	1991	1988–1993	−0.03	0.26	46.0	<0.001
Cape Rich	1996	1993	1992–1995	−0.14	0.35	256.7	<0.001
Grand Bend	1994	1990	1987–1994	−0.01	0.22	−2.0	0.001
South Bay	1997	1994	1992–1996	0.00	0.47	22.78	<0.001
Detour Village	2000	1992	1989–1994	−0.06	0.46	95.4	<0.001
Cheboygan	2000	1991	1988–1993	−0.08	0.30	134.6	<0.001
Naubinway	1994	1993	1990–1996	0.10	0.68	−213.4	0.01
§							
$\delta^{15}N$							
Southampton	1993	1992	1990–1994	0.11	−0.21	−200.0	<0.001
Cape Rich	1996	1995	1993–1997	0.09	−0.25	−160.8	<0.001
Grand Bend	1994	1999	1998–2000	0.07	−0.50	−118.7	<0.001
South Bay	1997	1992	1989–1996	0.02	−0.20	−25.09	<0.001
Detour Village	2000	2000	1998–2002	−0.01	−0.48	35.1	<0.001
Naubinway	1994	1999	1997–2001	0.01	−0.30	−12.6	0.001
¶							

Notes: Analysis was conducted on all locations without major breaks in samples among years. The best estimate for segmentation and the 95% confidence intervals are shown for each breakpoint. Slopes 1 and 2 are the slopes before and after breakpoints. *P* values from a Davies test were used to test for the significance of breakpoints.

† Intercept of the first segment.

‡ Indicates slope 3, after the 1989 breakpoint.

§ Thunder Bay and Whitefish Bay were not significantly segmented.

¶ Thunder Bay, Whitefish Bay, Glenora, and Cheboygan were not significantly segmented.

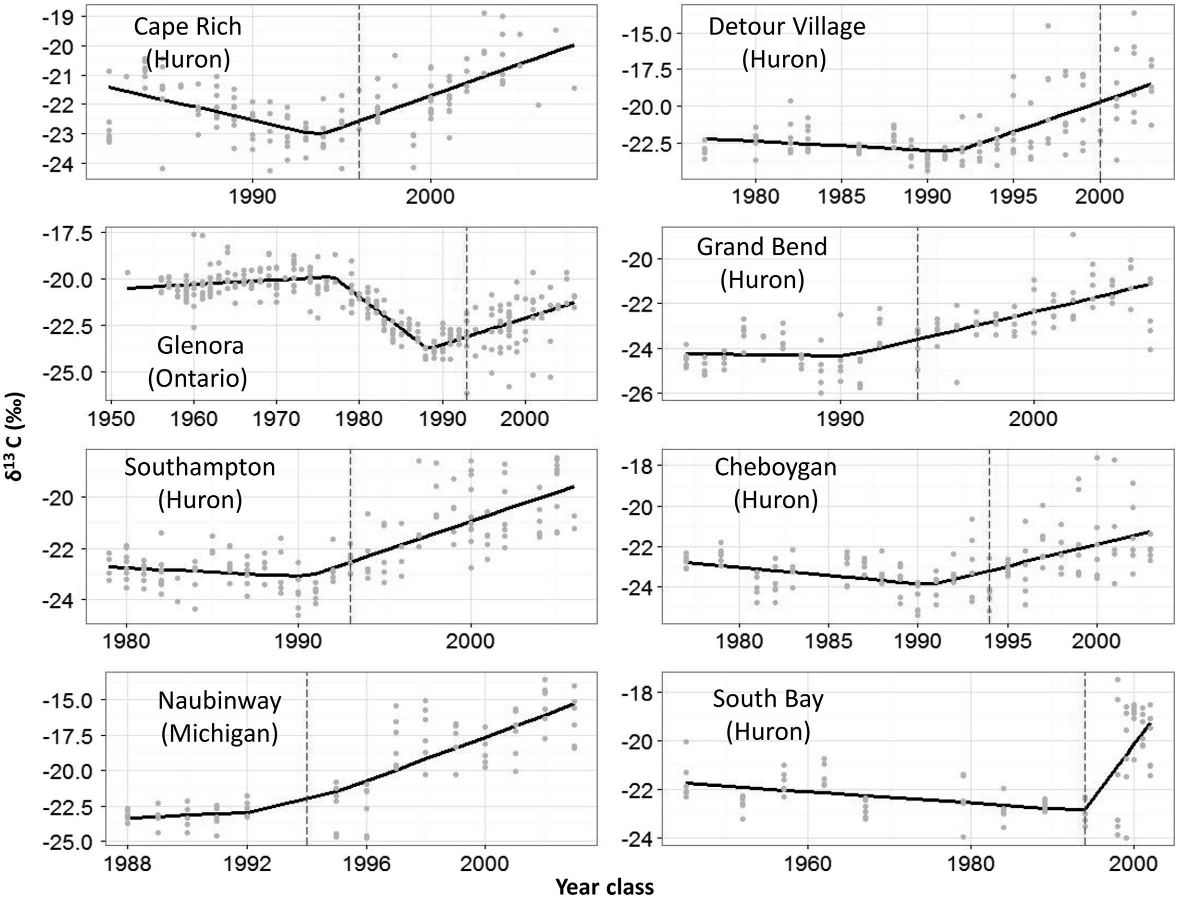

Fig. 4. Breakpoint regression for $\delta^{13}C$. Vertical line depicts the dreissenid establishment year. Only locations with significant breakpoints are shown. Values are Suess-corrected according to Verburg (2007). $\delta^{13}C$ values are shown by year class to which the individual fish was born. Points are individual measurements; lines are regression lines.

to breakpoints, and then negative (and steeper) following breakpoints; opposite to trends in $\delta^{13}C$.

Discussion

Our results provide compelling evidence for an increased reliance on nearshore resources by lake whitefish coinciding with the establishment of dreissenid mussels within the Great Lakes basin. In seven of 11 locations with established dreissenid mussel populations, $\delta^{13}C$ either became significantly more positive, or the slope of $\delta^{13}C$ vs. time indicated an increasing trend; trends in $\delta^{15}N$ when present were in the opposite direction. In contrast, two out of three locations in Lake Superior, where dreissenids have not had widespread establishment, did not show these trends. Breakpoints were observed in the isotope time series for most locations with established dreissenid mussels, but were not observed in Lake Superior. In several locations, breakpoints were within 0–5 yr of the dreissenid establishment year. These findings support the hypothesis that dreissenid mussels have altered the pathways and relative importance of nearshore vs. offshore production in Great Lakes food webs (Hecky et al. 2004), translating into effects observed in the isotopic ratios of a commercially harvested fish. Furthermore, the isotopic shifts first observed in Lake Whitefish within an embayment of Lake Huron (South Bay) where they were also accompanied by complementary shifts in depth distribution and diet (Rennie et al. 2009), have occurred over a broader geographical scale than first realized.

The most obvious pattern we observed was an enrichment of ^{13}C that occurred following dreissenid mussel establishment. $\delta^{13}C$ decreases with depth in freshwater lakes (Vander Zanden and Rasmussen 1999, Rennie et al. 2009; Appendix S2). Primary producers in shallower waters are enriched in ^{13}C relative to those in deeper waters, a trend that is maintained when moving to higher trophic levels in the food web. A change in $\delta^{13}C$ of a consumer can thus be indicative of a shift in the importance of nearshore vs. offshore production in the diet for that population, where the higher the $\delta^{13}C$, the more significant the nearshore contribution. Lake whitefish captured in locations with established

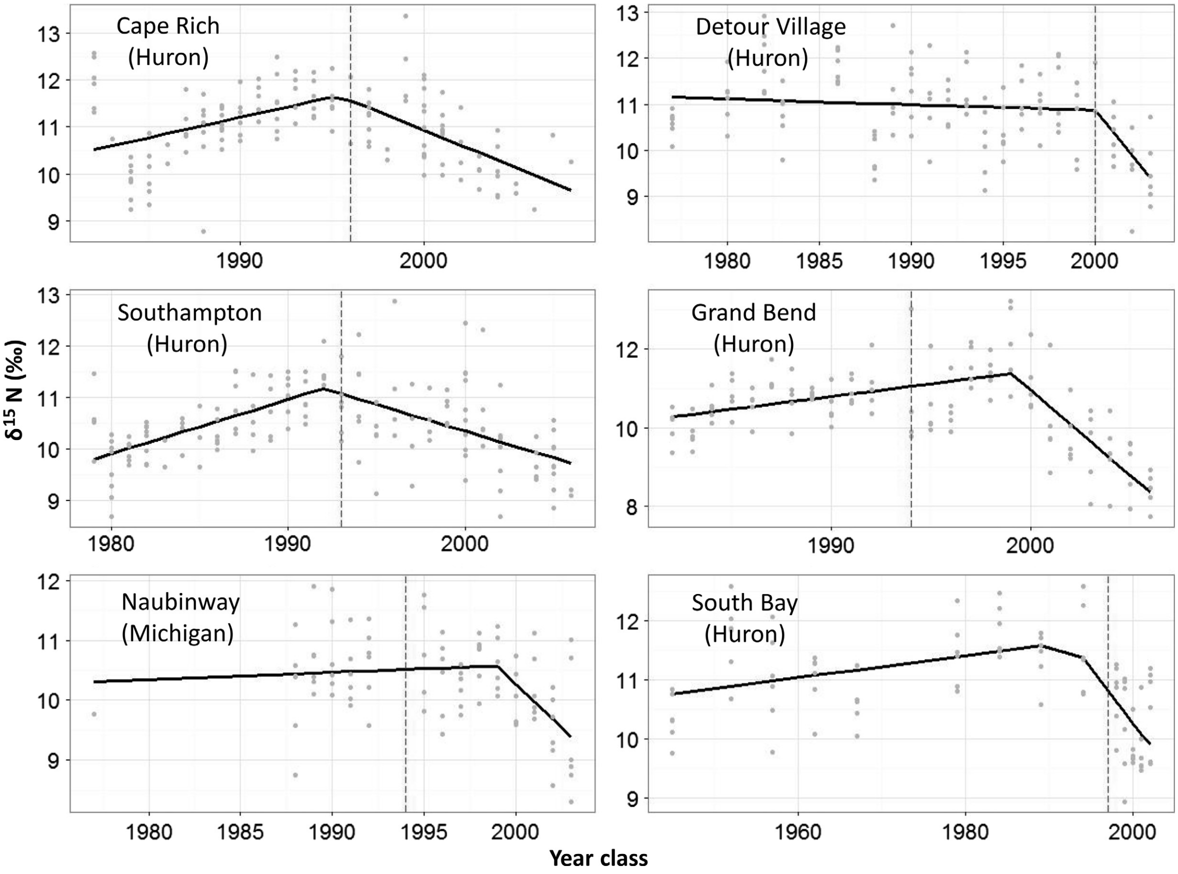

FIG. 5. Breakpoint regression for δ^{15}N. Vertical line depicts the dreissenid establishment year. Only locations with significant breakpoints are shown. δ^{15}N values are shown by year class to which the individual fish was born. Points are individual measurements; lines are regression lines.

dreissenid mussel populations often showed a shift to more positive δ^{13}C (i.e., an enrichment in ^{13}C), which reflects a shift to a greater reliance on nearshore-sourced carbon. In South Bay, the directional shift in δ^{13}C was accompanied by an increase in the proportion of nearshore prey items in the diet and a decrease in the depth-at-capture of lake whitefish (Rennie et al. 2009).

Increasing δ^{13}C values in lake whitefish could arise from two potential mechanisms, both resulting in a greater reliance on nearshore production. The first is a shift toward more nearshore feeding, which appears to be the case in South Bay where isotopic shifts were accompanied by an abrupt change to a more nearshore diet and depth distribution (Rennie et al. 2009). The second mechanism is an overall increase in benthic production in what were systems previously dominated by pelagic energy pathways, becoming apparent across multiple trophic levels in the lake. This was the pattern observed in Lake Simcoe, Ontario following the dreissenid mussel invasion (Rennie et al. 2013). Analysis of benthic samples (either biota or sediments) collected over time at different depths would help resolve which of the two mechanisms are occurring in these populations.

Regardless of the mechanism, the increased reliance on nearshore production supports the theory that the sources of energy, and thus energy pathways, have changed following dreissenid establishment in the Great Lakes (Hecky et al. 2004). These changes are broad, affecting lake whitefish populations from numerous locations where the benthic habitat and biota have been altered by the presence of dreissenid mussels. The fact that this redirection of energy is broadly affecting higher trophic levels as is indicated by our fish isotope results is a key finding of our study. There is uncertainty as to the extent to which fish populations have been impacted by dreissenid mussels (Bunnell et al. 2014) and whether some of the recent food web changes in the Great Lakes are being driven more predominately by bottom-up (e.g., mediated by dreissenids) vs. top-down (e.g., mediated by predation) effects (Bunnell et al. 2014, Riley and Dunlop 2016). Our findings for lake whitefish have relevance for other fish species; Rush et al. (2012) also found an increase over time in δ^{13}C for lake trout (*Salvelinus namaycush*) from Lake Ontario collected between 1995 and 2008, a pattern that was attributed to an increased reliance on carbon derived from nearshore sources. A study in Lake Michigan, also found evidence for increases in δ^{13}C between 2002–2003 and 2010–2012 in several other fish species, presenting this as evidence for a switch in energy pathways from pelagic to nearshore subsidies with the expansion of dreissenid mussels (Turschak et al. 2014). The findings of our study show the broad nature of these responses, the temporal scale of these effects, and the important role of bottom-up processes associated with dreissenid mussels. What is also of relevance is that these changes in energy pathways are having a geographically widespread effect on the resource use of one of the Great Lakes most valuable commercially harvested fish species.

Although the signal from dreissenids was less prominent for δ^{15}N than it was for δ^{13}C, the patterns were overall generally consistent with an increased reliance on nearshore-derived production. δ^{15}N tends to decline when moving from offshore to nearshore in freshwater lakes (Vander Zanden and Rasmussen 1999, Rennie et al. 2009; Appendix S2). It is also possible that a decrease in δ^{15}N is occurring because of an overall increase in benthic production, causing a pattern consistent with a reduction in food chain length. In four locations, we found obvious decreases and in two locations we found more recent decreases in δ^{15}N. In the six locations with significant breakpoints, there was a consistent pattern of positive or near zero slopes in δ^{15}N that switched to negative, increasingly steep slopes following the breakpoints that were within 0–5 yr of dreissenid establishment. In contrast, there were no trends in δ^{15}N for Lake Superior. Similar to δ^{13}C, sediment cores or other sources of baseline information for δ^{15}N would enable further understanding as to whether resource use shifts in lake whitefish are the result of increased benthic production or an increased prevalence of nearshore feeding.

A shift to more nearshore feeding in lake whitefish following dreissenid establishment could be related to the dramatic declines in *Diporeia* spp. that coincided with the population expansion of zebra and quagga mussels in Lakes Erie, Ontario, Michigan, and Huron (Dermott and Kerec 1997, Lozano et al. 2001, Nalepa et al. 2007, 2009*a*). Although Lake Whitefish feed on a variety of prey items that varies seasonally and geographically, the benthic amphipod *Diporeia* are frequently found in their diet when present (Rennie et al. 2009, Pothoven and Madenjian 2013, Sierszen et al. 2014) and appear to be higher in energy density than some of the more nearshore prey items consumed following dreissenid establishment (McNickle et al. 2006, Rennie et al. 2009). *Diporeia* declines tended to first occur at shallower depths in many of the open areas of the lakes (e.g., Nalepa et al. 2007), but perhaps with reductions occurring more quickly in some of the embayments such as South Bay, Lake Huron; this might explain variability in response time observed in isotopic signatures immediately following the dreissenid establishment year. This could also explain agency catch data, which shows a tendency toward deeper depth distributions of lake whitefish (and benthic fishes) in many areas following dreissenid establishment, with a subset of locations showing a subsequent shallower distribution of catches (Riley and Adams 2010, Rennie et al. 2015). Our result showing higher variability in δ^{13}C in post-dreissenid years in all but one location (Table 1) could also reflect a tendency of lake whitefish to move around more (Rennie et al. 2012), searching for remaining pockets of *Diporeia* or other food sources. Beyond the years included in our study, we might expect further shifts in isotopic signatures now that quagga mussels are expanding into more offshore areas (Bunnell et al. 2009, Karatayev et al. 2015) and Lake Whitefish are also increasing their reliance on round goby (*Neogobius melanostomus*), a more recent fish invader (Pothoven and Madenjian 2013).

Our study focused on the timing of dreissenid mussel establishment, but it is possible that other factors have affected lake whitefish dynamics and the isotopic signatures of their scale samples. This is an obvious conclusion given some of the trends apparent prior to dreissenid establishment and in the Apostle Islands of Lake Superior. For example, lake whitefish population abundance and climate could influence resource use in these populations. Other factors, such as changes in ecosystem productivity, atmospheric deposition, and terrestrial input could also affect the baseline isotopic signature of a system, which then alters the isotopic signatures of organisms feeding and living in that system. For example, interpreting the observed decline in δ^{13}C in Lake Erie is challenging because of sparse data, but it is possible that reduced phosphorus loadings led to the different response observed there (Appendix S4). We adjusted δ^{13}C for the Suess effect to account for baseline increases in δ^{13}C occurring as a result of anthropogenic activity (Verburg 2007, Appendix S3). However, previous research suggests that δ^{15}N in watershed sediments and fish tissue can be influenced by anthropogenic activity such as sewage effluent or industrial emissions, although the direction of trends differs depending on the proposed mechanism (Cabana and Rasmussen 1996, Hiriart-Baer et al. 2011, Holtgrieve et al. 2011). Baseline corrections have been done in studies examining isotopic trends of fish among multiple sites at single (or relatively few) points in time, for example by subtracting the isotopic signatures of unionid mussels (Cabana and Rasmussen 1996). However, in studies such as ours, where historical analysis is done on archived samples dating back decades, this type of correction is considerably more challenging. While sediments have been used to correct for δ^{15}N baselines in at least one other system (Rennie et al. 2013), published sediment isotopic data for the suite of locations within the Great Lakes and for the timelines we examined are not available.

Despite the potential contribution of other variables, several lines of evidence indicate that the timing of dreissenid mussel establishment remains a key driver of lake whitefish dynamics and changes in the isotopic ratios we measured. First, the changes in isotopic signatures were more abrupt than would be expected if gradual climate warming or gradual baseline changes in the environment as a result of anthropogenic change were the main driving factor of the fish isotopic trends. Second, trends in lake whitefish isotopes showed consistent patterns among most locations whereas trends in lake whitefish population abundance tended to be more inconsistent (e.g., either increasing, decreasing or not changing much; see Fera et al. 2015). Third, Lake Superior locations, where dreissenids have not had widespread establishment, either showed no trends in isotopic signatures, or in the case of Apostle Islands, showed a trend in $\delta^{13}C$ that was in the opposite direction compared to all other dreissenid-invaded locations (see Fera et al. 2015 for a description of lake whitefish dynamics in the Apostle Islands). Fourth, a previous study examining trends in growth for many of these same populations found that although lake whitefish population abundance (and to a lesser extent, air temperature) contributed to observed variation in growth, the timing of dreissenid mussel establishment was consistently a prominent variable in explanatory statistical models (Fera et al. 2015). Finally, in South Bay, the shift in isotopic signatures observed was greater and more abrupt than could be explained by a gradual shift in thermocline depth as a result of increasing temperatures, and were linked very clearly to changes in diet (Rennie et al. 2009). Nonetheless, future studies would benefit from additional research on whether system-wide baseline changes in isotopes might be altering isotopic ratios of fish in consistent and predictable ways.

Our study is an illustration of how the invasion of a lower trophic level species can have a broad and nearly consistent effect on a commercially harvested fish. We furthermore provide indirect evidence that dreissenid mussels have altered energy pathways within the Great Lakes (Hecky et al. 2004), a theory that has received much attention but with surprisingly little empirical support. The changes in feeding ecology of lake whitefish as revealed by our isotope results appear to be also having an effect on growth and recruitment of these valuable populations (Fera et al. 2015, Gobin et al. 2015), signaling that the carrying capacity for lake whitefish might have shifted as a result (Gobin et al. 2015). These changes have likely caused a reduction in the amount of harvest the populations can sustainably support, as is predicted from a harvest model built for the southern main basin of Lake Huron (Gobin et al. 2016). Given the large size and complexity of the Great Lakes, it is notable that the effects of dreissenid mussels on lake whitefish were as consistent as they were. If dreissenid mussels can cause increased reliance on nearshore production in the Laurentian Great Lakes where there is a high ratio of pelagic to nearshore area, the implication is that effects could be even more severe in smaller inland systems where the nearshore makes up a larger percentage of the total lake area and the offshore region is not nearly as large. This is a worrying finding considering the current expansion of quagga mussels into new habitats and waterways, including in North America and Europe (Karatayev et al. 2015, Marescaux et al. 2016).

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