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ARTICLE

Increased Piscivory by Lake Whitefish in Lake Huron

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Abstract
We evaluated the diet of Lake Whitefish *Coregonus clupeaformis* in Lake Huron during 2002–2011 to determine the importance of Round Goby *Neogobius melanostomus* and other fish as prey items. Lake Whitefish that had reached approximately 400 mm in length incorporated fish into their diets. The overall percentage of adult Lake Whitefish in Lake Huron that had eaten fish increased from 10% in 2002–2006 to 20% in 2007–2011, with a corresponding decrease in the frequency of Lake Whitefish that ate *Dreissena* spp. from 52% to 33%. During 2002–2006, Round Goby (wet mass, 38%), sculpins (Cottidae) (34%), and Ninespine Stickleback *Pungitius pungitius* (18%) were the primary fish eaten, whereas Round Goby accounted for 92% of the fish eaten in 2007–2011. Overall, Round Goby were found in the fewest Lake Whitefish stomachs in the north region of Lake Huron (6%) and in the most in the central (23%) and south (19%) regions of the lake. In the central region, Round Goby were eaten during all seasons that were sampled (spring through fall). In the south region, Round Goby were eaten only in the winter and spring but not in the summer when *Dreissena* spp. and spiny water flea *Bythotrephes longimanus* dominated the diet. Based on the 2007–2011 diet composition, an individual Lake Whitefish would need to have increased their consumption relative to that in 1983–1994 by 6% in the north region, 12% in the central region, and 41% in the southern region in order to achieve the same growth that was observed before dreissenid mussels arrived. However, Lake Whitefish weight adjusted for length only increased by 2% between 2002–2006 and 2007–2011 in the central region, decreased by 4% in the northern region, and remained constant in the southern region. This suggests that a shift toward more frequent piscivory does not necessarily improve the condition of a generalist feeder like Lake Whitefish.

Lake Whitefish *Coregonus clupeaformis* are one of the most important commercial fish species in the Laurentian Great Lakes, with annual harvests exceeding 6.9 million kg in 2000–2006, nearly half of which was taken from Lake Huron (Baldwin et al. 2009). Lake Whitefish have also been an ecologically important fish linking the upper and lower food webs in the upper Great Lakes. Historically, phytoplankton from the spring bloom settled to the lake bottom and were assimilated by the macroinvertebrate *Diporeia* spp. (Fitzgerald and Gardner 1993), which in turn were eaten by Lake Whitefish (Ward 1896; Hart 1931; Ihssen et al. 1981; Rennie et al. 2009a). This pathway provided an efficient link between pelagic and benthic food webs to cycle energy from primary production into a harvestable resource (Nalepa et al. 2005). However, following the disappearance of *Diporeia* spp. and the invasion of the Great Lakes by dreissenid mussels, this pathway was altered as primary production was now linked to Lake Whitefish through dreissenids (Pothoven et al. 2001). Although Lake Whitefish are flexible feeders, the shift from eating *Diporeia* spp. to eating dreissenids has been associated in part with declines in condition and growth (Pothoven

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et al. 2001; Rennie et al. 2009b), reduced energy content of the diet (Rennie et al. 2009a), and altered maturation schedules (Wang et al. 2008).

Like dreissenid mussels, Round Goby *Neogobius melanostomus* are native to the Ponto-Caspian region (Marsden et al. 1996). Round Goby were first found in the Great Lakes in 1990 in the St. Clair River (Jude et al. 1992) and soon thereafter in southern Lake Huron in 1994 (Marsden et al. 1996). Round Goby abundance increased between 1997 and 2003 in Lake Huron based on bottom trawl surveys (Schaeffer et al. 2005). Round Goby eat a variety of benthic invertebrates, including dreissenid mussels (French and Jude 2001; Schaeffer et al. 2005), and can alter benthic invertebrate communities (Kuhns and Berg 1999; Lederer et al. 2006).

As Round Goby became more common in the Great Lakes, piscivores, including Lake Trout *Salvelinus namaycush*, Burbot *Lota lota*, Walleye *Sander vitreus*, and adult Yellow Perch *Perca flavescens*, began incorporating them into their diets (Truemper et al. 2005; Dietrich et al. 2006; Fielder and Thomas 2006; Madenjian et al. 2011). Round Goby represent a new pathway that can convert dreissenid mussels into a food source for piscivores (Johnson et al. 2005; Dietrich et al. 2006) and may enhance piscivore growth rates (Steinhart et al. 2004). Interestingly, Round Goby have also been found in small quantities in the diets of the benthivorous Lake Whitefish in Lake Erie (CWTG 2009) and in Lake Huron (Pothoven and Nalepa 2006).

Our goals were to use data collected during 2002–2011 to (1) determine whether the importance of Round Goby as prey for Lake Whitefish changed over time in Lake Huron based on diet composition and frequency occurrence and (2) determine the importance of Round Goby and other prey in Lake Whitefish diets across seasons and regions in Lake Huron. We also used bioenergetics modeling to evaluate the implications that eating Round Goby could have on Lake Whitefish consumption demands.

METHODS

Lake Whitefish were collected in Lake Huron during 2002–2011 for various research projects by the Michigan Department of Natural Resources, the Ontario Ministry of Natural Resources, the Chippewa Ottawa Resource Authority, the U.S. Fish and Wildlife Service, and the National Oceanic and Atmospheric Administration using graded-mesh gill nets and bottom trawls. The lake was divided into three regions for analysis: north, central, and south (Figure 1). Sampling was apportioned into seasons: spring = April–May; early summer = June–July; late summer = August–September; fall = October–November; winter = December–March.

Upon capture, Lake Whitefish were measured and weighed (in most cases) and their stomachs were removed and frozen. To evaluate Lake Whitefish condition in each region, we used an analysis of covariance (ANCOVA) with fish weight as the response, total length as the covariate, and two periods, 2002–2006 and 2007–2011, as the treatments. The same approach was used by Pothoven et al. (2001) to document the change in condition of Lake Whitefish from Lake Michigan following the dreissenid mussel invasion. Fish length and weight were transformed ($\log_e$) to better meet assumptions of linearity and parallelism. Fulton's condition factor (K) was also determined and compared between time periods using analysis of variance (ANOVA).

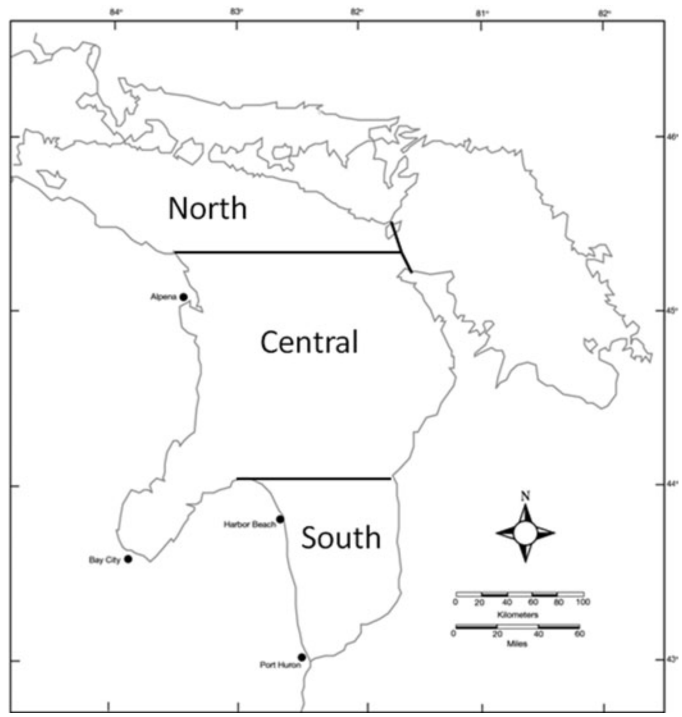

FIGURE 1. Map of Lake Huron showing the location of the north, central, and south sampling regions.

In the laboratory, the stomachs were dissected (esophagus to pyloric caeca) and prey items were identified and counted. Whole organisms and partial organisms (i.e., macroinvertebrates and zooplankton with heads, *Dreissena* spp. or Sphaeriidae with an intact septum) were counted as individuals. Zooplankton were classified as Cyclopoida, Calanoida, daphnia *Daphnia* spp., Bosminidae, Chydoridae, *Diaphanosoma* spp., *Leptodora kindtii*, and spiny water flea *Bythotrephes longimanus*. Benthic macroinvertebrates were generally classified to class (e.g., Amphipoda, Ostracoda, Gastropoda) or family (e.g., Chironomidae, Sphaeriidae), although some organisms were classified to species (e.g., opossum shrimp *Mysis diluviana*, quagga mussel *Dreissena rostriformis bugensis*). Fish prey were identified to species. Large samples of zooplankton or macroinvertebrates were subsampled prior to counting prey.

The lengths of whole prey organisms were measured using a computer image analysis system (Image-Pro 6.2). Prey length was converted to dry mass using length–weight regressions or species-specific mean weights. The dry mass of prey was converted to wet mass using published relationships. The wet mass of partially digested organisms was assumed to be equal to the mean mass of measured organisms. The mass of mollusks included shell mass. Unidentified fish prey were apportioned among species based on the composition of identified prey fish species from the diets of Lake Whitefish for each region and season. Overall, about 5% of the fish biomass in diets was classified as unidentified. Diet is reported as the percent of the total calculated wet mass for each respective region and season. The frequency of occurrence (%) for major prey items is also reported.

Visual inspection of the plot of the proportion of Round Goby in Lake Whitefish diet as a function of year indicated that Round Goby first became substantially more important in Lake Whitefish diets beginning in 2007. Because visual inspection of time series plots may be somewhat arbitrary (Madenjian et al. 2010), we applied change point regression analysis to the time series for the proportion of Round Goby in the Lake Whitefish diet. We assumed that this diet proportion remained constant during a set of early years, followed by a sudden shift in the diet proportion, and then another period of no change in the diet proportion. We determined the change point year that minimized the error sum of squares (Draper and Smith 1981). Change point year refers to the year in which the sudden shift in diet proportion occurred. Based on the change point analysis (see Results), we compared Lake Whitefish diets between the 2002–2006 and 2007–2011 periods.

To determine the effects of changes in diet composition on the rate of food consumption by Lake Whitefish, we used the version of the Wisconsin Lake Whitefish bioenergetics model modified by Madenjian et al. (2013). Energy densities of Lake Whitefish, energy densities of Lake Whitefish prey, and water temperature regimes experienced by Lake Whitefish were taken from our previous studies on Lake Whitefish feeding, growth, and energy density (Madenjian et al. 2006; Pothoven et al. 2006; Pothoven and Madenjian 2008). Growth and diet for Lake Whitefish prior to the dreissenid invasion (1983–1994) were taken from Pothoven and Madenjian (2008) to estimate consumption. We then determined the consumption needed to attain the growth that Lake Whitefish had achieved prior to the dreissenid invasion (i.e., 1983–1994) for three different diet scenarios: the 1983–1994 period, the 2002–2006 period, and the 2007–2011 period. Consumption estimates were made for Lake Whitefish ages 4–6, based on the sizes of fish used for diet analysis and available data.

RESULTS

Fish were incorporated into Lake Whitefish diets once they had reached approximately 400 mm (Figure 2), so further analysis was restricted to Lake Whitefish ≥400 mm. A total of 1,575 Lake Whitefish ≥400 mm were examined for diet analysis, and 1,197 had identifiable stomach contents.

There was an increase in the frequency of fish found in Lake Whitefish diets between 2006 and 2007 that was accompanied by an increase in the frequency of Round Goby found in diets (Figure 3). For 2002–2006, on average each year, 4–16% of Lake Whitefish were eating fish and <6% of the stomachs examined each year contained Round Goby. By contrast, for 2007–2011, 18–33% of Lake Whitefish were eating fish each year, with 13–16% of stomachs containing Round Goby. The change point year was determined to be 2007 ($R^2 = 0.91$, $F_{1,7} = 74.23$, $P < 0.001$; $R^2 < 0.66$ for all other years), thereby corroborating our conclusion from visual inspection of the diet proportion time series that the importance of Round Goby in Lake Whitefish diet first underwent a substantial increase in 2007. In addition to an increase in the frequency of fish in Lake Whitefish diets, there was a shift in the composition of fish eaten between time periods (Figure 4). During 2002–2006, Round Goby, sculpins (family Cottidae), and Ninespine Stickleback *Pungitius pungitius* were the primary fish eaten (% wet mass basis), with smaller contributions by Rainbow Smelt *Osmerus mordax* and other fish (i.e.,

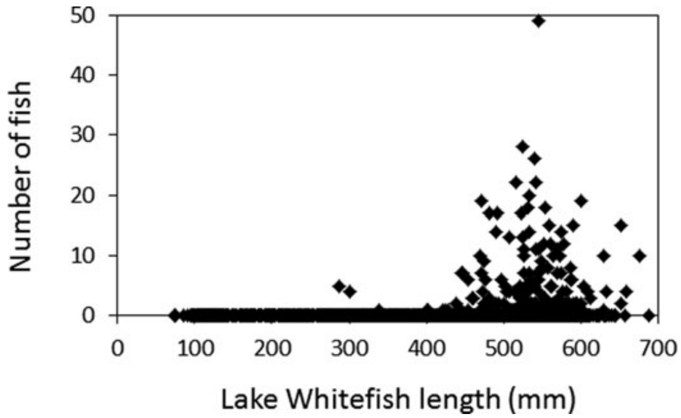

FIGURE 2. The number of fish found in Lake Whitefish stomachs as a function of Lake Whitefish total length in Lake Huron during 2002–2011.

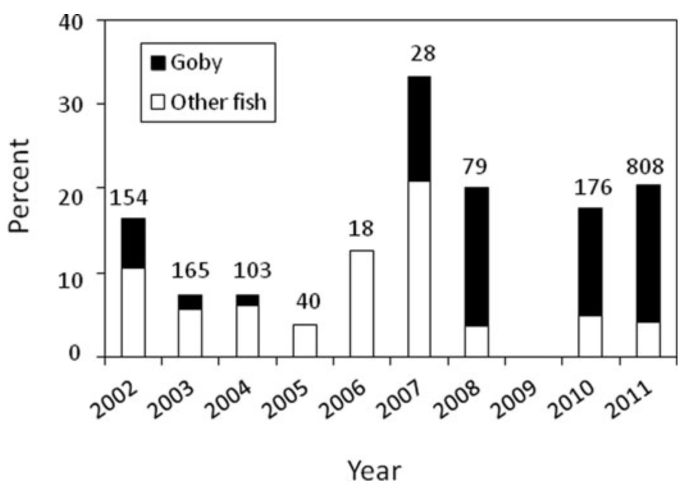

FIGURE 3. Percent of Lake Whitefish in Lake Huron that ate Round Goby and other fish each year during 2002–2011 (no sampling in 2009). The number of Lake Whitefish examined that had food in their stomachs is presented above each bar.

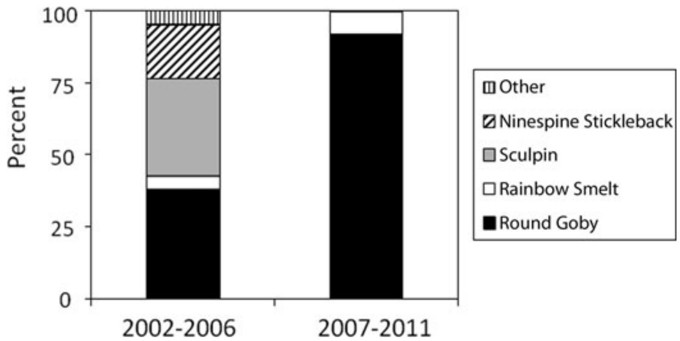

FIGURE 4. Percent composition (% wet mass) of fish prey found in Lake Whitefish diets during 2002–2006 and 2007–2011.

Alewife *Alosa pseudoharengus* and Johnny Darter *Etheostoma nigrum*). For 2007–2011, Round Goby accounted for nearly all the fish eaten, with a small contribution from Rainbow Smelt. The size range of Round Goby that were eaten was 17–95 mm and the mean $\pm$ SE length was 52 $\pm$ 0.9 mm.

In the north region during 2002–2006, Lake Whitefish diet (% wet mass) was mainly shelled prey, i.e., *Dreissena* spp. and Gastropoda (70–83%) during spring through summer (Table 1). Furthermore, *Dreissena* spp. were eaten by > 60% of the Lake Whitefish (Table 2). Fish were a relatively minor component of the diet (0–18%) in 2002–2006 in the north region.

In the north region during 2007–2011, *Dreissena* spp. and Gastropoda combined were never more than 33% of diet mass (Table 1) and *Dreissena* spp. were eaten by < 30% of the Lake Whitefish (Table 2). In turn, Round Goby accounted for 22–39% of the diet mass, except during the fall in 2007–2011 (Table 1), although they were only found in < 5% of the stomachs, except during late summer (Table 2). Other prey that were seasonally important in diets in the north region during 2007–2011 were Rainbow Smelt, opossum shrimp, and Chironomidae (Table 1).

In the central region during 2002–2006, *Dreissena* spp. and Gastropoda combined were 48–79% of the diet biomass during spring through summer (Table 3) and *Dreissena* spp. were found in > 40% of the stomachs (Table 2). Round Goby accounted for 37% of the diet biomass in spring (Table 3) but were only found in 8% of the fish stomachs (Table 2). In the summer, Round Goby accounted for < 2% of the diet biomass and other fish (i.e., Ninespine Stickleback and sculpin) accounted for 15–18% of the diet (Table 3).

In the central region during 2007–2011, *Dreissena* spp. and Gastropoda combined were 43% of the diet biomass in the spring but < 21% of the diet for all other seasons (Table 3). Round Goby accounted for 40–76% of the diet biomass (Table 3) and were found in 13–36% of stomachs in spring through summer and 4% of stomachs in the fall (Table 2).

In the south region during 2002–2006, few fish were collected for diet analysis and overall across all seasons the diet was mainly *Dreissena* spp. and Round Goby (Table 4). For 2007–2011, *Dreissena* spp. remained relatively important (>39% of diet biomass) except during spring. Round Goby accounted for over half the diet biomass in spring and winter (Table 4) and were found in 11–34% of stomachs during 2007–2011 (Table 2). By contrast, no Round Goby were found in diets in the south region during summer 2007–2011 when the spiny water flea was an important prey item (Table 4).

For the 2002–2006 diet composition, consumption by an individual Lake Whitefish would need to increase by 83% in the north region and 53% in the central region relative to 1983–1994 in order to achieve the same growth that was observed before dreissenid mussels arrived (i.e., 1983–1994 growth rates) (Figure 5). The bioenergetic analysis was not done for the south region for the 2002–2006 diet scenario because so few fish were available for diet analysis. With the 2007–2011 diet composition, an individual Lake Whitefish would need to have increased consumption relative to 1983–1994 only by 6% in the north region and 12% in the central region in order to achieve

TABLE 1. Diet (percent wet mass) of Lake Whitefish in northern Lake Huron during 2002–2006 and 2007–2011. Abbreviations are as follows: N = the number of Lake Whitefish with food in their stomachs and T = trace.

	2002–2006			2007–2011				
Prey and *N*	Spring	Early summer	Late summer	Spring	Early summer	Late summer	Fall	Winter
Spiny water flea	0	1	1	0	4	2	10	0
Chironomidae	4	6	2	10	21	57	13	67
Opossum shrimp	0	T	6	6	6	T	58	2
Dreissena spp.	47	43	81	11	28	1	5	1
Gastropoda	36	27	T	2	5	T	2	T
Round Goby	0	5	0	25	32	39	0	22
Rainbow Smelt	0	3	0	45	0	0	12	5
Other fish	8	10	0	0	0	0	0	0
Other	5	5	10	1	4	1	T	3
N	8	80	13	53	60	51	25	137

TABLE 2. Seasonal frequency of occurrence (percent of Lake Whitefish with the food type in their stomachs) for selected prey in Lake Whitefish diets in northern, central, and southern Lake Huron during 2002–2006 and 2007–2011.

			Frequency (%)			
Years	Season	Zone	*Dreissena* spp.	Round Goby	Rainbow Smelt	Other fish
2002–2006	Spring	North	75	0	0	13
	Early summer	North	60	1	1	9
	Late summer	North	77	0	0	0
	Spring	Central	54	8	0	16
	Early summer	Central	52	1	1	3
	Late summer	Central	40	0	0	9
	All	South	10	30	0	20
2007–2011	Winter	North	13	5	1	1
	Spring	North	25	4	11	6
	Early summer	North	30	3	0	7
	Late summer	North	16	20	0	0
	Fall	North	4	0	4	0
	Spring	Central	54	23	0	1
	Early summer	Central	19	13	0	1
	Late summer	Central	17	36	6	5
	Fall	Central	50	4	0	0
	Winter	South	53	34	2	3
	Spring	South	37	11	15	0
	Early summer	South	65	0	0	0
	Late summer	South	25	0	0	0

the same growth that was observed before dreissenid mussels arrived. By contrast, for the 2007–2011 diet composition in the south region an individual Lake Whitefish would have to increase consumption by 41% relative to 1983–1994 in order to achieve premussel growth rates.

There was a slight but significant interaction between the $\log_e$ length and time period in the north region ($F_{1,342} = 4.2$, $P = 0.04$), but the 95% confidence interval of the slopes relating $\log_e$ length and $\log_e$ weight overlapped, so we proceeded with an ANCOVA to evaluate condition. There was no interaction between the covariate and the factor in the central ($F_{1,659} = 0.89$, $P = 0.35$) or south regions ($F_{1,342} = 0.84$, $P = 0.36$). Mean weight adjusted for length increased slightly between 2002–2006 and 2007–2011 in the central region ($F_{1,661} = 7.4$, $P = 0.007$), decreased slightly in the northern region ($F_{1,343} = 17.6$, $P <$ 0.001), and remained the same in the southern region ($F_{1,61} =$

TABLE 3. Diet (percent wet mass) of Lake Whitefish in central Lake Huron during 2002–2006 and 2007–2011. Abbreviations are as follows: *N* = the number of Lake Whitefish with food in their stomachs and T = trace.

	2002–2006			2007–2011			
Prey and *N*	Spring	Early summer	Late summer	Spring	Early summer	Late summer	Fall
Spiny water flea	0	T	5	0	1	5	7
Chironomidae	15	8	T	10	38	1	T
Dreissena spp.	42	52	78	42	21	6	10
Gastropoda	6	16	1	1	T	0	5
Round Goby	37	2	0	43	40	76	74
Rainbow Smelt	0	1	0	0	0	12	0
Other fish	0	18	15	0	0	0	0
Other	T	3	1	4	T	T	4
N	37	146	58	102	70	103	24

TABLE 4. Diet (percent wet mass) of Lake Whitefish in southern Lake Huron during 2002–2006 and 2007–2011. Abbreviations are as follows: N = the number of Lake Whitefish with food in their stomachs and T = trace.

	2002–2006	2007–2011			
Prey and N	All seasons	Spring	Early summer	Late summer	Winter
Spiny water flea	1	0	11	56	0
Chironomidae	T	9	2	1	T
Dreissena spp.	39	11	87	41	45
Round Goby	47	53	0	0	53
Rainbow Smelt	0	27	0	0	0
Other	13	T	T	2	2
N	10	27	72	8	113

1.7, $P = 0.20$) (Table 5). Fulton's condition factor (K) followed identical patterns between time periods in each region as observed for length-adjusted mean weights (Table 5). Thus, it appears that Lake Whitefish condition in Lake Huron changed very little, if at all, between the 2002–2006 and 2007–2011 periods.

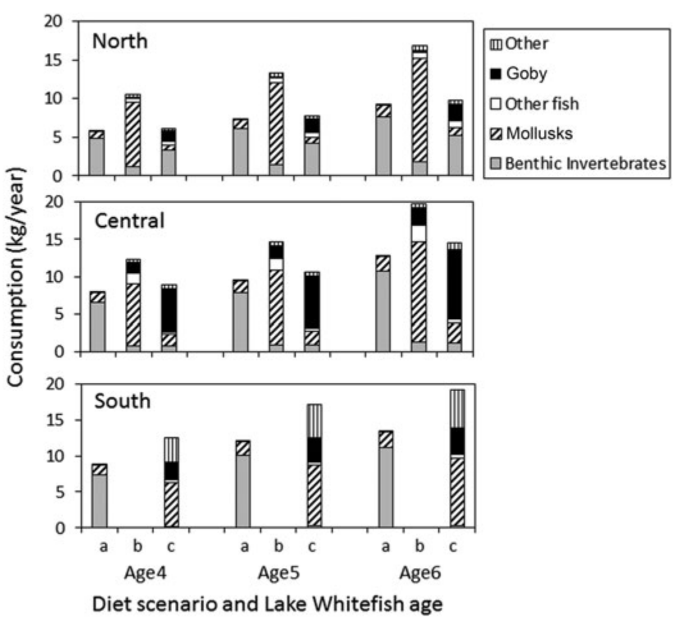

FIGURE 5. Annual consumption of an individual age-4, -5, or -6 Lake Whitefish needed to achieve the growth observed during the predreissenid period (1983–1994) in Lake Huron for each region under three diet scenarios: (a) predreissenid diet, (b) diet composition for 2002–2006, and (c) diet composition for 2007–2011. Annual consumption was estimated using the modified version of the Wisconsin Lake Whitefish bioenergetics model (Madenjian et al. 2013). Mollusks include *Dreissena* spp., Gastropoda, and Sphaeriidae. Benthic invertebrates include all nonmollusk benthic macroinvertebrates (e.g., Chironomidae, *Diporeia* spp., opossum shrimp, etc).

TABLE 5. Mean weight (adjusted for length; ANCOVA) and Fulton's condition factor (K) of Lake Whitefish in each region in Lake Huron for 2002–2006 and 2007–2011. Significant differences ($P < 0.05$) for each region are indicated by an asterisk. Mean total lengths were 489, 524, and 508 mm for the north, central, and south regions, respectively.

	Weight (g)			K		
Years	North	Central	South	North	Central	South
2002–2006	1,017*	1,251*	1,122	0.89*	0.88*	0.87
2007–2011	973	1,279	1,095	0.84	0.91	0.85

DISCUSSION

We demonstrated the dynamic nature of Lake Whitefish diets in the Great Lakes as invasive species continue to alter the ecosystem. In particular, we documented that the overall percentage of adult Lake Whitefish in Lake Huron that had eaten fish increased from 10% in 2002–2006 to 20% in 2007–2011. This increase in the occurrence of fish in the diets of Lake Whitefish was largely due to an increase in the frequency of the invasive Round Goby. We also noted a corresponding decrease in the frequency of *Dreissena* spp. from 52% to 33% of Lake Whitefish diets between the two time periods. *Dreissena* spp. and other shelled prey had been a dominant food item for Lake Whitefish following the declines of *Diporeia* spp. (Pothoven and Nalepa 2006).

The importance of Round Goby in the diet of Lake Whitefish from Lake Huron varied both spatially and seasonally during 2007–2011. Overall, Round Goby were eaten less frequently by Lake Whitefish in the north region (6%) and more frequently in the central (23%) and south (19%) regions. However, in the central region Round Goby were eaten during all seasons that were sampled (spring through fall), but in the south region, Round Goby were eaten only in winter and spring but not in the summer. During 2002–2006, only 1–2% of the Lake Whitefish in the north and central regions had eaten Round Goby, and although 30% of the Lake Whitefish had eaten Round Goby in the south, this sample was based on only 10 fish. Round Goby were initially most abundant in the southern and central regions of Lake Huron (Schaeffer et al. 2005), so it is not surprising that they were initially consumed more frequently in these regions than in the north. On the other hand, even though lakewide densities of Round Goby peaked in 2003 according to the Lake Huron bottom trawl survey (Roseman et al. 2013), they remained uncommon in Lake Whitefish diets until 2007. This suggests a substantial time delay between the attainment of relatively high abundance of Round Goby in Lake Huron and the switching to Round Goby in the diet of Lake Whitefish from Lake Huron. Predators might require a learning period to adapt to novel prey like Round Goby (Brownscombe and Fox 2013). On the other hand, the double-crested cormorant *Phalacrocorax auritus*, an avian predator, rapidly incorporated Round Goby into its diet in Lake Ontario (Johnson et al. 2010).

The diets of Lake Whitefish have reflected the shifting pathways for energy flow in the Great Lakes following the proliferation of invasive species over recent decades. After the decline of the benthic amphipods *Diporeia* spp. and the proliferation of dreissenid mussels, there was a shift from eating *Diporeia* spp. to eating more shelled prey, including dreissenids (Pothoven et al. 2001; Owens and Dittman 2003; Rennie et al. 2009a). This diet shift demonstrated the adaptability of Lake Whitefish, but it also was associated with lower growth and condition (Pothoven et al. 2001; Rennie et al. 2009b), increased feeding costs (Rennie et al. 2012), and decreased diet energy (Owens and Dittman 2003; Rennie et al. 2009a). The consumption of Round Goby indicates that, in addition to the direct pathway of energy flow between dreissenids and Lake Whitefish, there is now also an indirect pathway from dreissenids to Round Goby to Lake Whitefish.

A diet shift from invertebrates to fish is generally considered advantageous, especially for specialist piscivores during early ontogeny (Olson 1996; Post 2003), as well as older piscivores (e.g., Brown Trout *Salmo trutt*a; Jensen et al. 2012). Eating Round Goby has been linked to increased growth for some predators in Lake Erie by providing a new pathway for access to energy (i.e., dreissenids) that was not available and because they are abundant and relatively easy to capture (Steinhart et al. 2004; Johnson et al. 2005). This pathway of indirectly incorporating dreissenids into piscivore diets is becoming increasingly common in the Great Lakes (Johnson et al. 2005; Dietrich et al. 2006) and reflects a reengineering of the littoral food web and a shift to more benthic pathways (Southward-Hogan et al. 2007; Campbell et al. 2009; Rush et al. 2012).

From an energetic standpoint, we would expect that shifting from a diet dominated by shelled prey including dreissenids to a diet with more fish would be beneficial for Lake Whitefish. The energy density of Round Goby in Lake Huron (4,240 J/g; S. Pothoven, unpublished data) is comparable to that of *Diporeia* spp. (4,185 J/g) and much higher than that of dreissenids (1,703 J/g; see Pothoven and Madenjian 2008). Our bioenergetics analysis indicated that based on the diet composition during 2007–2011, Lake Whitefish that consumed similar amounts of food to the amounts consumed in the predreissenid period could attain predreissenid growth rates in the north and central regions, but not in the south region. In the south region, Round Goby were only consumed seasonally, low-energy dreissenids remained an important prey, and the summer diet was dominated by low-energy predatory zooplankton (Spiny water flea, 1,674 J/g; see Pothoven and Madenjian 2008). However, body condition did not increase between 2002–2006 and 2007–2011 in the north and south regions and only increased 2% in the central region. Thus, even though Round Goby are higher in energy than dreissenids, other factors might reduce the benefits of increased piscivory for Lake Whitefish.

A shift toward piscivory might not be as advantageous to a generalist feeder like Lake Whitefish as it would be for a specialist piscivore. For example, Yellow Perch are omnivorous generalists that are usually not piscivorous until at least age 1 (Keast 1985). A laboratory study found that growth was slower for Yellow Perch than for the specialist piscivore Walleye when both species were fed fish (Graeb et al. 2005). Generalist piscivores could have lower capture efficiencies of fish prey than specialist piscivores because of differing mouth morphologies and the lack of teeth (Graeb et al. 2005). Therefore, even though generalists are opportunistic and will feed on fish, the benefits of increased piscivory might not be as great as for specialized piscivores, depending on prey availability (i.e., encounter rates), handling time, pursuit time, search costs, and prey size availability (Truemper and Lauer 2005; Graeb et al. 2006; Campbell et al. 2009; Weber et al. 2011). Lake Whitefish are considered a benthivore and their subterminal mouth position could affect their ability to capture fish prey. On the other hand, a generalist feeding strategy is considered advantageous in a variable environment (Skúlason and Smith 1995).

Finally, the consumption of Round Goby by Lake Whitefish needs to be taken into consideration when evaluating piscivory in Lake Huron, and possibly other regions of the Great Lakes. Even if only a small fraction of the Lake Whitefish population is eating Round Goby, the magnitude of the biomass of Lake Whitefish in the main basin of Lake Huron (approximately 30,000 metric tons; J. He, Michigan Department of Natural Resources, personal communication) relative to that of the dominant piscivore Lake Trout (3,000 metric tons; J. He, personal communication) indicates that piscivory by Lake Whitefish could be substantial. Lake Whitefish should not only be considered a benthivore when evaluating the flow of energy in Great Lakes food webs but also a potential competitor with fish and avian piscivores.

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