

Resource switching in fish following a major food web disruption

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Abstract Dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) have re-engineered Great Lakes ecosystems since their introduction in the late 1980s. Dreissenids can have major indirect impacts on profundal habitats by redirecting nutrients and energy away from pelagic production (which supplies profundal production) and depositing nutrients and energy in the nearshore zones that they occupy. However, strong empirical evidence for the effects of this redirection of resources on fish populations is currently lacking. Here, we report significant shifts in isotopic signatures, depth distribution and diets of a coldwater profundal fish population that are all consistent with a greater reliance on nearshore resources after the establishment of dreissenid mussels in South Bay, Lake Huron. Isotopic signatures of scales collected from 5-year-old lake whitefish (*Coregonus*

clupeaformis) demonstrated remarkable stability over the 50-year period prior to the establishment of dreissenids (1947–1997) and a sudden and significant change in isotopic signatures (3‰ enrichment in $\delta^{13}\text{C}$ and 1‰ depletion in $\delta^{15}\text{N}$) after their establishment (2001–2005). These dramatic shifts in isotopic signatures were accompanied by a coincident shift in the mean depth of capture of lake whitefish towards the nearshore. A comparison of previously unpublished pre-invasion diets of lake whitefish from South Bay with contemporary diets collected between 2002 and 2005 also indicate a greater reliance on nearshore prey after the invasion of dreissenid mussels. This study is the first to report changes in the carbon source available to lake whitefish associated with restructured benthic communities after the appearance of dreissenid mussels. Further, this study contributes to a growing body of work that demonstrates the ecological insights that can be gained through isotopic analysis of archived fish bony tissues in ecosystems that have experienced significant levels of disturbance.

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Introduction

Once established, non-indigenous species can have profound effects on the ecosystems into which they are introduced and can frequently produce negative impacts on local economies (Forseth and Innis 2004; Wang et al. 2006; Smith and Tibbles 1980). In the Laurentian Great Lakes, the invasion and subsequent establishment of dreissenid mussels (*D. polymorpha* and *D. bugensis*) have altered both the structure and function of Great Lakes ecosystems. Changes in the Great Lakes following dreissenid establishment

include increased water clarity and chemistry (Barbiero and Tuchman 2004; Johannsson et al. 2000), alteration of plankton communities (Johannsson et al. 2000) and negative interactions with native benthic invertebrates (Dermott and Kerec 1997; Dermott 2001; Nalepa et al. 1998, 2007; McNickle et al. 2006). Further evidence suggests that the impact of dreissenids on profundal and pelagic habitats may be indirect, remotely affecting habitats that they do not themselves occupy (Nalepa et al. 2006). However, field-based studies to lend evidence to this indirect relationship have remained elusive.

A recently proposed conceptual model to explain the effects of dreissenids on Great Lakes ecosystems is the nearshore phosphorous shunt (Hecky et al. 2004), whereby phosphorous and other nutrients are directed and retained to a greater extent in nearshore areas than was observed prior to dreissenid establishment. A prediction of this model is that the importance of offshore production in ecosystems influenced by dreissenids should be greatly reduced relative to nearshore production. This implies that pelagic (and therefore profundal) communities where dreissenids are present may be faced with reduced nutrient (i.e., phosphorous) inputs and in turn lower productivity due to the redirection of energy nearshore. In support of this model, recent work has provided strong evidence of impacts of dreissenids on nearshore primary production (Depew et al. 2006), but investigations demonstrating clear links between the impacts of dreissenids—remote or otherwise—with offshore or profundal communities as proposed by the nearshore shunt hypothesis are rare (but see Pothoven and Madenjian 2008).

Lake whitefish (*Coregonus clupeaformis*) are an important component of the commercial fishery of the Great Lakes, representing over 45% of the total commercial harvest by weight, generating over \$18,000,000 USD landed value in 2000 (Kinnunen 2003). Recent declines in the growth rates and condition of lake whitefish have been associated with the dreissenid invasion (Mohr and Ebener 2005). As dreissenid mussels increased in abundance in the Great Lakes, the abundance of *Diporeia*, a deepwater amphipod and once a prominent member of the profundal food web, declined dramatically. *Diporeia* are widely cited to have been a key component of lake whitefish diets before the invasion of dreissenids (Pothoven et al. 2001; Lumb et al. 2007; Pothoven and Madenjian 2008). However, sufficient data to confirm this observation are lacking in the primary literature, and historical descriptions of whitefish diets that have been reported are based on small sample sizes and lack any seasonal resolution (e.g., Hart 1931; Ihssen et al. 1981).

Stable isotopes can be a valuable tool in helping ecologists better understand food web structure (Hecky and Hesslein 1995). Carbon isotopes can be used to distinguish

the importance of isotopically distinct energy sources to consumers, such as terrestrial versus aquatic inputs (France 1995), marine versus freshwater sources (Hobson 1990), or littoral versus pelagic or profundal sources (Vander Zanden and Rasmussen 1999; France 1998). Nitrogen stable isotopes typically provide insights into consumer trophic level (Vander Zanden and Rasmussen 2001; Post 2002). Because tissues in fish turn over relatively slowly compared to the retention of diet items in the gut, stable isotopic signatures of fish tissues can provide an integrated picture of the feeding ecology of organisms that would be laborious to construct using traditional point-in-time sampling of diets. Recent evidence has also shown strong correlations between stable isotopic signatures of fish muscle with that of fish scales and fin clips (Perga and Gerdeaux 2003; Kelly et al. 2006).

In this study, we tested the hypothesis that the feeding ecology and depth distribution of lake whitefish have changed with the establishment of dreissenid mussels in the Great Lakes. Contemporary samples of lake whitefish diets and catch records along with isotopic signatures of lake whitefish and benthic invertebrate tissues were contrasted with previously unreported historic data to demonstrate a greater reliance of lake whitefish on nearshore resources following dreissenid colonization.

Materials and methods

Study site

Fish and invertebrates were collected during 1947–2005 from the deep inner basin of South Bay, Lake Huron [Electronic supplementary material (ESM) S1] by the Lake Huron Research Unit of the Ontario Ministry of Natural Resources (OMNR). Evidence suggests that the population of lake whitefish occupying the inner basin is resident and does not mix with the population in the main basin of Lake Huron (Casselman et al. 1981; Henderson and Fry 1987). Benthic invertebrate samples collected from the inner basin were thus assumed to provide an accurate description of prey available to this population of lake whitefish.

Preliminary investigations

Before scale archives could be examined, preliminary investigations were required to gather basic information regarding lake whitefish isotopic signatures. First, we required relationships between lake whitefish scales and tissues in order to interpret variation in scale isotopic signatures over time. Second, acidification of scales has been proposed as a necessary step to remove the confounding effects of carbonate from scale carbon isotope signatures

(Perga and Gerdeaux 2003). We sought to test the necessity of scale acid treatment in our population. Last, we required an understanding of the effect of whitefish size on isotopic signatures to further reduce potentially confounding variation in fish isotopic signatures over time.

To provide this information, a subsample of 40 lake whitefish from across the size range captured during 2005 index netting was selected. Lake whitefish were collected between 29 August and 1 September 2005 using multi-mesh experimental gillnets. Each net was made up of 25-m-long by 2-m-high panels of 25-, 51-, 64-, 76-, 89-, 102-, 114- and 127-mm stretched monofilament mesh. All lake whitefish collected were measured for fork and total length, weighed, assigned a unique identification code, then individually bagged and frozen for later sampling.

In the laboratory, scales were removed from the left side of the fish, above the lateral line and below the dorsal fin, cleaned with distilled water and allowed to dry. A 3-mm-gauge punch was applied to the center of cleaned scales to remove scale tissue associated with zooplanktivory in early lake whitefish life histories (Reckahn 1970). Subsets of punched scales were treated with 10% HCl for 2 min (Perga and Gerdeaux 2003). This procedure has been reported to remove potentially confounding carbonate signatures from scales. A small (1–10 g) portion of skinless flesh was taken from the left side of the fish, above the lateral line and anterior to the dorsal fin. These muscle tissues were dried at 60°C to constant weight (24 h), ground with mortar and pestle, and stored in clean glass scintillation vials. Stable isotopes of all tissues were analyzed at the Environmental Isotope Laboratory at the University of Waterloo on a Delta continuous flow stable isotope mass spectrometer (Micromass) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108). Analytical error was reported to be 0.2 and 0.3‰ for carbon and nitrogen, respectively. To correct results and monitor data quality, international standards were employed for use with analyses of carbon (IAEA-CH6) and nitrogen (IAEA-N1, IAEA-N2), respectively.

Findings from these preliminary investigations showed that lake whitefish muscle tissue isotopic signatures were strongly related to those of scales ($\delta^{13}\text{C}$, Fig. 1a, $F_{1,38} = 91.98$, $P < 0.0001$; $\delta^{15}\text{N}$, Fig. 1b, $F_{1,38} = 131.85$, $P < 0.0001$). Scale $\delta^{13}\text{C}$ was consistently enriched compared with muscle tissue by 4.6‰ (± 1.8 ‰ standard error; Fig. 1a; t test that slope is not different from 1, $t = -0.83$, $P = 0.2$; t test that intercept is not different from 0, $t = -2.6$, $P = 0.013$). Scale $\delta^{15}\text{N}$ was not statistically different from that of tissues (Fig. 1b; t test that slope is not different from 1, $t = -0.18$, $P = 0.4$; t test that intercept is not different from 0, $t = -0.117$, $P = 0.907$). Acid treatment had no significant effect on lake whitefish scale isotopic signatures ($\delta^{13}\text{C}$, Fig. 2a, t test that slope is not different from 1,

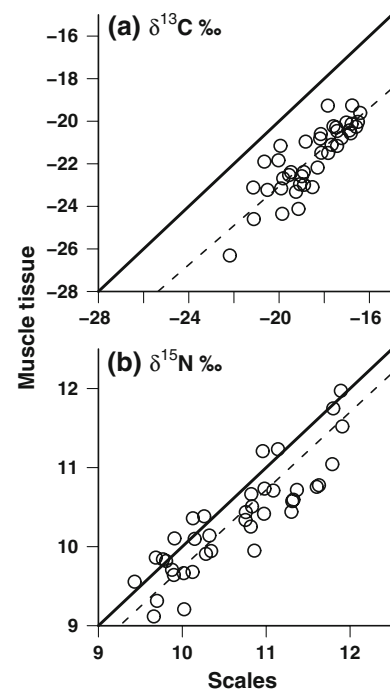


Fig. 1 Relationship between lake whitefish (*Coregonus clupeaformis*) isotopic signatures of muscle tissue and scales for **a** $\delta^{13}\text{C}$ and **b** $\delta^{15}\text{N}$. Dashed lines are from the regression of tissue isotopic signatures on those of scales; solid line is the 1:1 line

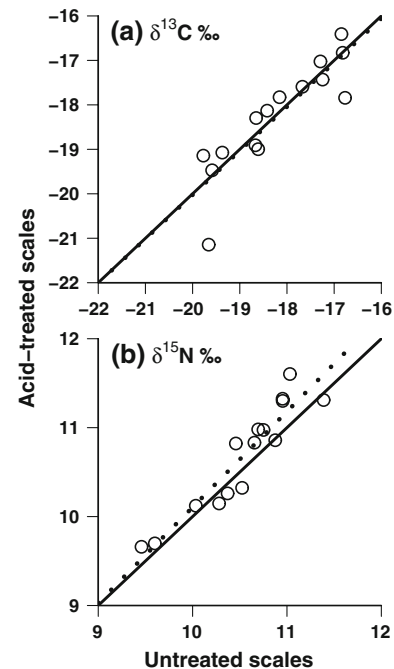


Fig. 2 Relationships between **a** $\delta^{13}\text{C}$ and **b** $\delta^{15}\text{N}$ signatures for acid-treated scales with untreated (not acid-treated) lake whitefish scales. Solid line is the 1:1 line; dotted line is the regression of acid-treated scales on untreated scales (behind 1:1 line in panel a)

$t = -0.06$, $P = 0.5$; t test that intercept is not 0, $t = -0.074$, $P = 0.942$; $\delta^{15}\text{N}$, Fig. 2b, t test that slope is not different from 1, $t = 0.66$, $P = 0.3$; t test that intercept is not 0,

$t = -0.543$, $P = 0.596$). Lake whitefish tissue $\delta^{13}\text{C}$ did not vary linearly with fish length ($P = 0.28$; Fig. 3a). The relationship between tissue $\delta^{15}\text{N}$ with whitefish body size was weak but significant (Fig. 3b, $F_{1,38} = 9.2$, $P = 0.004$; with outlier removed, $F_{1,37} = 7.7$, $P = 0.008$). The overall effect of this relationship is a reduction of approximately 1‰ (less than 1/3 of a trophic level) over the size range examined (210–515 mm fork length). Based on these findings, we proceeded with isotopic analysis of lake whitefish scales (without acid treatment) from archived collections to examine long-term patterns in lake whitefish isotopic signatures. In an attempt to avoid confounding effects of variation in mean fish size from year to year, we chose a single age class (age 5) for our analysis of archived scales. Age 5 was selected because this age class was well represented in archived samples and because we could reliably determine fish of this age based on scales. The determination of age from scales becomes increasingly less reliable for older aged fish compared with other structures, such as otoliths or fin rays (ESM S2; Mills and Chalanchuk 2004).

Archived scale collections

Based on our preliminary findings, three scales each from age 5 male and female whitefish were selected from each of the following years: 1948, 1955, 1960, 1965, 1970, 1982, 1987, 1992, 1997, 2001, 2002, 2003, 2004 and 2005. Scales

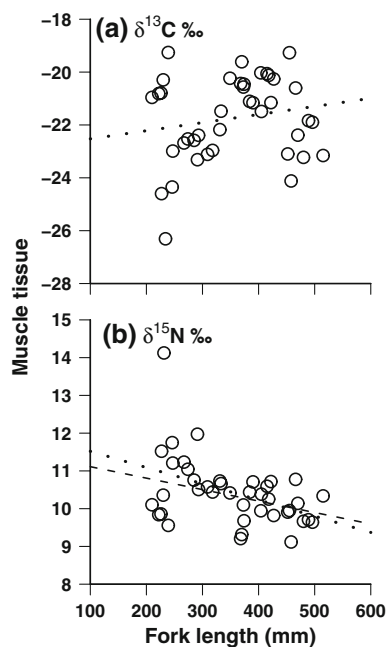


Fig. 3 Variation in lake whitefish tissue **a** $\delta^{13}\text{C}$ and **b** $\delta^{15}\text{N}$ isotopic signatures with body size expressed as fork length (mm). Dotted lines are the regression of tissue isotopic signatures on body size. In **b**, dashed line is the regression without the outlier in the top left-hand quadrant

were cleaned with deionized water, dried and the centers removed as described previously. Portions of the scales were then cut, weighed, placed in tin cups and sent for isotopic analysis. Fish from archived scale collections were all harvested during August to September using similar methods. Pre-invasion years spanned 1948–1997. Zebra mussels (*D. polymorpha*) were first detected in South Bay in 1995 (Ontario Federation of Anglers and Hunters Invasive Species Watch Program, <http://www.invadingspecies.com>) and were well established by 1997 (McNickle et al. 2006). Because we analyzed age 5 fish, we did not expect isotopic changes resulting from food web disruptions until 5 years after dreissenid establishment (i.e., 2001–2002). Post-invasion years included 2001–2005. To evaluate the effect of dreissenid invasion on lake whitefish isotopic signatures over time while controlling for random year-to-year variation, we used nested ANOVA, where YEAR was a random factor nested within INVASION status (invaded or not). Preliminary examinations excluded SEX as a significant variable when controlling for YEAR effects, so the sex of fish was ignored in subsequent analyses. Assumptions of homogeneity of variance and normal distribution were met for $\delta^{15}\text{N}$, but not for $\delta^{13}\text{C}$. We thus performed a restricted permutation test on our $\delta^{13}\text{C}$ results by randomly selecting 5 years of data (keeping isotopic signatures within years intact), assigning them to the “post-invasion” group, then assigning all remaining years to the pre-invasion group. This process was repeated 10,000 times. Nested ANOVA was performed on the randomized data, and the F -ratio for the INVASION effect was saved. The randomization P -value for INVASION was the proportion of F -ratios from the randomization that exceeded the INVASION F -ratio from the original nested ANOVA for $\delta^{13}\text{C}$. To evaluate the significance of YEAR within INVASION effects, we randomized observations across years within INVASION status and then randomly assigned years across INVASION as described above. Estimation of the YEAR randomization P -value was based on the number of F -ratios for the YEAR effect greater than that observed in the original nested ANOVA. All analyses were performed using R (R Development Core Team 2006).

Lake whitefish diet items

Benthic invertebrates were collected in September 2005 using a standard Ekman dredge. Samples were passed through a 500- μm mesh to remove fine sediments, immediately placed on ice and subsequently frozen within 12–24 h of capture. Vertical hauls of zooplankton were collected monthly (May–September 2005) at night using a 250- μm plankton net (45 cm diameter, 3 m long, Foster 2007) hauled from 4 m off bottom to the surface. Each month, three to five hauls were taken from each of two offshore

stations (30–40 m depth). Samples from all stations were combined and placed on ice for 2–4 h until they could be transferred to a freezer for later separation and analysis.

In the laboratory, invertebrate and zooplankton samples were thawed and organisms separated into taxonomic groups (Table 1). Once separated, organisms were placed in a drying oven at 60°C for 24 h until constant weight was achieved. Samples were then powdered and weighed into tin cups for isotopic analysis.

Uncertainty in isotopic determinations

To provide estimates of sub-sampling and analytical uncertainty for our isotopic analyses, periodic duplicate samples for lake whitefish scales and invertebrate tissue (zooplankton and benthos) were analyzed. Mean absolute differences among duplicates were compared using paired *t* tests.

Depth of benthic invertebrates and lake whitefish

The effects of collection depth on benthic invertebrate isotopic signatures were examined using linear regression. Further, invertebrate isotopic signatures were averaged over each of three depth categories (Table 1) used previously to distinguish benthic invertebrate distributions in South Bay (McNickle et al. 2006).

We examined the depth distribution of lake whitefish over time by weighting the mean depth of capture by lake whitefish catch per unit effort (CPUE). Briefly, CPUE was estimated as the geometric mean of whitefish biomass captured in standardized mesh sizes, and expressed in $\text{kg km}^{-1} \text{day}^{-1}$. Depth of capture was reported from soundings recorded at the time of net recovery. We estimated standard errors around weighted means according to Cochran (1977), a method that provides similar estimates of variance around weighted means to those of more intensive bootstrapping estimation methods (Gatz and Smith 1995). Comparisons of weighted mean depth of whitefish capture and thermocline depth between invaded versus non-invaded years were performed with *t* tests assuming unequal variance using the Welch modification of degrees of freedom (Zar 1999).

Description of lake whitefish diets

Unpublished data describing lake whitefish diets collected between May and December 1947 were provided by the OMNR. Stomach contents of all fish collected within a particular time period were pooled and then separated into taxonomic groups. The volume (mm^3) of each taxonomic group was estimated by displacement in water. These data are reported here as a proportion of all identifiable items for each time period.

To evaluate seasonal variation in contemporary diets, lake whitefish were collected in October 2004, May 2005, July 2005 and September 2002–2005. Seventeen to 60 stomachs were collected from fish in each sampling period from across the size range encountered. Contents were sorted to the lowest identifiable taxonomic level, counted and weighed. To make these data comparable to 1947 estimates, we summed the weights of each prey taxa across all fish sampled within each time period and report these totals as the proportion of identifiable items by weight within each time period.

Estimation of energy available to lake whitefish

To determine changes in energetic quality of lake whitefish diets after dreissenid colonization, we estimated annual proportions of prey items in whitefish diets over all seasons, weighted by the number of full stomachs observed in order to de-emphasize months in which lake whitefish were found not to be feeding. We applied published energy densities of whitefish prey items (ESM S3) to these proportions to estimate energy densities for diets before and after dreissenid invasion.

Comparison of measured and estimated lake whitefish isotopic signatures

Lake whitefish isotopic signatures can be influenced by factors besides food web change, such as changes in ecosystem productivity (Gerdeaux and Perga 2006). We therefore sought to determine how well measured changes in lake whitefish isotopic signatures compared with estimates based on diet information. To do this, we estimated lake whitefish isotopic signatures based on contemporary isotopic signatures of benthic prey groups and the relative proportions they contributed to past and present diets. Estimates of whitefish diet isotopic signatures were calculated for each time period; an annual mean diet was estimated as the mean over all time periods and weighted by the proportion of whitefish captured with stomach contents to de-emphasize diets during fall (when fewer fish actively feed). Isotopic means for benthic prey in the above estimate were selected to reflect the depths available to lake whitefish in each time period (Table 1). Benthic prey isotopic signatures were averaged over all depths for time periods without stratification (October to June), whereas averages excluded shallower (<30 m) depths during the summer stratified period, based on depth-of-capture data. To evaluate the possibility that lake whitefish always feed in the deepest parts of the bay regardless of season, we also estimated lake whitefish signatures using prey isotopic signatures at greatest depth (>30 m) in all time periods. An additional pre-invasion estimate of lake whitefish isotopic

Table 1 Isotopic signatures of lake whitefish prey items at three depth zones in South Bay, Lake Huron

Taxonomic group of prey	$\delta^{13}\text{C} \text{ ‰}$			$\delta^{15}\text{N} \text{ ‰}$			Grand Mean	n	Varies with depth? (P)
	Depth zone			Depth zone					
	1 (0–10 m)	2 (11–30 m)	3 (>30 m)	1 (0–10 m)	2 (11–30 m)	3 (>30 m)			
Amphipoda	–18.7	–22.6	–27.8	–23.5	9	0.0034*	6.2	9	0.0002*
Ceratopogoniidae	–21.3			–21.3	3	n/a	4.7	3	n/a
Chironomidae	–21.3	–21.9	–27.5	–22.9	14	<0.0001*	6.4	14	<0.0001*
Decapoda ^a	–19.0			–19.0	1	n/a	5.9	1	n/a
<i>Dreissena</i> ^a	–25.7	–27.3		–26.2	6	0.0069*	3.1	6	0.16
Ephemeroptera	–23.3	–22.5	–23.8	–23.1	5	0.93	5.1	5	0.0235*
Gastropoda ^a	–15.6	–19.0		–17.6	5	0.0328*	4.2	5	0.95
Isopoda	–19.7	–21.9		–20.4	3	0.42	4.7	3	0.0355*
Megaloptera	–21.6	–21.2		–21.4	2	n/a	5.0	2	n/a
Oligochaeta	–22.8	–22.8	–27.9	–24.5	6	0.0059*	4.8	6	0.0822*
Sphaeriidae ^a	–21.3	–28.2	–26.1	–25.2	3	0.46	7.5	3	0.0006*
Stickleback	–22.3			–22.3	1	n/a	7.7	1	n/a
Trichoptera	–21.5			–21.5	3	n/a	8.8	3	n/a
Grand Mean (all benthic taxa)	–21.6	–22.5	–27.2	–22.8	61	<0.0001*	4.6	63	<0.0001*
<i>Bythotrephes</i> ^b				–26.59	5	n/a	5.7	5	n/a
<i>Mysis</i> ^b				–26.70	1	n/a	8.3	1	n/a
Hymenoptera (Formicidae) ^c				–27.50	2	n/a	1.9	2	n/a

* Significant linear regression at $P < 0.05$ (see Fig. 6)^a Soft tissues only, shells removed^b Based on seasonal averages, May–September^c Literature value (Sanders and Planter 2007)

signatures was determined from diets of six lake whitefish collected October–November from South Bay in 1980, reported in Ihssen et al. (1981). Isotopic fractionation was assumed to be 3.4‰ for $\delta^{15}\text{N}$ and 1‰ for $\delta^{13}\text{C}$ between lake whitefish and their prey (Vander Zanden and Rasmussen 2001; Post 2002). We applied an error of 1‰ to isotopic estimates based on diet composition, corresponding to uncertainty in estimates of fractionation between diet and consumers (Vander Zanden and Rasmussen 2001; Post 2002).

Lake whitefish isotopic estimates based on diets were compared with estimates derived from scales. Because our fractionation value of 4.6‰ between scales and tissues was higher than those reported elsewhere (Kelly et al. 2006; Perga and Gerdeaux 2003), we chose a value of 4‰ for $\delta^{13}\text{C}$, since this is similar to that of the closely related European whitefish (Perga and Gerdeaux 2003) and falls well within the standard error of our estimate. Scale and tissue $\delta^{15}\text{N}$ were considered to be equivalent.

Results

Scales revealed significant changes in lake whitefish isotopic signatures between pre-invasion (before 2001) and post-invasion (2001 and later) time periods (Fig. 4). Differences between invaded and non-invaded years for $\delta^{13}\text{C}$ were significant (Fig. 4a, permutation $P = 0.0005$). Nitrogen signatures ($\delta^{15}\text{N}$) were significantly depleted post-invasion (Fig. 4b, nested ANOVA: $F_{1,12} = 13.6$, $P = 0.003$). Carbon signatures ($\delta^{13}\text{C}$) were particularly consistent over almost 50 pre-invasion years, whereas $\delta^{15}\text{N}$ were more variable during the same period; differences among years within invasion were non-significant for $\delta^{13}\text{C}$ (randomization $P = 0.9994$), but year effects within invasion were significant for $\delta^{15}\text{N}$ (nested ANOVA: $F_{12,70} = 3.83$, $P = 0.0002$).

Scale tissue duplicates were statistically indistinguishable for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\delta^{13}\text{C}$, mean absolute difference 0.19‰, paired sample t test, $t_{14} = 0.49$, $P_{\text{two-tailed}} = 0.63$; $\delta^{15}\text{N}$, mean absolute difference 0.32‰, paired sample t test, $t_{14} = 0.27$, $P_{\text{two-tailed}} = 0.79$). The same was true of invertebrate tissues ($\delta^{13}\text{C}$, mean absolute difference 0.19‰, paired sample t test, $t_8 = -0.39$, $P_{\text{two-tailed}} = 0.71$; $\delta^{15}\text{N}$, mean absolute difference 0.33‰, paired sample t test, $t_8 = 0.79$, $P_{\text{two-tailed}} = 0.45$). We also compared differences between duplicates of the same scale with different scales from the same fish. Differences were similar between scale duplicate types for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\delta^{13}\text{C}$, two sample t test, $t_{12} = 0.60$, $P_{\text{two-tailed}} = 0.56$; $\delta^{15}\text{N}$, two sample t test, $t_{14} = -0.46$, $P_{\text{two-tailed}} = 0.66$).

The depth of lake whitefish capture (weighted by CPUE) in South Bay was shallower after the invasion of dreisse-

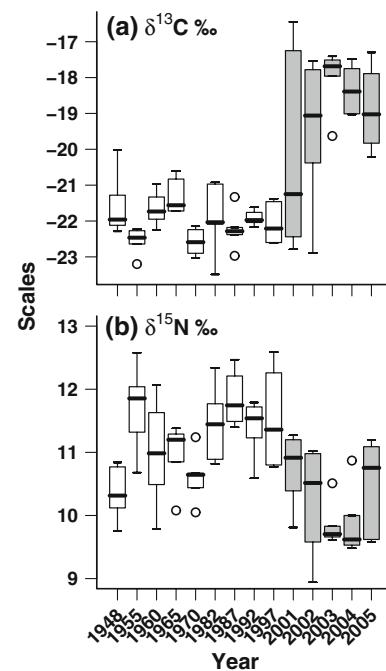


Fig. 4 Box and whisker plot of lake whitefish scale isotopic signatures of **a** $\delta^{13}\text{C}$ **b** $\delta^{15}\text{N}$ in South Bay, Lake Huron, collected from age 5 fish before dreissenid establishment (open boxes) and after establishment (2001–2005, shaded boxes)

nids (Fig. 5, t test, $t_{29,1} = 7.37$, $P_{\text{two-tailed}} < 0.0001$). Mean depth of capture was 8.7 m shallower post-invasion (24.5 m) than pre-invasion (33.2 m). Excluding set depths prior to 1965, when netting protocols were not standardized by depth as they were from 1965 onward, no significant difference was found in the depth of nets set (t test, $t_{5,3} = 2.39$, $P_{\text{two-tailed}} = 0.06$), suggesting changes in lake whitefish distribution are unlikely to be an artifact of sampling methodology. Mean thermocline depth was shallower post-invasion (14.9 m) than pre-invasion (19.1 m, t test, $t_{6,2} = 4.79$, $P_{\text{two-tailed}} = 0.003$; Fig. 5). To determine if changes in lake whitefish distribution were simply due to changes in thermocline depth, we subtracted the mean thermocline depth from the mean depth of capture. Post-invasion fish were found closer to the thermocline (mean depth 9.7 m below the thermocline) than in pre-invasion years (mean depth 14.1 m below the thermocline; t test, $t_{24,5} = 3.35$, $P_{\text{two-tailed}} = 0.003$).

Isotopic signatures were found to vary with depth for many benthic invertebrate taxa (Fig. 6; Table 1). Carbon signatures of invertebrates collected nearshore were more enriched in the heavy isotope for amphipods, chironomids, dreissenids, gastropods and oligochaetes (Fig. 6a, linear regression, all $P < 0.05$). In contrast, $\delta^{15}\text{N}$ for amphipods, chironomids, ephemeropterans, isopods, oligochaetes and sphaeriids was more enriched in the heavy isotope in profundal habitats (Fig. 6b, linear regression, all $P < 0.05$).

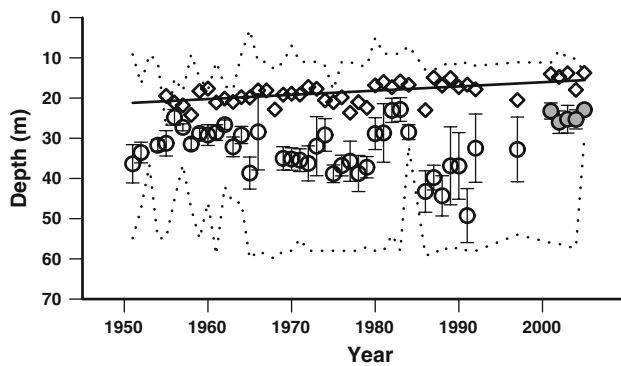
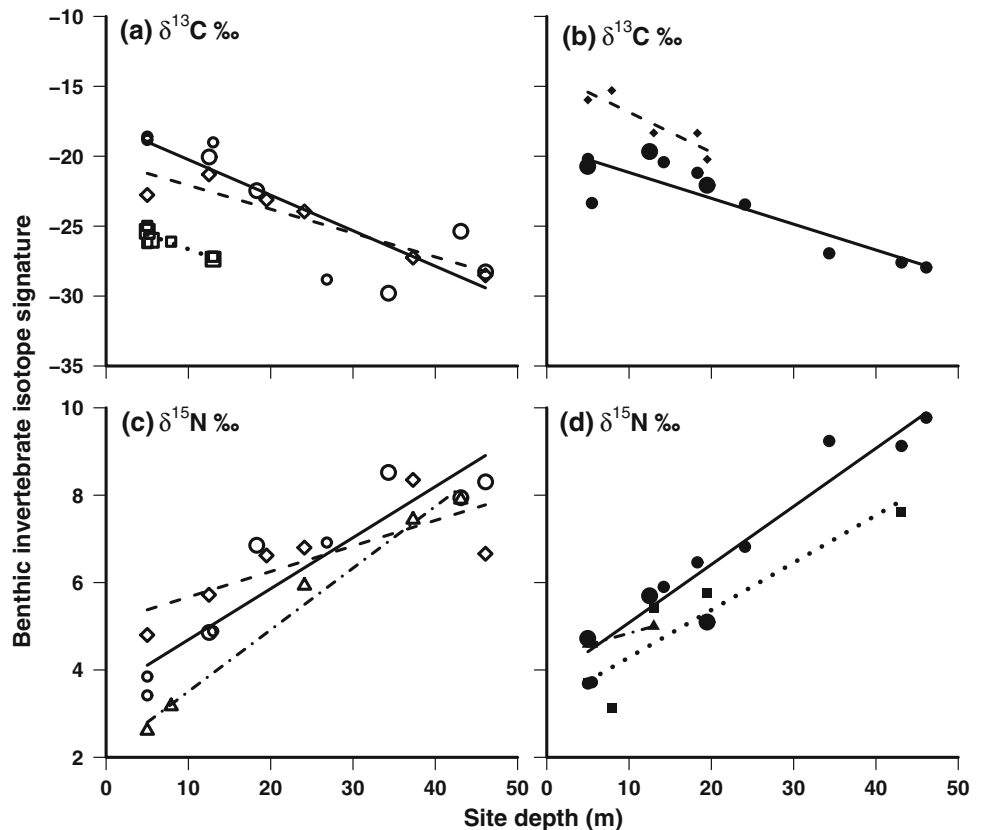


Fig. 5 Mean depth of capture of lake whitefish weighted by catch per unit effort (circles) in South Bay, Lake Huron before dreissenid invasion (open circles) and after dreissenid invasion (shaded circles). Error bars are weighted standard error estimates. Thermocline depth (diamonds) and trend in thermocline depth with time (solid line) are also shown. Dotted lines show minimum (top) and maximum (bottom) depth of net sets for each year of sampling. Note that the lake surface is 0 m depth

Diporeia fell on the same trajectory as other amphipods for both isotopes, so they were considered taxonomically equivalent (Fig. 6). Chironomids of the tribe Tanypodinae were grouped with other chironomids as they were found to lie on the same trajectory, as were *D. bugensis* and *D. polymorpha*, which were isotopically indistinguishable from one another (Fig. 6).

Fig. 6 Depth dependence of isotopic signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of benthic invertebrates collected from South Bay, Lake Huron, split among multiple panels for clarity. Note that only invertebrates with significant relationships with depth are shown ($P < 0.05$; Table 1). Symbols indicate (a, c) amphipoda (solid line, circles; larger circles are *Diporeia*); oligochaeta (dashed line, open diamonds); *Dreissena* (dotted line, open squares); *D. bugensis* are large squares, *D. polymorpha* are small; Sphaeriidae (dot-dashed line; open triangles) and (b, d); chironomidae (solid line, filled circles); tanypodinae are large circles; gastropoda (dashed line, filled diamonds); ephemeroptera (dotted line, filled squares); isopoda (dot-dashed line, filled triangles)



Lake whitefish diet data indicated a greater reliance on nearshore prey after the invasion of dreissenids than before (Fig. 7). Typically nearshore prey such as gastropods and dreissenids that contain a large proportion of indigestible material (shells) were a major component of post-invasion lake whitefish diets, whereas contributions of more typically profundal prey such as *Diporeia*, chironomids and sphaeriids were greatly reduced post-invasion. To further illustrate this point, we categorized all benthic organisms collected at depths >30 m to be profundal and all other benthic organisms (excluding fish) to be nearshore. Based on averages over all months (weighted by the number of fish with full stomachs, Fig. 7), profundal contributions to whitefish diets went from 71% in 1947 to only 30% in 2005, whereas littoral contributions increased from 23% in 1947 to 59% in 2005 (42% excluding non-native dreissenid mussels). Plankton contributed approximately 4% of 2005 diets, largely based on the presence of *Bythotrephes*, compared with less than 1% in 1947. Contributions of fish increased only slightly from 1.1% in 1947 to 2.6% in 2005. In both 1947 and in the post-invasion time period, the percentage of empty stomachs was lowest in spring and highest later in the season (Fig. 7). The estimated energy density of post-invasion lake whitefish diets was $2,517 \text{ J g}^{-1}$, 13% lower than pre-invasion diets ($2,897 \text{ J g}^{-1}$).

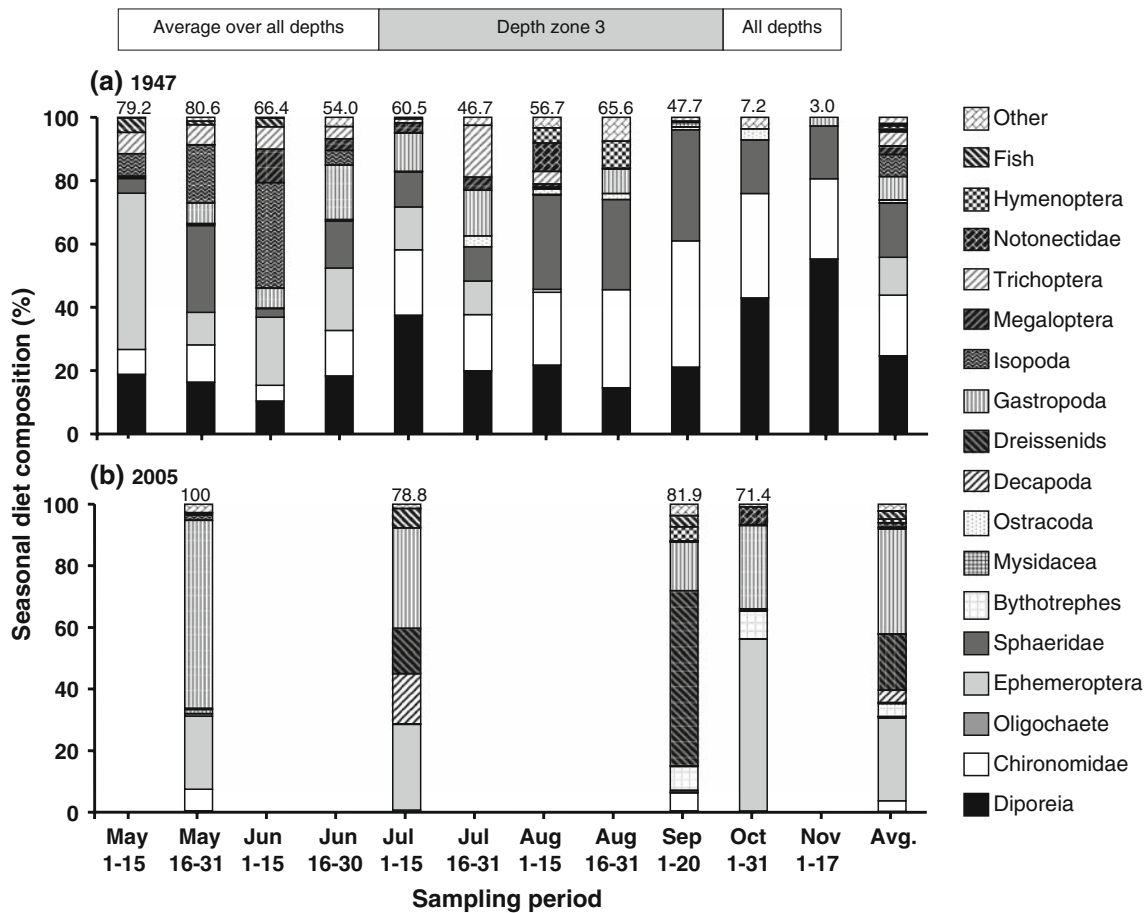


Fig. 7 Seasonal diet composition of lake whitefish in South Bay, Lake Huron, collected in **a** 1947 and **b** 2005. Predominantly profundal prey are *solid shades*; predominantly littoral prey are *patterned segments*; pelagic prey (primarily *Bythotrephes*) are *open segments with checkerboard pattern*. Numbers above *bars* are percentage of fish collected

with stomach contents. “Avg.” is the average diet composition over the entire year, weighted by the percentage of fish with stomach contents. *Bars* above panels show the depth used in estimating isotopic signatures in Fig. 8a, based on thermal stratification patterns. Depth zone 3 is >30 m depth, as per McNickle et al. (2006)

Whitefish isotopic signatures based on scales differed from those estimated from diet. However, the relative difference between isotopic signatures before and after dreissenid invasion was similar for both methods (Fig. 8a). Scale-based post-invasion whitefish signatures were enriched in $\delta^{13}\text{C}$ by 3‰ and depleted in $\delta^{15}\text{N}$ by 1‰ relative to pre-invasion estimates. Diet-based estimates of post-invasion whitefish signatures were enriched in $\delta^{13}\text{C}$ by 2.2‰ and depleted in $\delta^{15}\text{N}$ by 1.8‰ relative to pre-invasion estimates. Error bars between the pre- and post-invasion period did not overlap for either scale-based or diet-based whitefish isotopic signatures, suggesting differences beyond that which could be explained by uncertainty in fractionation estimates. Better correspondence between scale-based and diet-based whitefish signatures was found when we assumed isotopic signatures of diet items occupying the deepest section of the lake only (>30 m; Fig. 8b). Using this method, diet-based post-invasion whitefish isotopic signatures estimated from diets were enriched in $\delta^{13}\text{C}$

by 2.5‰ and depleted in $\delta^{15}\text{N}$ by 1.6‰ relative to pre-invasion estimates.

Discussion

Our study clearly demonstrates a greater dependence of lake whitefish on nearshore resources in South Bay after dreissenid colonization, whereas pre-invasion fish were more dependent on profundal resources. This conclusion is evident from three independent lines of evidence. First, the 3‰ enrichment in lake whitefish scale $\delta^{13}\text{C}$ isotopic signatures after dreissenid establishment, preceded by a relatively invariant signature for 49 years prior, reflects the more enriched $\delta^{13}\text{C}$ signatures of benthic organisms collected nearshore and a therefore a greater reliance of lake whitefish on nearshore resources. Second, the proportion of nearshore diet items in lake whitefish stomachs was higher in the post-invasion time period, and the isotopic shift

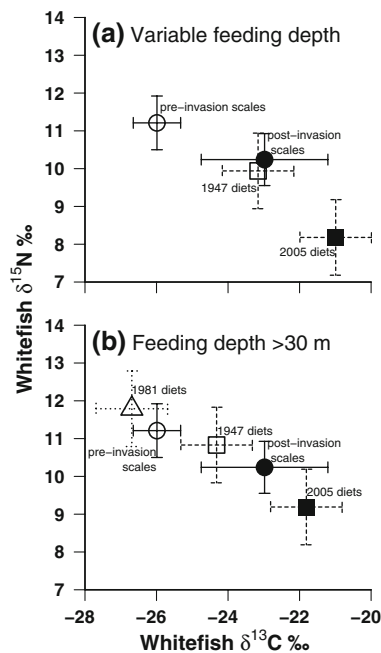


Fig. 8 Mean isotopic signatures of lake whitefish measured from scales (circles) and those estimated from diets (squares = 1947, 2005; triangles = 1981) before (open symbols) and after (shaded symbols) invasion of *Dreissena* to South Bay, Lake Huron. Error bars for scale measurements (solid) are ± 1 SD. Error bars for diets (dashed lines) represent previously reported uncertainty (variation) of 1‰ in fractionation estimates for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Panel **a** assumes lake whitefish feed nearshore in spring and fall, and isotopic values have been adjusted to reflect assumed shifts in depth (see Fig. 7). Panel **b**: lake whitefish isotopic signatures estimated from diets assuming prey items are consumed at depths >30 m year-round

between 1947 and 2002–2005 estimated from diets is comparable to that observed in lake whitefish scales. Third, lake whitefish were captured in shallower water after dreissenid establishment.

The observed shift of lake whitefish away from profundal and towards nearshore resources might be predicted from reduced offshore productivity, thought to be a result of the re-engineering of Great Lakes ecosystems by dreissenids as predicted by the nearshore phosphorous shunt model (Hecky et al. 2004). Because profundal productivity is so closely integrated with pelagic productivity, we believe our findings support a slight revision of this conceptual model to include more explicitly the reduction of the supply of energy from the pelagic to profundal zones of lakes after dreissenid colonization. The nearshore shunt model predicts both increased sequestration of pelagic material nearshore and a decreased rate of transport of nearshore nutrients offshore, both of which would act to reduce the vertical transport of nutrients from pelagic to profundal habitats. Though the nearshore shunt model also predicts an increased deposition of nearshore material into profundal habitats, this down-slope transport consists primarily of

large, inedible particles, which are less available to profundal organisms as a resource (Hecky et al. 2004). Continued declines in profundal benthic invertebrate abundance in the Great Lakes (McNickle et al. 2006; Nalepa et al. 2006, 2007) are not consistent with a scenario of nutrient subsidization, suggesting that any nearshore material being deposited in the profundal is subject to sedimentation and is not bioavailable.

It is likely that the isotopic changes in lake whitefish isotopic signatures we observed are somewhat conservative given changes in both $\delta^{13}\text{C}$ in air and $\delta^{15}\text{N}$ in dissolved inorganic nitrogen in the Great Lakes. Increasing emissions of fossil fuels due to anthropogenic activity have caused depletion of $\delta^{13}\text{C}$ in air (the Suess effect; Suess 1955) by approximately 1‰ since 1950 (Verburg 2007). Similarly, organic sediment $\delta^{15}\text{N}$ in the lower Great Lakes has become enriched by 1.5–2‰ during the same time period (Hodell and Schelske 1998). Both of these effects are opposite to the direction of changes observed in South Bay lake whitefish over time, and our ability to detect significant differences without accounting for either change indicates that our results are indeed robust.

It is unlikely that the observed enrichment in $\delta^{13}\text{C}$ is due to changes in nutrient levels in South Bay. Though positive relationships between $\delta^{13}\text{C}$ of European whitefish (*Coregonus lavaretus*) and mean annual total phosphorous (TP) concentrations have been observed in European lakes (Gerdeaux and Perga 2006), changes in nutrient status of the same magnitude in South Bay have not occurred. A 3‰ enrichment in carbon, according to the relationships reported by Gerdeaux and Perga (2006), would require an increase in mean TP concentrations between 50 and 70 $\mu\text{g}/\text{l}$. Phosphorous samples collected by the Ontario Ministry of the Environment in Robert's Bay (ESM 1) report spring phosphorous concentrations averaging 7.0 and 3.5 $\mu\text{g l}^{-1}$ in 1998 and 2006, respectively, where samples were collected between 8 and 15 m depth. Though phosphorous data are limited for South Bay pre-invasion, evidence from other sources suggests that changes in nutrient loading during this time period are unlikely. Spring surface phosphorous concentrations in the main basin of Lake Huron from 1983 to 2005 were relatively stable, ranging between approximately 3 and 6 $\mu\text{g l}^{-1}$ (Fernandez et al. in press). Thus, contemporary TP concentrations in South Bay would need to be a full order of magnitude above observed spring phosphorous levels to explain a 3‰ enrichment in $\delta^{13}\text{C}$. We believe a more parsimonious explanation for our results is an increased reliance on nearshore resources after the invasion of dreissenids, which is supported by both diet information and lake whitefish depth distributions.

It is however possible that climate change may play a role in the increased reliance of lake whitefish on nearshore resources. Summer thermocline depths have declined since

1950, which may provide lake whitefish with increased access to nearshore resources. Summer thermocline depths in South Bay and elsewhere vary negatively with increases in spring and summer air temperatures (King et al. 1997). Thus, shallower thermoclines may be a direct response to increasing mean annual air temperatures observed in the Great Lakes basin over the past 30–50 years (Jensen et al. 2007). Though post-invasion summer thermoclines are 4 m shallower on average, post-invasion whitefish are also captured on average 4 m closer to the thermocline compared with pre-invasion catches, suggesting that climate may contribute, but is not the only factor affecting changes in lake whitefish depth distributions and diets.

The increased reliance of lake whitefish on nearshore resources appears to result largely from the influence of zebra mussels (*D. polymorpha*) rather than the closely related quagga mussel (*D. bugensis*). *D. bugensis* can occupy deeper habitats and appears to out-compete *D. polymorpha* when resources are limiting (Hecky et al. 2004), and may therefore have a greater direct impact than *D. polymorpha* on profundal habitats once established. However, *D. bugensis* were only detected in South Bay in 2004 (M. Rennie, unpublished data) and were never detected during sampling 2 years prior (McNickle et al. 2006). Therefore, any dreissenid effect in our results stems primarily from the effects of *D. polymorpha*.

Lake whitefish diets post-invasion were 13% lower in energy content after the invasion of dreissenids compared with 1947 diets. McNickle et al. (2006) estimated that lake whitefish in South Bay foraging on post-invasion benthic communities faced a 16–43% reduction in energy based on previously reported diet data from this population (Ihssen et al. 1981) and various scenarios of post-invasion feeding habits. Using Ihssen's diet composition data, we estimated post-invasion diets contained 29% less energy than before invasion. We argue that our 1947 diet data are likely more representative than those of Ihssen et al. (1981), as their estimates are based on data from only six fish collected in July and August. In contrast, the data reported here from 1947 are based on collections of 1,625 fish examined from May to November. Regardless, our estimates of reduced diet energy densities are comparable to those estimated by McNickle et al. (2006) based on changes in the benthic community alone.

Contemporary lake whitefish populations may also face additional energetic costs of handling a greater proportion of shelled prey, which represents an increase in the consumption of indigestible material (shells) as well as potential additional handling costs. Evidence suggests that shelled prey are ingested whole by lake whitefish and then crushed by the stomach musculature (Owens and Dittman 2003). This increased processing requirement may negatively affect the net assimilation efficiency of

contemporary lake whitefish compared with historic populations.

Our study reveals a shallower depth distribution of lake whitefish in South Bay, while observations in the main basins of the Great Lakes suggest the opposite trend. Lake whitefish in Lake Ontario moved to deeper waters after the collapse of *Diporeia* populations in areas where whitefish were historically abundant (Owens and Dittman 2003). Additionally, increased offshore effort of commercial fishing vessels since the appearance of dreissenids has been observed in the main basin of Lake Huron, suggesting a deeper depth distribution of lake whitefish there (Mohr and Ebener 2005). In South Bay, our evidence from lake whitefish diets suggests that shallower depth distributions are associated with changes in foraging habits, where currently profundal organisms are poorly represented compared with nearshore organisms in the diet, despite the presence of a small remnant *Diporeia* population (McNickle et al. 2006). In the main basins of the Great Lakes, where dreissenids are established, *Diporeia* are currently limited to deep refugia (~200 m). It is possible that lake whitefish elsewhere in the Great Lakes will move inshore as *Diporeia* densities in deepwater refugia become depleted. Given that lake whitefish are a coldwater species with a thermal preferendum between 13.5 and 16.8°C (Jobling 1981; Edsall 1999), it is also possible that foraging at shallower depths (nearer or within epilimnetic waters) may be associated with suboptimal temperatures there, imposing further energetic costs in terms of both elevated standard metabolic rates and reduced feeding beyond what might be predicted based on changes in diet alone.

The difference in lake whitefish isotopic signatures before and after invasion based on either diets or from scales was strikingly similar and in the same direction. That signatures based on either diets or scales did not overlap to a greater degree is perhaps not surprising given some of the assumptions made in estimating diet-based isotopic signatures. First, our seasonal diet information is based on a single year before and after invasion, whereas mean annual isotopic signatures from lake whitefish scales are integrating 3–4 years of feeding history for each fish analyzed over the entire half-century that fish were collected. Second, we assumed that isotopic signatures of invertebrates in 1947 were similar to those in 2005. Additionally, there may be seasonal effects on benthic invertebrate isotopic signatures that are not accounted for in our study. Then again, the lack of fit between diet-based isotopic signatures and those observed may provide ecological insights. For instance, the improved alignment between scale-based and diet-based lake whitefish isotopic signatures, when assuming that lake whitefish feed in the deepest waters (>30 m) throughout the year, suggests that depth of capture might actually underestimate the depth at which whitefish feed. Further, the closer

alignment of estimates reported by Ihssen et al. (1981) with our observed pre-invasion lake whitefish isotopic signatures suggest that perhaps *Diporeia* were a larger component of pre-invasion diets than indicated by our 1947 data. Regardless, the striking similarity in direction and magnitude of differences in diet- and scale-based isotopic signatures before and after dreissenid establishment provides strong evidence that the increased reliance on nearshore resources observed in diets is the most probable cause for the isotopic changes observed in lake whitefish.

The isotopic signatures of many (though not all) of the benthic organisms examined in South Bay were shown to vary with depth. Whereas *Diporeia* on Lake Superior demonstrated the greatest change in isotopic signatures between 40 and 300 m (Sierszen et al. 2006), various South Bay benthos showed changes of similar magnitude and direction but over much shallower (5–50 m) depth ranges. In agreement with our findings, Vander Zanden and Rasmussen (1999) also demonstrated that both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ varied between habitat types across a range of lakes, decreasing in $\delta^{13}\text{C}$ and increasing in $\delta^{15}\text{N}$ from littoral to profundal habitats. Further, it is unlikely that this pattern is an artifact of depth-specific changes in species composition within the taxa we analyzed. For instance, chironomids of the tribe Tanypodinae were found to lie on the same trajectory as other chironomids (Fig. 6), indicating that their typically more predaceous lifestyles were less important than depth in affecting their isotopic signatures. This suggests the depth at which benthic organisms are collected could greatly affect the conclusions drawn by food web studies, particularly if they are being used as baseline organisms for estimating of food chain length (Vander Zanden and Rasmussen 1999; Post 2002). As in our study, we recommend that depth distribution data for consumers be used to best determine at which depths fish are likely to be feeding during particular times of the year. Though depletion of benthic invertebrate $\delta^{13}\text{C}$ with depth in South Bay is consistent with these other studies where dreissenids are absent (Sierszen et al. 2006; Vander Zanden and Rasmussen 1999), it is possible that the enriched $\delta^{13}\text{C}$ in South Bay nearshore invertebrates and post-invasion lake whitefish may be further exaggerated due to increased benthic algal productivity under increased light penetration (Fernandez et al., in press, possibly associated with dreissenid establishment).

Our relationship between scale and tissue isotopic signatures is consistent with those reported elsewhere for lake whitefish (Lumb 2005), for the closely related European whitefish, *Coregonus lavaretus* (Perga and Gerdeaux 2003), and other species comparing bony tissues with those of muscle (Kelly et al. 2006). In contrast to data presented by others investigating European populations of fish (Syvaranta et al. 2008; Perga and Gerdeaux 2003), we found no significant effect of acid treatment on scale $\delta^{13}\text{C}$ signatures.

Acidification of scales has been shown to have little effect in other North American fish species as well (Sinnatambay et al. 2007), and a recent study on roach (*Rutilus rutilus*) showed an enrichment of only 0.14% with regards to $\delta^{13}\text{C}$ after acidification (Syvaranta et al. 2008). This discrepancy among multiple studies may suggest geographic differences in the carbonate content of scales between fish species and/or populations. However, three of four studies (those above and ours) now show either negligible or only slight effects of acidification on scale isotopic signatures. Until the issue is better resolved, investigators should determine the necessity of scale acidification before undertaking temporal or comparative studies that use scales as a primary source of isotopic information.

To conclude, our study is among the first to provide empirically based evidence for proximate explanations of declines in lake whitefish growth and condition following dreissenid colonization. A reduction in the energetic value of diets, increased costs of handling shelled prey and potential costs of foraging in shallower, warmer waters will all contribute to reductions in growth and condition of lake whitefish where dreissenids are established. However, the possible contribution of warmer regional temperatures to shallower lake whitefish depth distributions suggests further research is required to better tease apart the effects described here from other coincidental changes, such as climate change and variation in population density.

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