Article

Increased dependence on nearshore benthic resources in the Lake Simcoe ecosystem after dreissenid invasion

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Abstract

Changes in the lower trophic level of Lake Simcoe, Canada, coincident with the invasion of dreissenids have been well documented, but little is known regarding the effects of these changes on the pathways of energy flow to higher trophic levels. To evaluate pathways of energy flow, we analyzed stable isotopes of zooplankton, benthic invertebrates, and fish over a 26-year period. Using stable isotopes of carbon (C) and nitrogen (N), we found evidence for a dramatic increase in the importance of benthic-derived nearshore primary production in Lake Simcoe after the invasion of dreissenids; $\delta^{13}C$ of benthos collected at 5 and 10 m depth increased by 4–5‰ on average, and benthic warmwater fishes demonstrated a similar increase. In contrast, $\delta^{13}C$ of profundal (≥ 20 m) benthos and pelagic zooplankton were not significantly different during this time period, while offshore pelagic and profundal fishes changed more subtly in magnitude but in the same direction as nearshore benthos and warmwater fishes. The range of $\delta^{13}C$ values observed across the fish community increased from 3 to 10‰, primarily due to a positive temporal shift among warmwater fishes. Our study highlights the increase in functional heterogeneity in Lake Simcoe after dreissenid invasion, likely due to an increase in nearshore benthic production. Accounting for increased contributions of benthic-derived C with time is critical in accurately modelling C and energy transfer in the lake, and for better understanding the degree of nearshore–offshore coupling in the lake.

Key words: diversity, *Dreissena polymorpha*, energy flow, nearshore shunt, stability, stable isotopes, trophodynamics

Introduction

The resilience and stability of ecosystems following disturbance events are related to their degree of structural and functional diversity. A recent summary of the empirical and theoretical work on the stability of food webs shows that ecosystem stability results from a diversity of interaction strengths among slow and fast energy channels (Rooney and McCann 2012). In aquatic environments, benthic energy channels are often characterized by higher diversity, weaker interaction strengths, and slower rates of energy transfer relative to pelagic channels (Rooney et al. 2006, Rooney and McCann 2012). Thus, systems dominated primarily by fast channels (e.g., lakes dominated by phytoplankton-derived pelagic production) are characterized by strong interactions among trophic levels and may be less stable or resilient to large-scale disturbance than systems with both fast (pelagic) and prominent slow (benthic) channels.

Types of disturbance that diversify energy flow through ecosystems may therefore increase ecosystem resilience and stability. The dreissenid mussels (*Dreissena*

polymorpha and *D. rostriformis bugensis*), which are non-indigenous to North American ecosystems, seem to fit this category. Described as "ecosystem engineers," dreissenids are hypothesized to direct energy and production away from offshore pelagic energy channels and toward nearshore benthic energy channels. This process has been termed "benthification" (Mills et al. 2003) and conceptually formalized as the "nearshore phosphorus shunt" (Hecky et al. 2004). Dreissenid invasions have also been accompanied by an increase in benthic invertebrate diversity (Ricciardi et al. 1997, Ward and Ricciardi 2007, Ozersky et al. 2011) and a decrease in the abundance of nondreissenid profundal benthos (e.g., Lozano et al. 2001, McNickle et al. 2006, Rennie and Evans 2012). Previous work revealed that lake whitefish (*Coregonus clupeaformis*) in South Bay, Lake Huron shifted toward more nearshore resources following dreissenid invasion (Rennie et al. 2009). The authors concluded that this change was likely due to a decline in profundal offshore production; however, the effects of dreissenid establishment on the resource use of other ecosystem components (e.g., benthos, zooplankton, and the overall fish community) are not currently well known.

The establishment of zebra mussels, *D. polymorpha*, in the mid-1990s in Lake Simcoe, Ontario, Canada (Evans et al. 2011) has contributed to major ecological changes. While total benthic invertebrate abundance declined overall (Jimenez et al. 2011), total benthic invertebrate biomass increased by 17-fold at shallow sites (5–15 m depth), which could be almost entirely attributed to dreissenid biomass (Rennie and Evans 2012). A recent compilation of data from multiple surveys conducted between 2005 and 2010 found that the highest densities and biomass of dreissenid mussels occurred within the 5–15 m isopleths (North et al. 2013). Using the compiled estimates, North et al. (2013) calculated that the biomass of dreissenids in Lake Simcoe had the capacity to filter the entire volume of the lake some 47 times during its 11.9 yr residence time; therefore, these organisms have had a strong influence on the ecology of the lake.

A number of changes in water chemistry seem to have accelerated coincident with the establishment of dreissenids in the mid-1990s; water clarity increased (Eimers et al. 2005, Young et al. 2010), algal biovolume declined at some lake stations (Winter et al. 2011), and significant changes in phytoplankton community composition were observed (Winter et al. 2011). Daily filtration rates by dreissenid mussels for Lake Simcoe (25% of the total lake volume per day; North et al. 2013) are within the range of those reported for the Great Lakes, where the nearshore shunt hypothesis was initially developed. The invasion of dreissenid mussels in Lake Simcoe and subsequent ecosystem-scale changes therefore provide an opportunity to evaluate the nearshore shunt hypothesis outside of the Great Lakes.

Our objective was to determine whether changes at lower trophic levels that coincided with the establishment of dreissenids (i.e., improved water clarity, reduced algal biovolume, change in phytoplankton community structure) were reflected in the pathways of energy flow to fish species in the nearshore and offshore communities. We evaluated stable isotopic values of carbon (C) and nitrogen (N) from archived and contemporary biological samples of benthic invertebrates, zooplankton, and fish. Isotopic signatures of fish species representing warmwater (i.e., nearshore, shallow, benthic/epilimnetic), midwater (i.e., metalimnetic) and coldwater (i.e., offshore, pelagic, profundal) habitats were compared for temporal changes, as were changes in the prey for these fishes (i.e., shallow, midwater, and profundal benthos, and pelagic zooplankton).

Study site

Lake Simcoe, located approximately 80 km north of Lake Ontario and the city of Toronto, Canada, is the largest lake in southern Ontario outside of the Laurentian Great Lakes, with a surface area of 722 km². The lake is relatively shallow; mean depth is 14–15 m and maximum depth is 42 m (Rawson 1930, Winter et al. 2007). In 1982, the numerically dominant fish species in the lake (as indicated by winter fishery census) were yellow perch (*Perca flavescens*) and rainbow smelt (*Osmerus mordax*); dominant species by biomass were yellow perch and lake whitefish (Evans and Waring 1987). Lake trout (*Salvelinus namaycush*) and lake whitefish populations were in decline, with intensive stocking programs initiated for each species during the 1960s and 1980s, respectively. The offshore winter fishery is now dominated numerically by yellow perch (Lake Simcoe Fisheries Assessment Unit, Ontario Ministry of Natural Resources, unpublished data). Lake trout and lake whitefish continue to be stocked, although some natural recruitment for both species has been observed during the last decade (J.K.L. La Rose, Ontario Ministry of Natural Resources, pers. comm.).

Methods

Sampling

Zooplankton were sampled between 1986 and 2009 by the Ontario Ministry of Environment at approximately biweekly intervals during the open water period and preserved in 5% buffered formalin. Additional details on sampling methods can be found in Kelly et al. (2013).

Zooplankton used for isotopic analyses in this study were taken from samples collected at station K45 (for location see Fig. 1 in North et al. 2013), a midlake sampling site. We picked large cladoceran herbivores (Daphniidae) for isotopic analysis to provide a baseline for pelagic primary production (Marty and Planas 2008). Years were chosen to distribute observations as evenly as possible across the pre- (1986–1993) and post-dreissenid (1996–2009) invasion time periods, according to sample availability. Based on these criteria, pre-invasion years were represented by 1986, 1990, and 1991, and post-invasion years by 1997, 1999, 2005, and 2008. Sample dates within each year were selected to capture at least one observation per month, but inclusion of particular sample dates within each year ultimately depended on the availability of daphnids in samples. Daphnids from 51 sampling events were analyzed over all years, with an average of 7 sampling events for each year.

Benthic invertebrates ("benthos") were sampled less frequently than zooplankton, with surveys conducted in 1982, 1983, 1986, 1993, 2008, and 2009. Benthic samples were collected from 6 discrete depths (5, 10, 15, 20, 25, and 30 m) along a transect extending from Sibbald Point to station K45 (see Fig. 1 in Rennie and Evans 2012 for sampling locations). Depths were classified into 3 distinct strata, based on the portion of the water column they typically occupied. Sites at 5 and 10 m depths, typically exposed to epilimnetic waters, were assigned to stratum 1; 15 m sites, representative of the metalimnion, were assigned to stratum 2; and 20, 25, and 30 m sites, exposed to hypolimnetic waters, were assigned to stratum 3. All benthos collected were sieved on 500 μm mesh screens and preserved in 10% buffered formalin. Additional details can be found in Rennie and Evans (2012).

Eight common benthic taxa were selected for isotopic analysis; Chironomidae, Oligochaeta, Amphipoda, Ephemeroptera, Pelecypoda (nondreissenid taxa, including Sphaeriidae and Psididae), Gastropoda, Isopoda, and *Dreissena*. In total, 275 benthic samples separated by taxa were analyzed. Chironomids were best represented over all years ($n = 91$), followed by oligochaetes ($n = 56$), whereas isopods ($n = 12$) and dreissenids ($n = 12$) were represented by the fewest observations. All other taxa had sample sizes >20 (Supplementary material, Table S1). Stratum 1 samples were best represented ($n = 142$), followed by stratum 3 ($n = 96$) and stratum 2 ($n = 37$).

Fish were sampled in 1982, 1983, and 2009 using identical multimesh gillnets along the same transect, targeting the same sites and discrete depth classifications as benthic samples. During a 2-week period between August and September, 3 nets were set for a 3 h period at each of 3 stations daily until each depth was sampled 3–4 times. Gillnets consisted of 11 panels, each 15.2 m in length and 2.4 m in height, strung together into a 137.2 m net. Panels were arranged randomly and consisted of 12, 19, 25, 38, 51, 64, 76, 89, 102, 114, and 127 mm stretched mesh. Fish were sampled at the time of collection; weight, length, sex, and maturity were determined, and ageing structures collected. Fish collected in both time periods were assigned to one of 3 preferred stratum; coldwater, deep offshore habitats (stratum 3); warmwater, shallow nearshore habitats (stratum 1) and midwater intermediate metalimnetic habitats (stratum 2; Table 1). Five fish of each species were selected from each time period for stable isotope determinations from within their preferred strata.

To the greatest extent possible based on the samples available, we reduced the influence of body size on fish isotopic values by matching scale samples from fish of similar sizes (total length) in both time periods (Table 1). Stable isotopes were determined from scales for all fish species (listed in Table 1) except sculpin, for which fins were analyzed. Relationships between fish scales and muscle tissues are typically strong (e.g., Kelly et al. 2006,
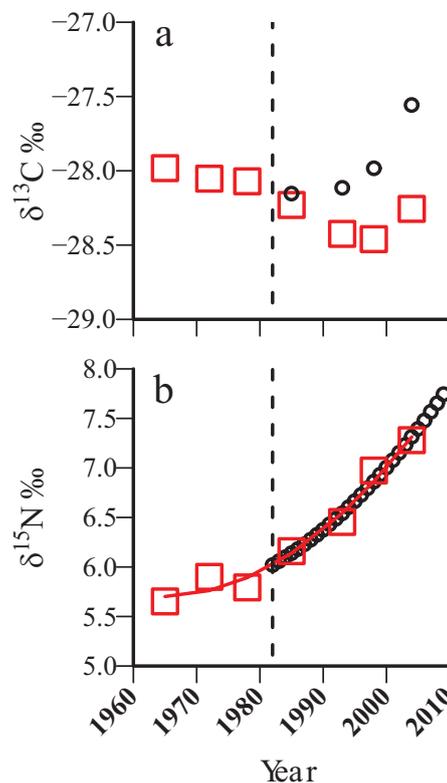

Fig. 1. Sediment isotope values for the main basin of Lake Simcoe, Canada, from Hiriart-Baer et al. (2011). Panel a: sediment organic carbon (C) isotope values (squares), and Suess correction applied to isotopic values, corrected to 1982 atmospheric δ^{13}C (circles). Panel b: sediment nitrogen (N) isotope values (squares) and the quadratic function best fit to describe the pattern in N isotopes in the lake from ca. 1964 to 2004 (line). Circles are the predicted values for each year between 1982 and 2009, used to correct δ^{15}N isotope values of organisms collected 1982–2009 to 1982 values.

Table 1. Mean and 1 standard error (SE) of total length of fishes analyzed for stable isotopes from Lake Simcoe, Canada. Means and SEs are based on a sample size of 5 fish for each species. *n/p* = not present in the lake at that time period; *n/c* = not collected or observed during the survey. Species abbreviations also apply to Table 4 and Fig. 7.

Habitat*	Species common name	Latin name	Abbreviation	1982-83 Mean (mm)	SE	2009 Mean (mm)	SE
Warmwater, shallow	Pumpkinseed	*Lepomis gibbosus*	PS	172	9	172	8
(Stratum 1)	Smallmouth bass	*Micropterus dolomieu*	SB	360	6	362	6
	White sucker	*Catostomus commersonii*	WS	401	3	402	2
	Yellow perch	*Perca flavescens*	YP	180	1	181	1
	Emerald shiner	*Notropis atherinoides*	ES	91	3	*n/c*	
	Spottail shiner	*Notropis hudsonius*	SS	75	8	*n/c*	
	Round goby	*Neogobius melanostomus*	RG	*n/p*		80	0.2
Midwater	Logperch	*Percina caprodes*	LP	92	0.2	*n/c*	
(Stratum 2)	Trout perch	*Percopsis omiscomaycus*	TP	84	1	*n/c*	
Coldwater, deep	Lake herring	*Coregonus artedi*	LH	284	1	284	1
(Stratum 3)	Lake trout	*Salvelinus namaycush*	LT	409	74	639	20
	Lake whitefish	*Coregonus clupeaformis*	LW	454	3	452	2
	Rainbow smelt	*Osmerus mordax*	RS	121	0.1	121	0.1
	Slimy sculpin	*Cottus cognatus*	Sc	*n/c*		78	8
	Spoonhead sculpin	*Cottus ricei*	Sp	*n/c*		74	4

*Stratum designations: 1 = 5 and 10 m; 2 = 15 m; 3 = 20, 25, and 30 m.

Rennie et al. 2009) and have been used elsewhere to reveal ecosystem-level change (Gerdeaux and Perga 2006, Rennie et al. 2009). For species that undergo ontogenic shifts (e.g., from a planktivorous to benthivorous or piscivorous stage), we removed the centres of scales with hypodermic needles or biopsy punches (depending on species and scale morphology) and analyzed only the outer portion to represent adult growth. This procedure was applied to scales of lake whitefish, yellow perch, smallmouth bass, and lake trout. Lake trout were not captured during the 2009 survey and were instead taken from an assessment survey conducted the previous year. The assessment survey targeted similar depths (>20 m), but different geographical sites in the main basin than our survey.

Stable isotope determination

All tissue samples analyzed (except scales) were dried for 24 h at 60 °C to a constant weight, ground to a fine powder using mortar and pestle, and weighed into tin cups. Scales were cut to capture the period of interest (i.e., adult feeding stage) and provide the weight necessary for analyses. Samples were analyzed at the Environmental Isotope Laboratory at the University of Waterloo, Ontario,

Canada, on a Delta continuous flow stable isotope mass spectrometer (Micromass) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108). The isotope laboratory reported analytical error of C and N determinations at 0.2‰ and 0.3‰, respectively. We determined more precise analytical error independently based on duplicate submissions from our own samples (mean difference, $\delta^{13}C = 0.03‰$, $\delta^{15}N = 0.16‰$). Differences among duplicate samples were insignificant based on paired t-tests (12 observations, $P \gg 0.05$ for both C and N). International standards for both isotopes were used to provide quality assurance and control on samples.

To account for preservation effects on isotopic signatures of formalin-preserved benthos, we used a generic correction factor of 2‰ for $\delta^{13}C$ and no correction for $\delta^{15}N$ (Rennie et al. 2012). This correction was applied to all preserved benthic organisms analyzed from samples collected between 1982 and 2008. Samples collected in 2009 were processed fresh (i.e., sorted, dried, and immediately prepared for isotopic analyses). Isotopic preservation effects on freshwater zooplankton stored for more than 1–2 years are minor and fall within the range of reported laboratory measurement error (Rennie et al. 2012); thus, preservation corrections were not applied to zooplankton. Although benthic invertebrate samples from

all 3 strata were analyzed, those from stratum 2 were excluded from statistical analysis due to high variability. The data were presented in plots for comparison.

Isotopic signatures of fish scales and fins are typically enriched by ~4‰ compared with muscle tissues (Kelly et al. 2006, Rennie et al. 2009). Because we were interested primarily in relative changes in stable isotopic signatures within fish species between time periods, we did not adjust fish isotopic signatures from scales/fins to reflect tissues because relative differences between time periods would be the same regardless of whether or not such correction factors were applied.

Isotopic values of C and N in aquatic ecosystems require corrections when investigated over long time series (Schmidt et al. 2009). Isotopic values of both atmospheric C (as CO_2, commonly referred to as the Suess effect; Verburg 2007) and N (Holtgrieve et al. 2011) have changed over time due to anthropogenic impacts. $\delta^{15}N$ in aquatic sediments and biota is also known to be highly sensitive to changes in anthropogenic activity in the surrounding watershed, specifically to sewage and the application of agricultural fertilizer (Hodell and Schelske 1998). Over the current period of investigation (1982–2009), atmospheric CO_2 is predicted to have depleted by 0.91‰ (using the equation of Verburg 2007). To isolate isotopic changes in organisms due to changes in energy source not confounded by changes in atmospheric C, and to demonstrate the effect of our correction on previously reported sediment C isotopic values for Lake Simcoe during the study period (Hiriart-Baer et al. 2011), we applied a Suess correction (Verburg 2007) by standardizing $\delta^{13}C$ values of all material analyzed to 1982 levels. We similarly used down core trends in $\delta^{15}N$ from dated sediments (Hiriart-Baer et al. 2011) to isolate isotopic changes in organisms due to changes in trophic position not confounded by anthropogenic changes. Lake Simcoe sediment $\delta^{15}N$ trends from 1964 to 2004 corresponded best with a second-order polynomial (sediment $\delta^{15}N = 3.957 - 4.023\times Year + 1.024\times Year^2$; $F_{2,4} = 84.31$, $R^2 = 0.98$, $P = 0.0005$). This function was used to estimate annual sediment $\delta^{15}N$ from 1982 to 2009; we estimated our annual $\delta^{15}N$ correction factor as the difference between $\delta^{15}N$ for any year and $\delta^{15}N$ in 1982. These annual correction factors were then subtracted from the $\delta^{15}N$ of all organisms, corresponding to the year in which they were collected.

Statistical analysis

Zooplankton have rapid turnover rates relative to benthic invertebrates or fishes and as such can have a strong seasonal component in stable isotope values (Matthews and Mazumder 2005). We therefore attempted to evaluate the influence of season on zooplankton stable isotopic values to better interpret interannual differences. Seasonal patterns were evaluated with nonlinear ANCOVA, using second- and third-order polynomial functions (Huitema 2011). These analyses revealed significant Year×Season interaction terms ($P < 0.05$), indicating that seasonal patterns were statistically different among years and could not be effectively described by a single general pattern in all years; therefore, the biweekly zooplankton isotopic values were averaged annually, and the annual open water means were used to test for differences before and after dreissenid establishment. Seasonal values were presented graphically to provide context for variation in annual means. Differences in zooplankton stable isotope values before and after dreissenid establishment were evaluated using a nested ANOVA, where the observations in each year were nested within dreissenid "Invasion" status.

Temporal changes in benthic invertebrate taxa for both $\delta^{13}C$ and $\delta^{15}N$ were evaluated using linear mixed effects models. In our models, Year was a random factor and nested within Invasion status (before/after dreissenid establishment, fixed effect). The general (full) model was:

$$Isotope(‰) = Stratum + Invasion + Stratum \times Invasion + (Invasion/Year) + Stratum \times (Invasion/Year) + \varepsilon. \quad (1)$$

We tested the significance of the Stratum×Invasion interaction term by comparing the full model with one where the effects of Stratum and Invasion were additive (i.e., one with the multiplicative effect of Stratum×Invasion removed).

To evaluate the consistency of effects due to dreissenid establishment (Invasion effect), versus annual variation, we compared the full model to one without an Invasion term:

$$Isotope(‰) = Stratum + Year + Stratum \times Year + \varepsilon. \quad (2)$$

In the event that the interaction term was not significant, additive models were evaluated for effects of Stratum. Strata effects were evaluated comparing the full or additive model to one where Stratum was not considered:

$$Isotope(‰) = Invasion + (Invasion/Year) + \varepsilon. \quad (3)$$

Or, in the case where Invasion effects were nonsignificant, the comparison was made with either the full or additive model to one with only random Year effects.

In cases where data from only a single stratum were available, we evaluated the significance of dreissenid

invasion by comparing model (3) above to one with only random Year effects:

$$\text{Isotope(‰)} = \text{Year} + \varepsilon. \qquad (4)$$

We used log-likelihood to conduct all model comparisons and determine P-values for factors of interest. Model fits were evaluated by examining residual plots, and all showed distribution around zero with no patterns in the residuals (sample sizes for each taxa by year and stratum in Supplementary Table S1).

Temporal changes in both benthos and zooplankton between time periods were summarized as means (by Invasion and, in the case of benthos, additionally by Stratum) and compared to changes in the fish community.

Trophic changes in the fish community were evaluated several ways. First, centroids of biplots were used to compare changes in fish community structure from 1982–1983 to 2009. Second, we evaluated directional change in $\delta^{13}C$ and $\delta^{15}N$ for both inshore and pelagic species common to both time periods; changes were evaluated using Welch 2-sample t-tests. Critical P-values were adjusted using a Benjamini-Hochberg procedure to control for false discovery rate (Benjamini and Hochberg 1995, Waite and Campbell 2006). All statistical procedures and graphics were produced using R (R Development Core Team 2010).

Results

Temporal isotopic corrections

Suess corrections revealed 0.70–0.91‰ enrichment in sediment organic ^{13}C isotopic values for material collected or dated between 2004–2009 relative to samples collected in 1982 (Fig. 1a); recently deposited organic C in sediments was slightly more enriched in the heavier isotope compared with organic C deposited in 1982, accounting for background changes in atmospheric C. The relationship we derived to describe sediment $\delta^{15}N$ with time (1964–2004) fit the data well, and we extrapolated this relationship to estimate sediment $\delta^{15}N$ to 2009 (Fig. 1b). Based on this relationship, N isotopes in sediments were estimated to have increased by 1.72‰ from 1982 to 2009.

Change in invertebrate isotopes

Zooplankton $\delta^{13}C$ (Suess-corrected) and $\delta^{15}N$ (sediment-corrected) varied seasonally in all years. While not significant statistically, plots of zooplankton $\delta^{13}C$ with season generally seemed to follow a convex pattern, peaking midsummer (Jul-Aug), while $\delta^{15}N$ seemed to

follow a convex pattern with a midsummer minimum, followed by a peak and decline late in the season, possibly coincident with lake turnover (Fig. 2). Nested ANOVA revealed significant interannual variation in zooplankton $\delta^{13}C$ and $\delta^{15}N$ that was unrelated to the establishment of dreissenids (Fig. 3; Table 2).

Benthic invertebrate Suess-corrected $\delta^{13}C$ differed significantly in years before and after dreissenid invasion for all taxa investigated in at least one depth stratum (Fig. 4; Table 3). For benthic taxa distributed among both strata 1 and 3 (chironomids and oligochaetes), dreissenid invasion interacted significantly with depth strata (Fig. 4). For taxa that occurred pre- and post-dreissenid establishment, mean (±1 standard error) benthic invertebrate $\delta^{13}C$ values in depth stratum 1 increased by 5.1 ± 1.2‰ after dreissenid invasion (Fig. 4). In contrast, $\delta^{13}C$ values for chironomids and oligochaetes in stratum 3 were more stable after dreissenid invasion. Pelecypod $\delta^{13}C$ did increase in stratum 3 over time by nearly 3‰, but due to a lack of contemporary samples from stratum 1, we could not compare this pattern to Pelecypoda from more shallow sites.

In contrast, only chironomids demonstrated any significant change in sediment-corrected $\delta^{15}N$ values after dreissenid establishment (Fig. 5; Table 3). Chironomid $\delta^{15}N$ values were relatively stable at deep sites (stratum 3) but tended to decrease after dreissenid invasion at shallow sites (stratum 1). On average, benthic invertebrate $\delta^{15}N$ declined by 1.2 ± 1.1‰ in stratum 1.

Mean invertebrate isotopic values were summarized pre- and post-dreissenid invasion in pelagic, profundal, and nearshore habitats (Fig. 6). On average, Suess-corrected $\delta^{13}C$ values were similar for both zooplankton and profundal benthos before and after dreissenid establishment, each within 1‰ of pre-invasion values. By contrast, $\delta^{13}C$ values of shallow benthos (i.e., from stratum 1) were enriched by 3.9‰. Sediment-corrected $\delta^{15}N$ values tended to be lower by approximately −2‰ after dreissenid invasion among benthos from shallow sites, but less so among zooplankton (−1.2‰) or profundal benthos (−0.6‰).

Change in fish community isotopes

Overall, the fish community was isotopically more variable and occupied a larger range on the biplot (especially with regards to $\delta^{13}C$) after dreissenid invasion compared to the pre-invasion data (Fig. 7). Based on the biplot centroids, the fish community was significantly enriched in the heavier isotope of C after dreissenid invasion (pre-invasion $\delta^{13}C = -22.8$, post-invasion $\delta^{13}C = -20.8$, $t_{64.4} = 4.67$, $P < 0.0001$) but was not significantly different in N (pre-invasion $\delta^{15}N = 12.3$, post-inva-

Table 2. Results of nested ANOVA on preserved zooplankton isotopic values, 1982–2008.

Isotope	Year nested in Invasion			Invasion		
	$F_{5,44*}$	df	P	$F_{1,5}$	df	P
$\delta^{13}C$	10.42	5,44	<0.0001	0.07	1,5	0.8
$\delta^{15}N$	2.50	5,43	0.045	4.44	1,5	0.09

Table 3. *P*-values of model comparisons evaluating the significance of factors of interest in explaining variation in benthic invertebrate isotopic signatures. Significance of factors was determined via comparisons of nested models using log likelihood. "Stratum×Invasion" effects were evaluated by comparing the full model with an additive model. "Invasion" effects were evaluated by comparing the full model with one where Invasion as a fixed factor was excluded. Where data were from a single stratum only, the reduced full model (no stratum effect) was compared to one with only a random year effect. The stratum effect was only evaluated when the additive model was not significant. *n/a* = not applicable (see notes below).

Organism	$\delta^{13}C$			$\delta^{15}N$		
	Stratum×Invasion	Stratum	Invasion	Stratum×Invasion	Stratum	Invasion
Chironomidae	0.011		0.004	0.020		0.47
Oligochaeta	0.020		0.29	0.99	.55	0.34
Amphipoda*	*n/a*	*n/a*	0.012	*n/a*	*n/a*	0.20
Ephemeroptera*	*n/a*	*n/a*	0.0011	*n/a*	*n/a*	0.71
Gastropoda*	*n/a*	*n/a*	0.0029	*n/a*	*n/a*	0.99
Isopoda*	*n/a*	*n/a*	0.048	*n/a*	*n/a*	0.99
Plecypoda**	*n/a*	*n/a*	0.0097	*n/a*	*n/a*	0.99
Dreissena	*n/a*	*n/a*	*n/a*	*n/a*	*n/a*	n/a

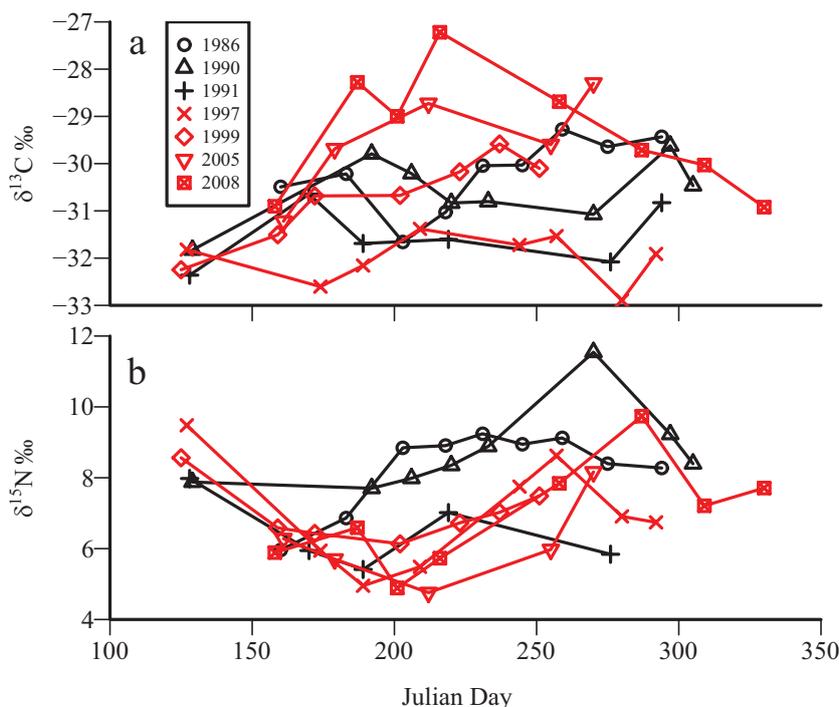*statistical analysis for stratum 1 only.
**statistical analysis for stratum 3 only.

Fig. 2. Seasonal patterns in zooplankton isotopic values of $\delta^{13}C$ (panel a) and $\delta^{15}N$ (panel b) collected from station K45 in Lake Simcoe, Canada. Isotopic values for a given year were corrected for Suess effect ($\delta^{13}C$) and anthropogenic N influences ($\delta^{15}N$). Years prior to dreissenid establishment (<1995) are indicated in black; years after dreissenid establishment (>1995) are shaded red.

sion $\delta^{15}N = 11.9$, $t_{97.2} = 1.08$, $P = 0.28$). We compared the difference and directional change among 4 offshore, coldwater fish species (lake trout, lake whitefish, lake herring, rainbow smelt) and 4 nearshore, warmwater species (yellow perch, pumpkinseed, white sucker, smallmouth bass) over this time period (Table 4). Following Benjamini-Hochberg corrections for false discovery rate, all warmwater species had significantly more positive $\delta^{13}C$ values after dreissenid invasion (Fig. 7; Table 4). Similarly, coldwater fish species demonstrated an increase in $\delta^{13}C$ following dreissenid invasion (significant changes with the exception of rainbow smelt), but the changes were of lower magnitude than observed in the warmwater species. Only 2 warmwater species demonstrated significant change in $\delta^{15}N$; both yellow perch and smallmouth bass had lower $\delta^{15}N$ after dreissenid invasion (Table 4, Fig. 7). Of all fish species analysed, only lake whitefish showed a significant increase in $\delta^{15}N$ in 2009 (Fig. 7, Table 4).
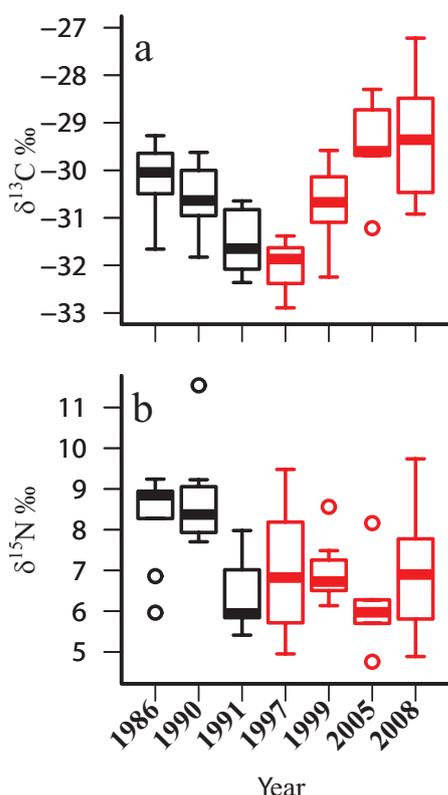

Fig. 3. Box plot of annual patterns in zooplankton isotopic values of $\delta^{13}C$ (panel a) and $\delta^{15}N$ (panel b) collected from station K45 in Lake Simcoe, Canada. Isotopic values were corrected for Suess effect ($\delta^{13}C$) and anthropogenic N influences ($\delta^{15}N$). For each year, boxes represent the interquartile range (25th to 75th percentile of the data), and whiskers indicate 95th percentile range. Solid bar indicates the median value for each year, and outliers are shown as circles. Years prior to dreissenid establishment (<1995) are indicated in black; years after dreissenid establishment (>1995) are shaded red.

Discussion

Our stable isotope data clearly indicate a major change in the source of C supplying both fish and nearshore (stratum 1) invertebrates after the establishment of dreissenid mussels in Lake Simcoe. The mean $\delta^{13}C$ of all benthic invertebrate taxa occupying shallow depths (5–10 m) increased by 5‰ after dreissenid establishment. Nearshore fish species that tend to inhabit warmer shallow waters (yellow perch, smallmouth bass, white sucker, and pumpkinseed) exhibited a similar average increase of 3.4‰ after dreissenid establishment. Offshore fish species demonstrated an increase in $\delta^{13}C$, but of much smaller magnitude (0.9% on average). The consistency of this pattern (increasing $\delta^{13}C$ across both primary and secondary nearshore consumers) clearly indicates a profound shift in the source of C at the base of the nearshore food web, as opposed to a simple change in consumer diets.

Changes in the source of C were primarily isolated to shallow benthic regions of the lake and were not similarly reflected in pelagic or profundal habitats. Pelagic zooplankton $\delta^{13}C$ values, while variable among seasons and years, were not systematically different between years when dreissenids were present versus those when they were absent. Profundal benthos on average did not change following dreissenid establishment; however, $\delta^{13}C$ values of coldwater pelagic/profundal fish species changed by 0.9‰ on average, only one-quarter of the increase observed in nearshore fishes, but of similar magnitude as profundal benthos. This shift is small ecologically, given that enrichment factors for $\delta^{13}C$ between trophic levels can vary by as much as 1‰. Thus, it is difficult to say with certainty that increases in profundal or pelagic fish on the order of 1‰ represent any significant increase in benthic production, but it is very plausible that the much greater increases in nearshore fishes can be attributed to reported increases in benthic-derived nearshore production (Ozersky et al. 2012).

Our results suggest the importance of benthic production in the shallow regions of Lake Simcoe increased sometime between 1993 and 2008 with the establishment of dreissenid mussels occurring in 1996. Although $\delta^{13}C$ of shallow benthic invertebrates was variable from 1982 to 1993, this variation was much less than the magnitude of the shift to higher $\delta^{13}C$ in 2008 and 2009. While we have no earlier isotopic estimates of shallow benthos after dreissenid establishment, our 2008 and 2009 data reveal a major and consistent increase in the importance of benthic production in the nearshore of Lake Simcoe. In another study, Ozersky et al. (2012) compared the contemporary (2008–2009) isotopic signatures of nearshore invertebrates collected from rocky substrates in Lake Simcoe to only a single pre-invasion

Table 4. Statistical evaluation of change in isotopic values prior to (1982–1983) and after (2009) dreissenid invasion. Significance was based on comparison of estimated probability from *t*-tests against Benjamini-Hochberg corrected critical *P*-value (P_{crit}) to correct for false discovery rate. Δ denotes change in mean isotopic signature between time periods. Warmwater species are in bold font. Two-letter acronyms denote fish species as in Table 1.

Isotope	Species	Δ	*t*	*df*	*P*	P_{crit}	Significant
δ^{13}C	RS	0.4	−1.30	3.8	0.2668	0.05	no
	WS	**3.0**	**− 3.62**	**4.3**	**0.0195**	**0.043**	**yes**
	LW	1.4	− 3.34	6.3	0.0144	0.038	yes
	LT	1.0	− 3.16	7.7	0.0140	0.031	yes
	LH	0.8	− 3.68	5.8	0.0111	0.025	yes
	YP	**2.6**	**− 4.60**	**4.6**	**0.0071**	**0.019**	**yes**
	PS	**5.0**	**− 7.71**	**5.5**	**0.0004**	**0.013**	**yes**
	SB	**3.3**	**− 8.01**	**7.9**	**0.0000**	**0.0063**	**yes**
δ^{15}N	LT	− 0.1	0.42	8.0	0.6856	0.05	no
	LH	− 0.2	0.65	7.3	0.5361	0.043	no
	PS	**− 0.9**	**1.95**	**5.7**	**0.1022**	**0.038**	**no**
	WS	**− 1.2**	**2.36**	**8.0**	**0.0463**	**0.031**	**no**
	RS	− 0.7	2.73	7.0	0.0292	0.025	no
	LW	1.1	− 2.94	8.0	0.01869	0.01875	yes
	YP	**− 1.6**	**5.23**	**5.9**	**0.0021**	**0.0125**	**yes**
	SB	**− 1.1**	**5.30**	**7.2**	**0.0010**	**0.0063**	**yes**

year (1993). The temporal consistency among both pre- and post-invasion years reported in our study provides confirmation that changes before/after dreissenid invasion are not an artifact of random interannual variation but rather represent a major change in the importance of benthic-derived C in the nearshore regions of the lake.

The most reasonable explanation for this increase in the importance of benthic-derived C is the benthification of Lake Simcoe due to dreissenid filtration in the nearshore and shallow offshore regions of the lake. The major increase in total invertebrate abundance in sites 5–15 m in depth was almost entirely due to dreissenid biomass (Rennie and Evans 2012). Dreissenids, which are concentrated in this depth zone of the lake and filter an estimated one-quarter of the total lake volume each day (North et al. 2013), likely have had an impact on the deposition of nutrients directly from the water column to benthic habitats via dreissenid biodeposits (Hecky et al. 2004, Cha et al. 2011, Ozersky et al. 2012). The increase in water clarity in the lake by 30–50% since 1980 (Young et al. 2010) would also have increased the area of lake bottom available to support benthic production. This is the first example we are aware of to demonstrate such a significant shift in the routing of C at multiple trophic levels and habitats (i.e., among many nearshore and offshore fish species and benthic invertebrate taxa occupying a range of habitats) after dreissenid invasion.

Increased whole-lake productivity as an alternative explanation for the increase in organism δ^{13}C we observed does not seem to apply to Lake Simcoe. Enrichment in δ^{13}C of ecosystem components has been observed elsewhere with an increase in lake productivity (Schelske and Hodell 1991, Perga and Gerdeaux 2004). In Lake Ontario, an estimated increase in spring total phosphorus (TP) from 5 to 30 µg L^{-1} resulted in an increase in sediment-deposited organic δ^{13}C by 1.5‰ (Schelske and Hodell 1991). A relationship developed between lake whitefish scale δ^{13}C and lake TP in Lake Geneva and predicted a 2‰ enrichment when lake TP doubled from 40 to 80 µg L^{-1} (Perga and Gerdeaux 2004). In Lake Simcoe, spring TP has significantly declined from 1980 to 2008, and ice-free TP has been variable and without trend since the mid-1990s (Young et al. 2011); therefore, the isotopic enrichment we observed in the nearshore was not likely due to increasing whole-lake productivity.

These changes may have significant consequences for ecosystem stability. An increase in the diversity of sources of energy to a system should promote ecosystem stability in the face of disturbance (Rooney and McCann 2012). The increased importance in shallow benthic C represents a massive increase in an energy source that was previously of lesser importance. The positive shift in δ^{13}C of shallow benthic fish and invertebrates in recent years has led to an increase in the breadth (i.e., range) of δ^{13}C values present in

the ecosystem, and therefore the trophic and functional diversity in the Lake Simcoe ecosystem compared to the period before dreissenid establishment. In 1983, the fish community had a $\delta^{13}C$ range of approximately 3‰. This range tripled to 10‰ in the 2009 fish community, with most of that increase being due to species shifting in a direction consistent with an increase in benthic resources. Similarly, the differentiation between shallow benthic and profundal invertebrate signatures has nearly doubled after dreissenid establishment (based on patterns among Chi-
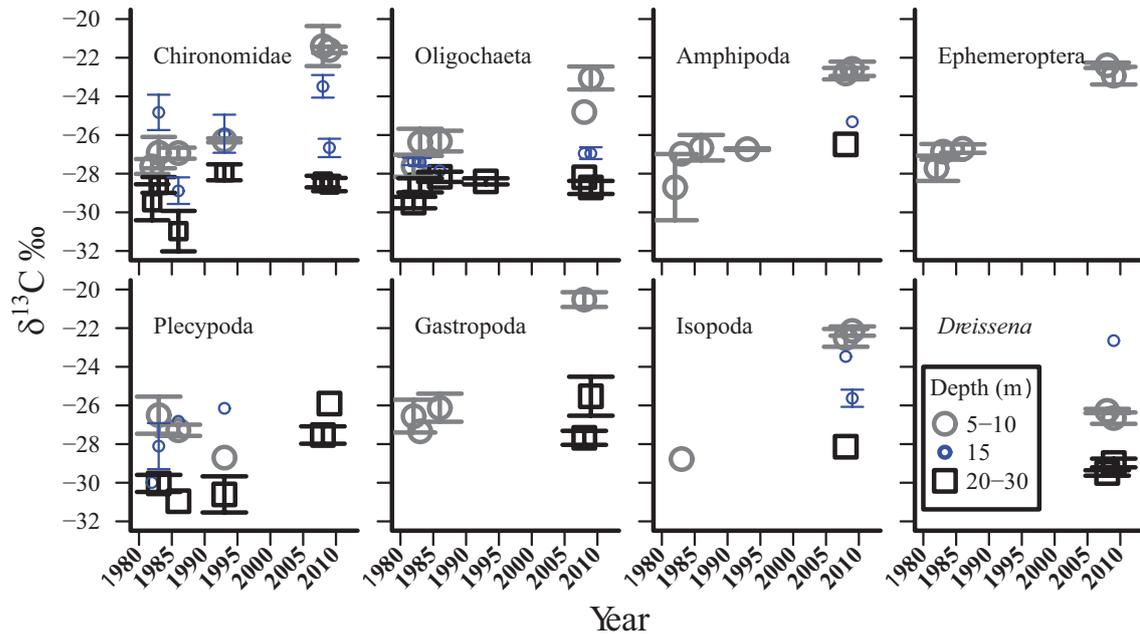
Fig. 4. Temporal patterns of benthic invertebrate $\delta^{13}C$ values, 1982–2009, by depth stratum. Stratum 1 (5–10 m depth) are shaded circles, stratum 2 (depth = 15 m) are small shaded circles, and stratum 3 (depths 20–30 m) are black squares. Isotopic values were corrected for Suess effect. Error bars are ±1 standard error. Each panel is identified by the taxon it represents.
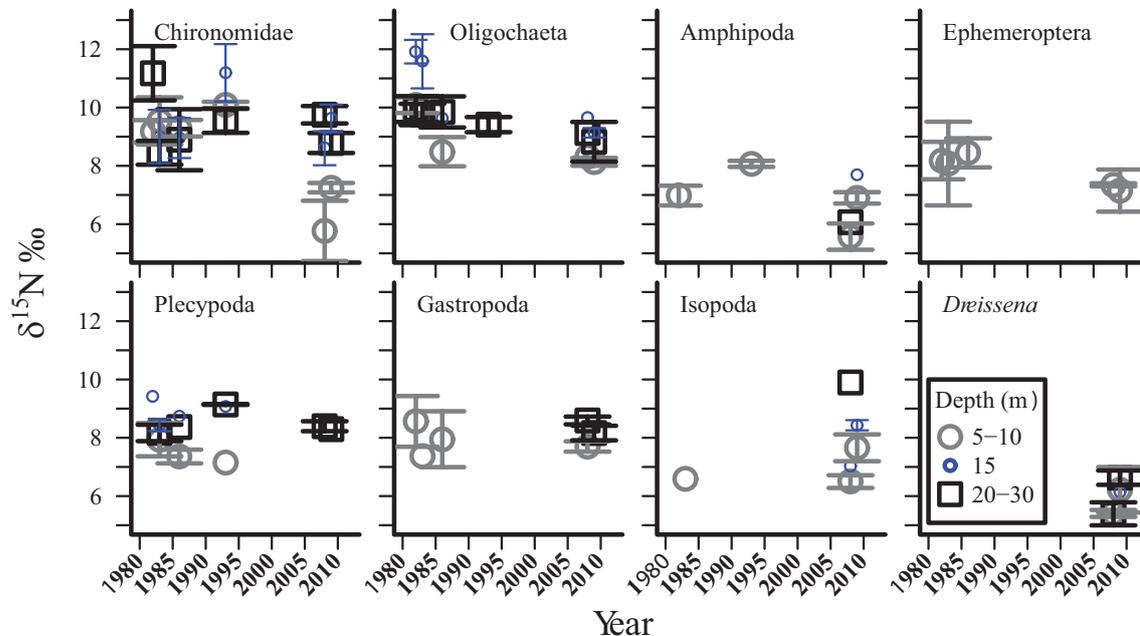
Fig. 5. Temporal patterns of benthic invertebrate $\delta^{15}N$ values, 1982–2009, by depth stratum. Stratum 1 (5–10 m depth) are shaded circles, stratum 2 (depth = 15 m) are small shaded circles, and stratum 3 (depths 20–30 m) are black squares. Isotopic values were corrected for anthropogenic N influences. Error bars are ±1 standard error. Each panel is identified by the taxon it represents.

ronomidae and Oligochaeta; Fig. 4). Another study reported an increase in spatial distribution and taxonomic diversity of macrobenthos in the shallow, rocky littoral zone in Lake Simcoe (Ozersky et al. 2011), which also suggests increased ecosystem stability in the nearshore of the lake.

While our study clearly demonstrates an increased importance of shallow benthic-derived C to the Lake Simcoe ecosystem, we cannot partition the overall fraction of primary production in the lake that originates from nearshore benthic versus offshore pelagic primary production. However, the increase in importance and significance of the nearshore benthic channel of C and energy in the lake may influence our understanding of the relationships between phosphorus loading, chlorophyll, TP, and deep-water oxygen levels. While the empirical relationships between these variables derived prior to the arrival of dreissenids still seem to hold in the lake (Young et al. 2011), the underlying mechanisms that drive those relationships may have changed (e.g., photoacclimation; Guildford et al. 2013). Ecosystem models based on process and function rather than empirical relationships may be better able to reveal what role the dramatic ecosystem changes accompanied by dreissenids are playing in nutrient cycling and deposition of organic particulate matter in the lake.

The application of the sediment correction for $\delta^{15}N$ ensures that the temporal trends we observe here were due to factors other than atmospheric inputs from development (Brown et al. 2011) or watershed influences such as
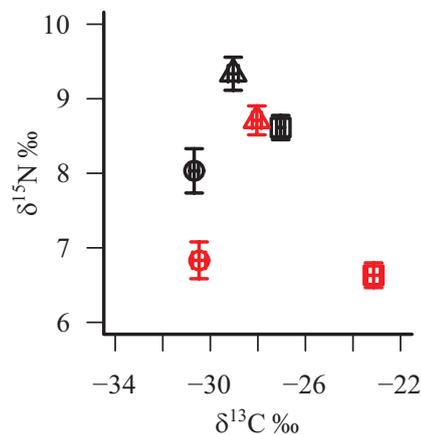

Fig. 6. Biplot of mean estimates for $\delta^{13}C$ and $\delta^{15}N$ from zooplankton (circles), profundal benthos (depth stratum 3, triangles), and shallow benthos (depth stratum 1, squares) across all taxa encountered. Black symbols are values prior to dreissenid establishment; red-shaded symbols are after dreissenid establishment. Isotopic values were corrected for Suess effect ($\delta^{13}C$) and anthropogenic N influences ($\delta^{15}N$). Error bars are ±1 standard error.

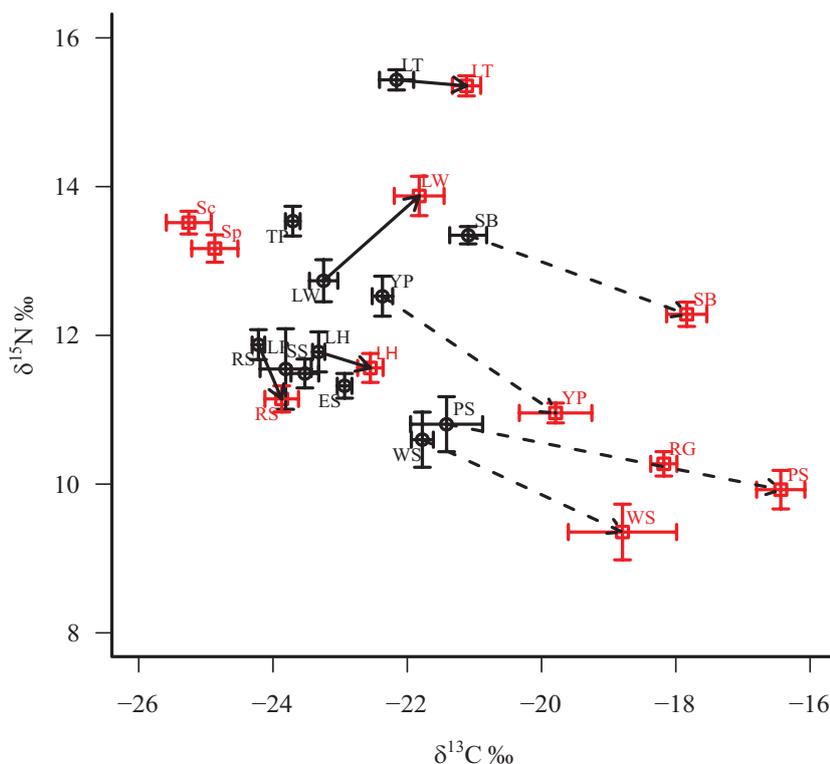**Fig. 7.** Biplot of mean estimates for $\delta^{13}C$ and $\delta^{15}N$ for fish species encountered in surveys of the fish community in Lake Simcoe, Ontario in 1983 (pre-dreissenid establishment, black circles), and 2009 (post-dreissenid invasion, red-shaded squares). Black solid lines denote shift in coldwater pelagic/profundal fish species, and dashed lines denote shift in shallow, warmwater fish species. Two-letter designations of fish species are in Table 1.

sewage or agricultural inputs (Evans et al. 1996, Winter et al. 2002, Eimers et al. 2005), all of which tend to contain heavier N versus that derived within the lake (Teranes and Bernasconi 2000, Lake et al. 2001). Prior to this correction, nearly every ecosystem component we investigated (sediments, zooplankton, benthos, fish) increased in δ^{15}N with time, particularly for profundal benthos and coldwater fishes (results not shown). Following this correction, the δ^{15}N signatures of some benthic organisms, zooplankton, and 2 shallow, warmwater fishes (yellow perch, smallmouth bass) actually declined with time. With the anthropogenic signal removed, this decline at multiple trophic levels and ecosystem components (benthic, pelagic) suggests that lighter δ^{15}N signatures may be reflecting changes at the base of the foodweb (e.g., algae).

While a decline in δ^{15}N signatures could also result from an increase in N-fixation, and therefore an increase in N-fixers (i.e., cyanobacteria) among the algal community (Gannes et al. 1998), recent evidence suggests it is unlikely this is occurring in Lake Simcoe. Winter et al. (2011) reported an overall decline in cyanobacteria (typically the major N-fixers in the algal community) in Lake Simcoe from 1980 to 2007. Further, cyanobacteria are not frequently consumed by grazers and therefore are often not incorporated directly into food webs.

A similar shift in δ^{15}N could also occur with a decline in the relative proportion of mixotrophic/heterotrophic algae or an increase in autotrophs among the algal community; however, mixotrophic algae often make up only a small fraction of the nanoplankton community in freshwater lakes of similar trophic status as Lake Simcoe (Arenovski 1994). We are unaware of any evaluations of the degree of mixotrophy among the algal community in Lake Simcoe, past or present.

Lighter δ^{15}N values are often associated with benthic resources obtained at shallower depths (Vander Zanden and Rasmussen 1999, Siersen et al. 2006, Rennie et al. 2009), which may explain the declines in the δ^{15}N of fishes feeding at shallower depths now versus 1983, but not the decline in shallow, warmwater benthos (Chironomidae) obtained from similar sites (i.e., depths) over time. Additional work is required to determine the causes for lighter (post-correction) δ^{15}N values among zooplankton and nearshore benthos in Lake Simcoe.

Some isotopic trends differed from our general patterns, specifically for profundal pelecypoda (Psididae and Sphaeriidae) and lake whitefish. Lake whitefish demonstrated the greatest increase in δ^{13}C among the coldwater species evaluated in this study (Table 4). Lake whitefish has been found elsewhere to increase its use of nearshore resources following dreissenid invasion (Rennie et al. 2009). Unlike any other taxon following sediment δ^{15}N corrections, lake whitefish δ^{15}N values were significantly

greater after driessenid establishment. This observation is counter to what might be expected if lake whitefish were relying on resources from shallow benthic regions (Rennie et al. 2009), and suggests a possible increase in the trophic position of this species in Lake Simcoe.

Lake whitefish have been observed to be piscivorous in some systems, and some piscivory has been reported for this species in Lake Simcoe (Hart 1931, Amtstaetter 2002), although no fish remains were found in the stomachs of 29 lake whitefish sampled during our study in August 2009. The predatory cladoceran, *Bythotrephes longimanus*, invaded Lake Simcoe in 1993 and was prominent in lake whitefish stomachs collected in 2001 (Amtstaetter 2002) and 2009 (M. Rennie and D. Evans, unpublished data) and might account for slightly elevated δ^{15}N signatures.

Profundal pelecypoda are filter feeders and thus have the capacity to filter resources directly from the water column; therefore, it is possible that these organisms are filtering ^{13}C-enriched detrital particles from the water column. Given their distribution in the profundal zone closely associated with the sediments, however, it is surprising that their signatures are not more similar to those observed for sediments and other profundal taxa, with only slight (e.g., ≤1‰) or no increases with time.

In summary, we describe a major increase in the importance of benthic-derived C resources in the nearshore of Lake Simcoe after the establishment of dreissenid mussels, resulting in a major increase in the breadth of resources available to organisms in the lake. Our observations provide evidence in support of the nearshore shunt occurring in Lake Simcoe, suggesting that the conceptual model applied to explaining dreissenid effects in the Great Lakes also applies to other systems. Our data suggest that nearshore benthic-derived C in Lake Simcoe may also be influencing energetic resources of coldwater offshore fishes like lake whitefish in addition to nearshore fishes like catostomids, percids, and centrarchids.

Nearshore resources and benthic-derived C have been frequently shown to be disproportionately important to whole-lake processes (Vadeboncoeur et al. 2002, Hampton et al. 2011). As such, modest increases in the routing of energy through benthic pathways may have amplified effects on ecosystem function, structure, and stability. If true, then there are likely important functional differences between the current-day Lake Simcoe ecosystem versus the past. We suggest that understanding these changes may be critical to a progressive, sustainable approach to management of the lake. Ultimately, whole-ecosystem modelling approaches will be required to better understand the mechanistic changes that have occurred in the lake. The information provided here should assist in those endeavors by illustrating the emergence of the nearshore benthic community in Lake Simcoe as a likely and

significant energy channel in the production of recreationally important fish species.

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