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Re-engineering the eastern Lake Erie littoral food web: The trophic function of non-indigenous Ponto-Caspian species

Linda M. Campbell [a,*], Robert Thacker [b,1], David Barton [c,2], Derek C.G. Muir [d,3], Dixie Greenwood [e,4], Robert E. Hecky [f,5]

[a] School of Environmental Studies and Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6
[b] Department of Astronomy and Physics, Saint Mary's University, Halifax, Nova Scotia, Canada B3H 3C3
[c] Department of Biology, University of Waterloo, 200 University Avenue, Waterloo, ON, Canada
[d] National Water Research Institute, Environment Canada, Burlington ON, Canada
[e] Port Dover Research Station, Ontario Ministry of Natural Resources, Port Dover, ON, Canada
[f] Large Lakes Observatory, University of Minnesota, Duluth, 10 University Drive 204 RLB Duluth, MN 55812-2496

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ABSTRACT

The trophic roles of key Ponto-Caspian invaders (quagga mussels *Dreissena bugensis*, amphipods *Echinogammarus ischnus* and round goby *Apollonia melanostomus*) within the littoral food web of eastern Lake Erie were quantified using stable isotopes (δ^{13}C, δ^{15}N). A dual stable isotope parameter search with a mass balance component was used to assess the isotopic importance of quagga mussels and amphipods as dietary items to two size classes of round goby. The utility of the mass balance simulation was also evaluated as a tool to approximate isotopic contributions of feasible prey and identify gaps incurred by "missing" prey items not included in the sampling. The mass balance dietary simulation, confirmed by stomach content data, indicated that isotopically important prey to small round goby (<11.2 cm) were chironomids and Ponto-Caspian amphipods, while large round goby (≥11.2 cm) showed strong preference for quagga mussels. The dietary mass balance simulation output also supported the isotopic importance of round goby to the somatic growth of smallmouth bass, rock bass and freshwater drum. The isotopic mass balance output for yellow perch was more ambiguous, which may be in line with their known broadly omnivorous diet. The white bass output was in line with published data indicating increasing consumption of round goby for this species, while the brown trout output strongly favoured alewife isotopic contributions. However for white perch and walleye, the mass balance simulations were not in line with their known published diets in Lake Erie, probably due to a lack of key prey items in the sample set (e.g. zooplankton for white perch and shiner species for walleye). As expected, the Ponto-Caspian species have integrated themselves into the littoral food webs, and the "quagga mussel–round goby–smallmouth bass" food chain forms one of the key components within the trophodynamics of Lake Erie.

Introduction

Unintentional introductions of aquatic species from the Ponto-Caspian region of Europe have been one of the most significant anthropogenic impacts in the lower Laurentian Great Lakes (Holeck et al., 2004). The most successful of these non-indigenous species (NIS), the zebra mussel *Dreissena polymorpha* and quagga mussels *Dreissena bugensis*, the amphipod *Echinogammarus ischnus*, and the round goby *Apollonia* (*Neogobius*) *melanostomus* have spread rapidly throughout the nearshore littoral environments of Lake Erie over the past two decades (Vanderploeg et al., 2002). Those NIS are interfering or competing with native species, such as unionid clams, *Gammarus* spp., and mottled sculpins *Cottus bairdi* (Vanderploeg et al., 2002). NIS are also preyed upon by other native species such as smallmouth bass *Micropterus dolomieu* (Steinhart et al., 2005), so NIS may become important conduits of nutrients and contaminants to higher trophic levels (Morrison et al., 2000, Johnson et al., 2005). The role of the Ponto-Caspian NIS in re-engineering the littoral ecosystems is now of concern (Hecky et al., 2004) but, the direct importance and role of round goby, *Echinogammarus* and *Dreissena* within the littoral fish food webs of Lake Erie have not been quantified.

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* Corresponding author. Tel.: +1 613 533 6602.
E-mail addresses: linda.campbell@queensu.ca (L.M. Campbell), rthacker@ap.smu.ca (R. Thacker), drbarton@sciborg.uwaterloo.ca (D. Barton), Derek.Muir@ec.gc.ca (D.C.G. Muir), dixie.greenwood@ontario.ca (D. Greenwood), rhecky@d.umn.edu (R.E. Hecky).
[1] Tel.: +1 902 420 5105.
[2] Tel.: +1 519 888 4567x32559.
[3] Tel.: +1 905 319 6921.
[4] Tel.: +1 519 583 3565.
[5] Tel.: +1 218 726 7926.

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The objective of this study is to assess the importance of key Ponto-Caspian NIS, *D. bugensis*, *Echinogammarus* and round goby, in the diets of fish within the littoral food web of eastern Lake Erie using stable isotopes of carbon and nitrogen. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes have been widely used to characterize food web structure in lakes because $\delta^{13}C$ and $\delta^{15}N$ values reflect assimilation of food by consumers integrated over time (Peterson and Fry, 1987). In temperate lakes, stable nitrogen isotope values increase from prey to consumer, typically by about 2–4‰, providing a continuous, integrated trophic position measure (Vander Zanden et al., 2001). Stable carbon isotope values increase up to 1.2‰ between trophic levels and can indicate habitat type or dietary carbon source (Hecky and Hesslein, 1995). Isotopic mass balance approaches (simulations) can be developed to approximate the range of potential prey that may be "isotopically important" to a predator species, meaning that the isotopic values of the prey are directly assimilated into the somatic tissue of the predator (Phillips and Gregg, 2003; Campbell et al., 2005).

Table 1
Sampled benthos and their average stable isotope values.

Benthos	Code	*n*	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
Invertebrates						
Chironomidae	CH	17	−19.3	(1.1)	10.9	(1.2)
Dreissena bugensis	DB	18	−22.7	(1.6)	9.8	(0.5)
Echinogammarus ischnus	EI	4	−19.6	(1.6)	10.2	(0.5)
Gammarus fasciatus	GA	5	−16.8	(1.0)	9.1	(1.0)
Other						
Benthic algae (mixed scrapings)	BA	10	−17.1	(2.2)	6.9	(1.5)
Cladophora spp.	CL	1	−18.1		5.6	
Spirogyra spp.	SP	3	−13.2	(2.1)	8.2	(1.2)
Dreissena feces	DF	11	−15.6	(1.5)	7.1	(0.6)
Gammarus feces	GF	1	−16.6		9.7	
Detritus	DE	15	−9.5	(1.8)	7.0	(0.5)
Macrophyte (mixed)	MA	7	−15.9	(6.3)	7.8	(4.5)
Seston	SE	17	−24.7	(2.2)	6.0	(1.2)

Standard deviations are listed in brackets. The species codes, as used in Fig. 1, are listed here.

Methods

Underwater benthic sampling (Table 1) was undertaken by divers on June 14 and October 9, 2002 along a 10-m transect off Peacock Point near Port Dover in the eastern basin of Lake Erie (Barton et al., 2005). Invertebrates were collected with an airlift system (Barton and Hynes, 1978), using air from a pressurized diving air tank to draw benthos and debris, dislodged by hand or a blunt knife, upwards a 1.3-m long 5-cm diameter ABS tube, topped with a 90° elbow attachment leading into an attached 243-μm mesh bag. A single qualitative collection was made on each visit at each depth (2, 5 and 10 m) representing 3–5 min of sampling effort. Invertebrates were sorted from associated algae and inorganic debris and identified to genus or species where possible. All of the dreissenids were quagga mussels (*D. bugensis*). Amphipods and chironomids were the most abundant non-mussel benthic macrofauna. Organisms were allowed to evacuate their guts for approximately 12 h in vials of aerated lake water prior to drying and analysis (Gu et al., 1997). Amphipod feces were collected from the vials for isotope analyses. *Dreissena* feces and pseudofeces were also collected from groups of 15–20 mussels placed in a clean jar of lake water and allowed to empty their guts and mantle cavities over 3–5 days. Any material found on the bottom of the jar was assumed to have originated from the mussels. No attempt was made to distinguish between feces and pseudofeces, and both will be referred as *Dreissena* "feces".

Cladophora glomerata, *Spirogyra* spp. and mixed algal scrapings (short filaments and diatoms) were collected at depths of 2 m from hard surfaces (rocks and dreissenid shells), rinsed with distilled water and visually inspected to ensure no contamination by organic matter or other organisms before drying. Detritus or particulate organic material (e.g. settled seston particles, sloughed body parts, dead organisms and plants) were collected with a piston-scraper device described by Barton and Carter (1982) or by suction with 60 mL syringes, and all pieces of shell and small pebbles removed. Water samples sampled for seston were collected using a Van Dorn bottle at approximately 1 m above the lake bottom at each sampling site, prefiltered with 300 mm mesh, then filtered to clogging through a 0.8 mm quartz filter. Examination of the filters showed seston to be composed of phytoplankton, zooplankton, detritus and inorganic particulate material. All samples of algae, detritus, feces and seston filter included high inorganic content so were acidified with 10% hydrochloric acid to remove inorganic carbon prior to drying and isotope analysis. Amphipods and invertebrates were not acidified because this method can significantly alter $\delta^{15}N$ values (e.g., Carabel et al., 2006).

Fish (Table 2) were obtained from weekly Ontario Ministry of Natural Resources nearshore gill net surveys during late July and early August of 2002 and 2003 between Port Dover and Peacock Point in Long Point Bay. While the focus was on monitoring littoral species, in late July 2003 we happened to collect several species (large brown

Table 2
Sampled fish species, and their average total length, average stable isotope values and species codes.

Common name	Scientific name	Code	*n*	Total length (mm)		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
Alewife	*Alosa pseudoharengus*	AW	8	191.0	(5.65)	−22.7	(2.0)	12.3	(0.6)
Brown bullhead	*Ictalurus nebulosus*	BB	1	271		−21.1		14.4	
Brown trout	*Salmo trutta*	BT	3	626.7	(112.0)	−21.6	(0.02)	15.5	(0.4)
Common carp	*Cyprinus carpio*	CC	2	594.0,	60.0	−22.0,	−17.7	13.2,	14.1
Freshwater drum (sheepshead)	*Aplodinotus grunniens*	FD	15	385.0	(57.14)	−19.0	(1.3)	15.9	(0.7)
Gizzard shad	*Dorosoma cepedianum*	GS	6	311.0	(113.10)	−21.1	(1.0)	12.7	(1.9)
Shorthead redhorse	*Moxostoma macrolepidotum*	SR	2	500.0,	547.0	−19.6,	−18.5	12.8,	12.9
Pumpkinseed	*Lepomis gibbosus*	PS	1	~		−22.1		12.5	
Quillback	*Sebastes maliger*	QB	1	441.0		−19.0		14.2	
Rainbow smelt	*Osmerus mordax*	RS	1	13.4		−22.0		13.6	
Rainbow trout	*Oncorhynchus mykiss*	RT	3	327.0	(16.7)	−21.6	(0.5)	13.8	(0.1)
Rock bass	*Ambloplites rupestris*	RB	18	182.4	(39.2)	−18.7	(1.9)	15.8	(1.1)
Round goby —large	*Apollonia melanostomus*	RG_S	53	77.3	(16.3)	−18.8	(1.6)	14.1	(0.6)
Round goby —small	*Apollonia melanostomus*	RG_L	41	145.42	(20.8)	−20.9	(1.3)	13.6	(0.5)
Smallmouth bass	*Micropterus dolomieui*	SB	30	324.8	(68.8)	−19.3	(0.9)	15.9	(0.4)
Walleye	*Sander vitreus*	WE	6	384.2	(33.4)	−20.6	(0.3)	15.1	(0.3)
White bass	*Morone chrysops*	WB	6	195.0	(41.0)	−20.0	(0.5)	15.7	(0.3)
White perch	*Morone americana*	WP	10	231.2	(35.7)	−20.8	(1.1)	14.7	(0.6)
White sucker	*Catostomus commersoni*	WS	10	357.3	(86.6)	−20.9	(1.8)	13.5	(0.5)
Yellow perch	*Perca flavescens*	YP	33	195.3	(56.8)	−19.1	(0.9)	15.3	(0.9)

Round goby data have been indicated for large ($\geq$11.2 cm) and small (<11.2 cm) individuals. Standard deviations are indicated in brackets. Samples with $n = 2$ have all values listed.

trout and alewife) which are more typically associated with offshore pelagic environments. All fish were filleted, wrapped in foil and frozen at −60 °C until analyses.

Skin-free sub-samples of 2002 fish muscle tissue and whole invertebrates were dried and ground to fine powder for stable isotope analyses using a Micromass VG-Isochrom Continuous Flow Isotope Ratio Mass Spectrometer (CF-IRMS) at the Environmental Isotope Laboratory, University of Waterloo. Subsamples of dried and powdered skin-free 2003 fish muscle tissue were sent to the National Water Research Institute Stable Isotope Hydrology and Ecology Research Laboratory in Saskatoon and analyzed using GV Instruments online elemental analyzers. Working standards used to determine inter- and intra-run variation and accuracy of the results included the International Atomic Energy Agency (IAEA) standards CH6, N1, N2, plus internal standards (Campbell et al., 2003). Replicate fish samples were included in every run to determine between-run variation and inter-laboratory variation. Standard deviations of both the standards and replicate samples were ±0.3‰ for δ^{15}N and ±0.2‰ for δ^{13}C for both laboratories. Inter-laboratory variation for duplicate samples were insignificant (paired *t*-test $p \gg 0.1$) so, data from both laboratories were pooled.

Statistical analyses were performed using JMP version 6.0.2 for Windows (SAS Inc). One outlier was excluded from the round goby data prior to analyses on the basis of a *z*-test (>3 standard deviations). Change-point analyses using a modified CUSUM approach with bootstrapping with the Change-Point Analyzer 2.0 software (Taylor, 1998) were carried out on the round goby dataset to determine significant changes in trends in stable isotopes vs. length. The yellow perch and smallmouth bass datasets were also analyzed for change-points but none was found.

Knowledge of stomach contents, prey and predator feeding behaviour and zonal classification are necessary when assessing the relative likelihood of possible diets. Stable isotope research does not remove the need to investigate and quantify stomach contents and ecological behaviour, but fish caught via overnight gill nets frequently have nothing identifiable in their stomachs. In those situations, dietary approximations based on stable isotope data can be used. This leads to two modes of usage for stable isotope models, one where they are used in a purely *postdictive* fashion to determine relative dietary contributions based upon known stomach content and feeding habits, vs. an *interpretive* mode when the possible number of prey items is enlarged to include items that may or may not be consumed. The latter case still includes the former as a subset of possible solutions, but interpretation will be more complex by the inclusion of spurious matching diets that do not reflect true feeding habits. Recognition of spurious dietary items can be based on published records of stomach contents and observed predatory behaviour. In absence of supporting information, the stable isotope mass balance approach can still provide useful albeit limited information. At minimum, the model will reject prey with isotopic signatures that are incompatible with those of the predator.

Computerized approximations of dietary contributions to a predator, technically called a parameter search, were coded in FORTRAN (Campbell et al., 2005) and run on the SHARCNET high performance computational infrastructure (http://www.sharcnet.ca/). Technically, we have conducted a "parameter search", but in this paper we will refer to this as a "mass balance simulation". We took a "convergence" approach by combining a simple static linear mixing model (with a mass balance component) and a parameter search to estimate the potential contribution of different dietary items to the somatic growth of seven fish species. Our approach is equivalent to that of the "IsoSource" stable isotope mixing simulation (Phillips and Gregg, 2003, Phillips et al., 2005), and we have run the same isotopic scenarios on both programs, with nearly identical results. However, our program has the distinct advantage of being designed specifically to run on a high performance parallel multiple-processor computer platform (as opposed to a single processor running Visual Basic) which allows solutions to be found within seconds, rather than several hours. The mixing model (Eqs. 1 and 2) assumed a fractionation rate of 3.4‰ for δ^{15}N and 1.0‰ for δ^{13}C based on mean isotope fractionation rates for temperate freshwater ecosystems (Post, 2002).

$$\text{Estimated predator } \delta^{15}\text{N} = \left(\left(\delta^{15}\text{N}^{\text{prey}}_{i} {*}\%\text{diet}_i\right) + \left(\delta^{15}\text{N}^{\text{prey}}_{j} {*}\%\text{diet}_j\right) \ldots\right) + 3.4‰ \tag{1}$$

$$\text{Estimated predator } \delta^{13}\text{C} = \left(\left(\delta^{13}\text{C}^{\text{prey}}_{i} {*}\%\text{diet}_i\right) + \left(\delta^{13}\text{C}^{\text{prey}}_{j} {*}\%\text{diet}_j\right) \ldots\right) + 1.0‰. \tag{2}$$

This algorithm works by considering all possible fractions of different prey items and discards those which do not reproduce the stable isotope values of the predator under the mass balance approach. We tested for sensitivity by varying the fractionation rates as measured in diverse food webs (e.g., Post, 2002), but it did not significantly affect the output results. To reduce the size of the searched parameter space, different proportions of potential prey for each species were adjusted by 2% (including the possibility of a 0% contribution), with the final sum always equalling 100%. Note that the relative contributions of each dietary item can be changed by 1% or 2%. The latter gives a faster but marginally less accurate calculation, although in practice, the differences between searches with 1% and 2% changes are far smaller than the variances in prey stable isotope values. As mentioned, the mass balance simulation for each species was continued until the estimated isotopic values of the species matched the actual mean values for *both* δ^{15}N and δ^{13}C (±0.2‰). Because both δ^{15}N and δ^{13}C values had to be simultaneously matched, the number of possible dietary combinations was constrained. The maximum number of possible saved diets was set at 80 million, a limit set to ensure enough memory is available within the computer for storing all matching diets. In practice the 2% granulation employed prevented this from being reached.

We stress that no single matching diet can be considered more correct than any other, and the interpretation of means and variances, while somewhat crude, is the best method we have for interpreting the potential "isotopic importance" of prey items in the absence of long-term stomach content data. The method will, however, ensure that any prey items that have isotopic signatures that are incompatible with the predator under the mass balance model are excluded, and this is perhaps the most powerful aspect of the models when used in an interpretive mode. We again emphasize that while this is true regardless of the number of prey items considered in the model, increasing the number of potential prey will tend to weaken the discriminatory power of the model since increasing the number of prey items always tends to increase the number of matching diets. This is not surprising since the model is considering two simultaneous equations with as many variables as there are prey, and if the number of prey exceeds two then the system of equations represents an underdetermined mathematical problem (e.g. Farin and Hansford, 2005).

The simulated dietary patterns are the result of a computed "list" of all possible combinations of inputted prey values, adjusted for trophic fractionation addition that would yield the measured mean δ^{15}N and δ^{13}C values for the fish species in question. Mass balance simulations were run for nearshore species known to be at least partially piscivorous (smallmouth bass, rock bass, freshwater drum and yellow perch) and two size classes of round goby, using benthic items and forage fish as potential prey. Round goby individuals were separated by size (>and ≤11.2 cm) based on change-point analyses, and predicted diets were compared to detailed stomach content data for a subset of the sampled fish (Barton et al., 2005). Several species not associated with littoral benthic food webs–brown trout, white perch and walleye–were included although we did not have the full list of known pelagic prey items associated with those species. We assumed that all nine fish species included in the simulations are highly mobile, and averaged potential prey items across depths (e.g., we did not simulate depth-specific dietary sources).

Results and discussion

Food web structure

Stable isotope values of benthic invertebrates from the littoral zone of Peacock Point ranged from −22.7‰ (*D. bugensis*) to −16.8‰ (*Gammarus fasciatus*) for δ^{13}C, and from 9.1 to 10.9‰ for δ^{15}N (Table 1, Fig. 1A). Seston collected from 1 m above the bottom had more depleted ^{13}C and ^{15}N values compared to benthic algae and detritus. Stable isotope values differed little among benthic primary producers. Fish had narrower δ^{13}C ranges than those for invertebrates (−25 to −16‰) and higher δ^{15}N values (12 to 17‰; Fig. 1A). Rock bass, smallmouth bass, freshwater drum and yellow perch shared overlapping δ^{15}N and δ^{13}C values (Table 2, Fig. 1B) suggesting common littoral habitats and diets. Common carp and white sucker shared similar δ^{15}N values and overlapping δ^{13}C values with those of the round goby. Brown trout and walleye had slightly lower δ^{15}N values (15–17‰) and were more ^{13}C-depleted (−22 to 20‰) than smallmouth bass, freshwater drum and rock bass. Pelagic planktivores (alewife and gizzard shad) and omnivorous predators (rainbow trout and rainbow smelt) were also ^{13}C-depleted relative to smallmouth bass and freshwater drum. These isotopic differences between the presumptive littoral species (rock bass, freshwater drum, yellow perch and smallmouth bass) and the presumptive pelagic species (brown trout, walleye, and lake trout) are suggestive of greater reliance on a seston-based food web in offshore waters (Fig. 1).

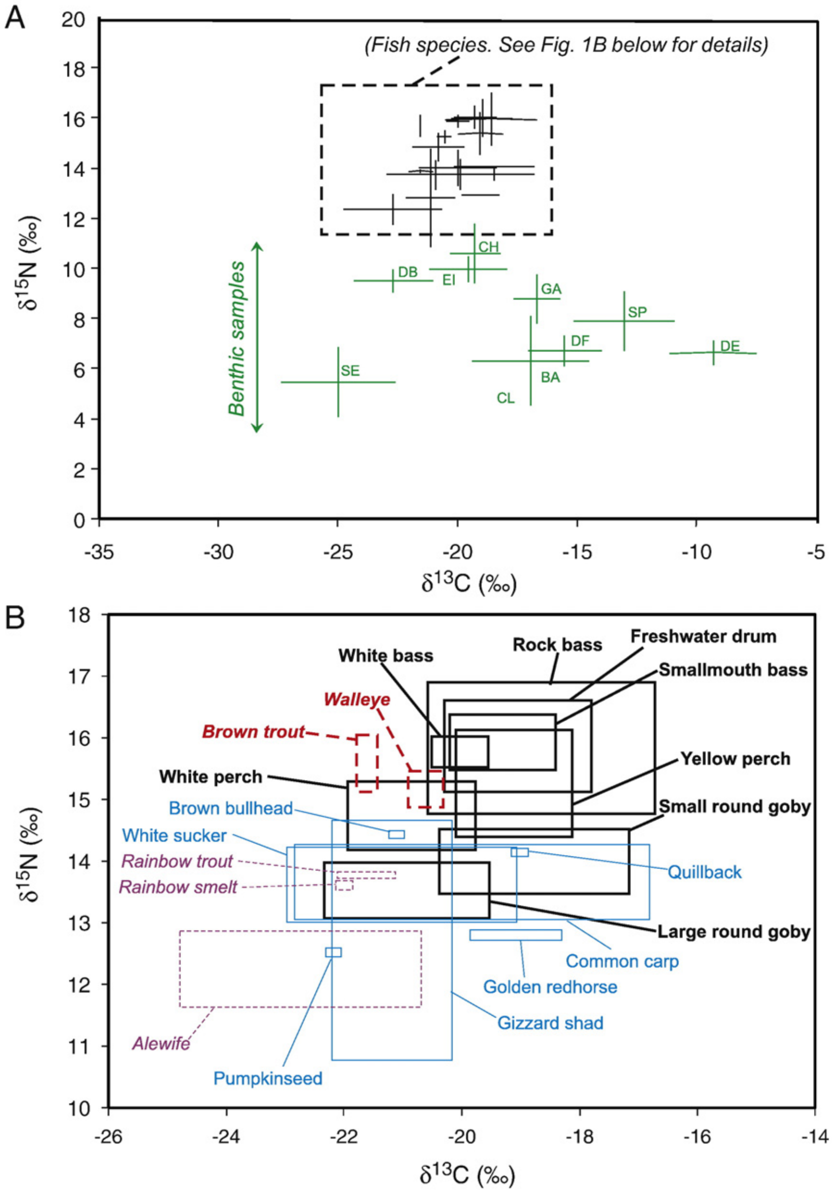

Fig. 1. Stable isotope diagram of the Lake Erie food web. (A) shows the average (± standard deviation) distribution of all fish and invertebrates, while (B) shows the minimun - maximum distribution of δ^{15}N and δ^{13}C values for each collected fish species. Bold fonts and thicker lines denote the species used in the mass balance dietary simulations. Italic fonts and dotted lines indicate putative "pelagic" fish species (e.g., offshore). The very small squares denote sample numbers $N = 1$. For sample numbers, see Tables 1 and 2.

Round goby diets: comparing stable isotopes and stomach contents

The most significant size-related change in $\delta^{15}N$ values for round goby (Fig. 2A) occurred at 11.2 cm, as indicated by change-point analyses (confidence interval: 9.8 cm to 11.3 cm; confidence level 100%). In contrast, $\delta^{13}C$ values (Fig. 2B) show steady trends in ^{13}C-depletion with increasing length, and no significant change-points were detected. This lack of change-points for $\delta^{13}C$ was confirmed by regressing length against $\delta^{13}C$ data separately for fish< and ≥11.2 cm and for all fish (Table 3). The slopes were not significantly different from each other (0.25–0.30, $p>0.5$) or from that for the significant regression using the entire dataset ($p>0.30$; Table 3).

In the isotopic mass balance simulation for round goby, we incorporated all of the invertebrates as well as benthic algae, *Dreissena* feces and detritus on the assumption that round goby would consume those incidentally along with the intended prey. The mass balance simulation for small round goby (Fig. 3A) suggests that Chironomidae are the most important prey, followed by *Echinogammarus*. It is interesting to note that *G. fasciatus* was not as isotopically significant as *Echinogammarus* even though *G. fasciatus* was 3× to 15× more abundant in the study area (Barton et al., 2005). For larger round goby (≥11.2 cm), *Dreissena* was clearly the most isotopically significant prey item, followed by Chironomidae and *Echinogammarus*. The minimum potential dietary contribution by *Dreissena* was 60%; possible contributions for all other prey items included 0% (Fig. 3B).

Table 3
Linear regression equations for $\delta^{15}N$ and $\delta^{13}C$ versus total length (TL) for small (<11.2 cm), large (≥11.2 cm) and all round goby samples (RG).

Regression	Intercept	Slope	R^2_{adj}	*p*-value
Small RG $\delta^{15}N$ vs. TL	13.0	0.15	0.16	0.002*
Large RG $\delta^{15}N$ vs. TL	15.0	−0.10	0.12	0.014*
All RG $\delta^{15}N$ vs. TL	14.5	−0.06	0.15	0.002*
Small RG $\delta^{13}C$ vs. TL	−16.89	−0.24	0.04	0.075
Large RG $\delta^{13}C$ vs. TL	−17.88	−0.21	0.093	0.030*
All RG $\delta^{13}C$ vs. TL	−16.50	−0.30	0.40	<0.001*

* Significant regressions.

The ontogenetic changes in round goby stable isotope values and mass balance simulation results are consistent with the stomach contents (Fig. 4), suggesting that a threshold gape size and jaw strength are achieved at a body length of about 11 cm. Stomach contents (Fig. 4) indicate a similar shift from Amphipoda and Chironomidae to increasing amounts of *Dreissenia* at lengths of 10–15 cm (Barton et al., 2005). Increasing consumption of dreissenids with increasing body size has been observed in round goby from the southern shoreline of Lake Erie, the Detroit River, Lake Ontario and elsewhere in the Great Lakes (Ray and Corkum, 1997; Schaeffer et al., 2005; Walsh et al., 2007; Johnson et al., 2005). The results of our stomach content and isotopic mass balance analyses suggest that a "Ponto-Caspian food chain" has been established in Lake Erie with the round goby feeding heavily upon invertebrate species from its native environments.

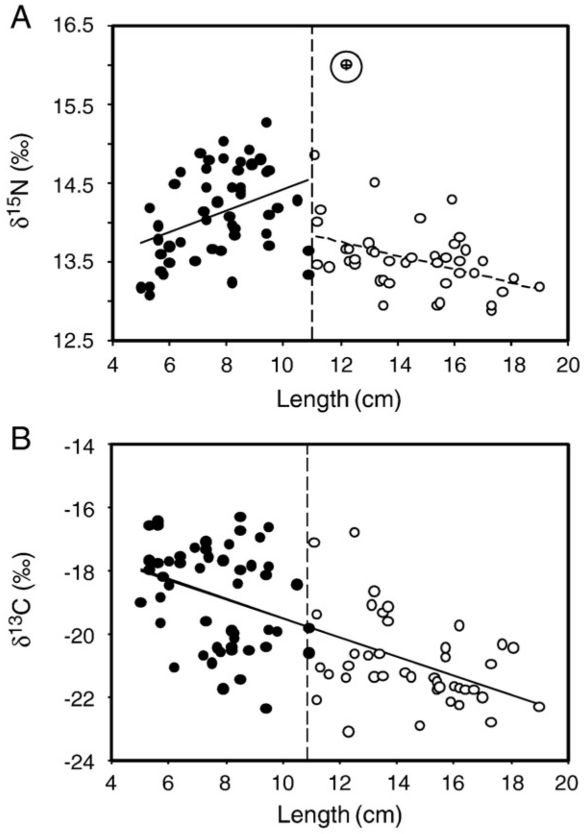

Fig. 2. Round goby $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values vs. total length. Closed circles indicate smaller round goby, open circles indicate the larger round goby, and the crossed circle indicates an outlier. Change-point analyses (see Methods) were applied to the round goby $\delta^{15}N$ dataset to determine the length at which $\delta^{15}N$ values changed significantly which was determined to be 11.2 cm (indicated by vertical dashed line). Change-point analyses for round goby $\delta^{13}C$ values were not significant. See Table 3 for regression equations.

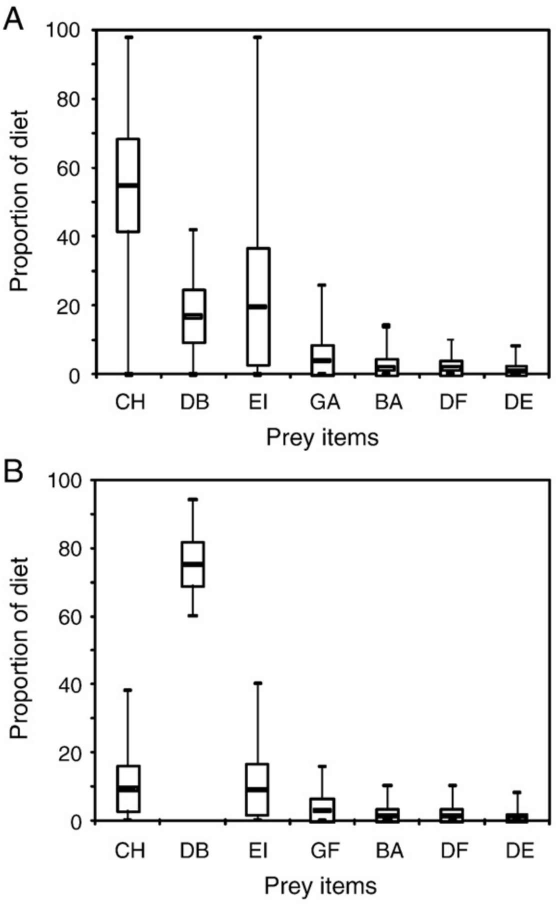

Fig. 3. Round goby stable isotope mass balance simulation output: (A) "small" round goby (<11.2 cm; see Fig. 2 A); (B) "large" round goby (≥11.2 cm). Prey codes are as defined in Table 1. Box sizes correspond to the variance of a prey measure over all possible diets. The whiskers denote the maximum and minimum possible contributions found in matching diets. The mean value is plotted as the central line.

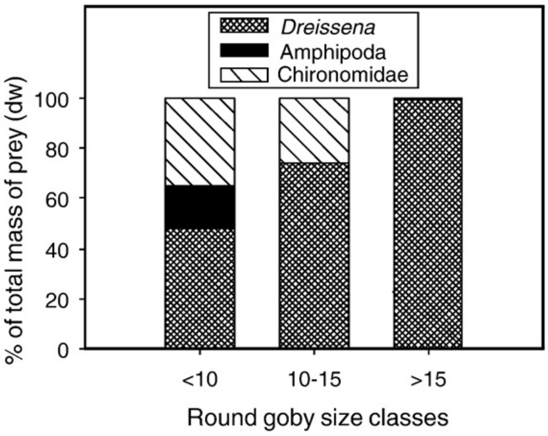

Fig. 4. Round goby stomach contents for three size classes. The data is from Barton et al. (2005) from the same fish analyzed for stable isotopes (Fig. 2).

Isotopic mass balance estimates for potential round goby predators

Keeping in mind that the mass balance simulation (parameter search) program is useful for assessing potential isotopic contributions of known dietary items (as opposed to predictive estimates of dietary composition), the results for smallmouth bass (Fig. 5A) confirm that small fish, especially round goby in both size categories, are isotopically important to this species. This is consistent with reported diets of smallmouth bass in Lake Erie. Steinhart et al. (2004) reported an increase in the growth rate of juvenile smallmouth bass in western Lake Erie following the round goby invasion; the stomachs of first-year smallmouth bass over 100 mm contained up to 100% round goby by weight. Similarly, Johnson et al. (2005) reported higher proportions of round goby in the diet of larger smallmouth bass with the mean annual dietary contribution exceeding 50% (dry weight) in 2002. While round goby appear to have been the primary prey of smallmouth bass during 2002–2003, our isotopic data and published

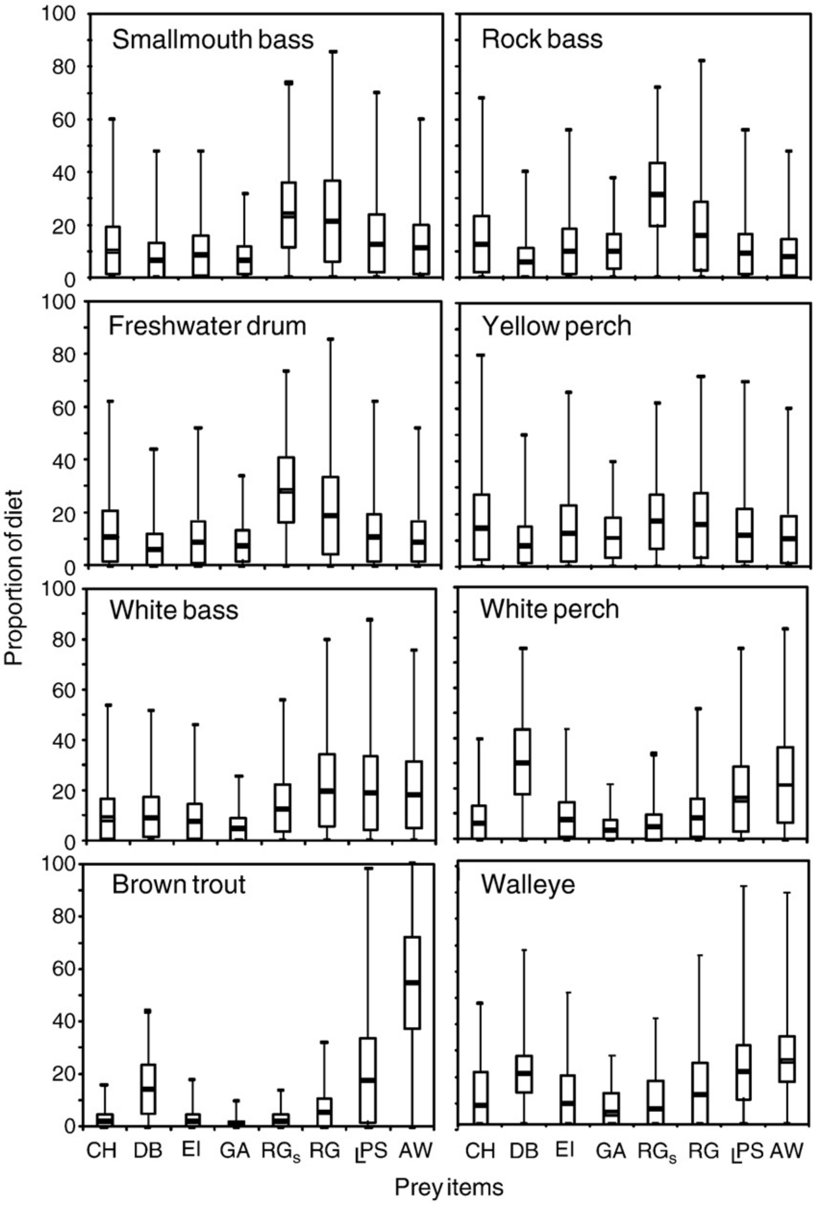

Fig. 5. Stable isotope mass balance simulation output for 8 species of fish. Prey codes are as defined in Tables 1 and 2. RG_S and RG_L indicate small and large round goby (see Table 2 and Fig. 2A). Box sizes correspond to the variance of a prey measure over all possible diets. The whiskers denote the maximum and minimum possible contributions found in matching diets. The mean value is plotted as the central line.

stomach contents indicate that other prey items, especially small fish were also important.

Mass balance simulation indicated similar diets for freshwater drum and rock bass, with fish, especially small round goby, and Chironomidae as the most important prey (Figs. 5B, C). The negligible simulated contribution from *Dreissena* in the diet of freshwater drum is surprising. After the establishment of zebra mussels in 1990 but before the appearance of round goby, the importance of *D. polymorpha* increased with fish size, reaching 60–70% of the total average volume of stomach contents in large freshwater drum (>375 mm in length) from western Lake Erie (French and Bur, 1996). Very few published data exist for rock bass diets in Lake Erie. Our data suggest that the importance of round goby as a conduit from *Dreissena* and *Echinogammarus* is not limited to smallmouth bass, but may also be important to other littoral omnivorous fish.

Yellow perch are opportunistic predators that “eat practically any available form of animal life”(Price, 1963). This was reflected by the lack of any dominant prey items in our mass balance simulation (Fig. 5D), with *Echinogammarus* and round goby being somewhat more emphasized in terms of potential isotopic contribution. Johnson et al. (2005) found that round goby contributed roughly a quarter of Lake Erie's yellow perch's total diet each year since 1998, and that benthos, zooplankton, and small fish also were important. Yellow perch became increasingly piscivorous at larger size in southern Lake Michigan, but the prey species consumed changed with availability between 1982 and 2002, as perch switched from alewife and rainbow smelt to round goby (Truemper et al., 2006). It is interesting to note that all of those prey species are NIS, emphasizing the opportunistic dietary flexibility of the yellow perch.

Results of our mass balance simulation also confirm the piscivorous diet of white bass in Lake Erie that have increasingly included round goby in recent years (Johnson et al., 2005).

Somewhat different results were obtained for three species of fish. Mass balance simulation indicated that *Dreissena* contributed about 30% to the diet important for the somatic growth of white perch, 20% to walleye and 15% to brown trout. This seems unlikely given the strong preferences for Cladocera, Chironomidae and fish reported in white perch (Couture and Watzin, 2008; Parrish and Margraf, 1994) and for alewife in brown trout (Crawford, 2001). However, the mass balance simulations for all three species appropriately indicated the importance of fish to their diets. Walleye in Lake Erie are primarily offshore piscivores whose stomachs often contain gizzard shad, shiners *Notropis* spp, rainbow smelt and juvenile yellow perch (Johnson et al., 2005). As a result, we re-ran the mass balance simulation for walleye with a new dietary list including gizzard shad, rainbow smelt, white perch and yellow perch, but the program failed to find any feasible matches. The brown trout we analyzed were collected along with alewife in gill nets in late July of 2003, an uncommon occurrence at those littoral sites (Greenwood, unpublished OMNR catch data) which suggests that the brown trout had been following their preferred prey, alewife, into littoral zones, supported by the mass balance simulation emphasizing alewife for this species. The unexpected isotopic contribution from *Dreissena* to brown trout, walleye and white perch conflicts with previous dietary studies. This pattern probably reflects direct or incidental consumption (e.g., alewife stomach contents) of pelagic zooplankton by white perch and brown trout, or small cyprinids, such as spottail or emerald shiners, to walleye. Those planktivorous prey items also should have planktivorous isotopic signatures similar to *Dreissena*. This illustrates the utility of the mass balance simulation (parameter tool) as a tool to evaluate isotopic contributions of feasible prey and identification of probable “missing” prey items.

Re-engineering trophodynamics in nearshore littoral Lake Erie

Ponto-Caspian species, e.g., round goby, *Echinogammarus* and *Dreissenia* spp. have introduced new links allowing energy flow to from detritus via *Echinogammarus* to smaller round goby, and from phytoplankton via *Dreissena* to larger round goby. Subsequently, larger fish species feeding upon small and large round goby are profiting from the new linkages (re-engineering) of the littoral food web. Round goby, within a relatively short time frame, have established themselves as keystone prey species within the littoral community of eastern Lake Erie, and are now a dominant prey item for many littoral fish.

To explain the sudden re-appearance of the nuisance green alga, *C. glomerata*, in the lower Great Lakes, it has been postulated that *Dreissenia* spp. are now acting as a ‘shunt’ of pelagic phosphorus (P) to benthic environments, leading to littoral P-enrichment, resulting in luxurious growth of *Cladophora* and the re-engineering of nearshore environments (Hecky et al., 2004). Round goby are amplifying the nearshore P shunt, accessing the energy in *Dreissena* spp. and its biodeposits (feces and pseudofeces), and trophically transferring this to long-lived littoral fish species. Juvenile smallmouth bass in Lake Erie have likely benefited from the pelagic subsidy, since this species has shown an increase in growth rate coinciding with increased round goby in their diet (Steinhart et al., 2004). The influence of round goby extend well beyond the littoral zone. In Lake Ontario, round goby have started to include *Mysis relica* in their diets (Walsh et al., 2007), and salmonids, such as lake trout *Salvelinus namaycush*, are beginning to feed upon round goby (Dietrich et al., 2006). It is clear that impacts upon energy flow between profundal, pelagic and littoral environments due to round goby in the Great Lakes are still in flux.

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