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Hemimysis anomala in Lake Ontario food webs: Stable isotope analysis of nearshore communities

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ABSTRACT

Hemimysis anomala, a littoral freshwater mysid native to the Ponto-Caspian region, is the newest invader to the Laurentian Great Lakes basin. Discovered in 2006, they have since been found in all of the Great Lakes (except Lake Superior) and have the potential to offset the dietary energy sink caused by invasive dreissenid mussels (*Dreissena bugensis* and *D. polymorpha*) in the littoral zone. We evaluated nearshore food web structure at four sites along Lake Ontario's north shore spanning a gradient of *Hemimysis* density to determine: 1) if dominant nearshore food web pathways change seasonally, and 2) whether fish are exhibiting a dietary shift towards consumption of *Hemimysis*. No *Hemimysis* were found in any of the 431 fish (alewife *Alosa pseudoharengus*, round goby *Neogobius melanostomus*, and yellow perch *Perca flavescens*) stomachs analysed. We used stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) collected from invertebrates and fish to characterise trophic linkages and fish dietary preference. Yellow perch and round goby exhibited significantly higher $\Delta\delta^{15}N$ at Bronte (high *Hemimysis* density) compared to Cobourg, Waupoos and the Bay of Quinte. $\Delta\delta^{13}C$ of alewife is more enriched at Bronte and is comparable to the $\Delta\delta^{13}C$ of *Hemimysis*. Our results suggest that *Hemimysis* are being incorporated into diets of round gobies, alewife and small yellow perch and their reliance on *Hemimysis* as a dietary component increases with *Hemimysis* density. As *Hemimysis* populations continue to establish and stabilize, fish may incorporate this species into their diets at a higher rate.

Introduction

Hemimysis anomala, the bloody red shrimp, (hereafter *Hemimysis*) were first detected in 2006 in both Lake Michigan and Lake Ontario (Pothoven et al., 2007; Kipp and Ricciardi, 2007). Since then, the extent of their distribution in the Great Lakes basin has increased dramatically (Marty et al., 2010), with the highest recorded densities found in Lake Ontario at over 1800 m^{-3} (Taraborelli et al, (2012-this issue)). Frequency of occurrence of *Hemimysis* at shore-based sampling stations in the Canadian waters of Lake Ontario increased from 65% to 90% over a 12-month period between 2008 and 2009, and their densities increased about one order of magnitude during this period suggesting the population is still expanding (Taraborelli et al. (2012-this issue)).

Although *Hemimysis* prefer shallow water near structural features (e.g. rocky substrate with deep interstices, around man-made structures including piers), they have been reported out to depths of 20 m in the Laurentian Great Lakes (LGL) (Pothoven et al., 2007). *Hemimysis* undergo diel vertical migration moving up into the water column at night, and seek refuge in the substrate during the day (Boscarino et al, (2012-this issue)). Dense swarms of *Hemimysis* have been reported both in the nearshore and at depths of ~20 m during daytime, although the factors influencing the formation of these aggregations remain unclear (Lantry et al., 2010; Minchin and Boelens, 2010). Their diet is variable, including zooplankton, algae, phytoplankton and detritus (Ketelaars et al., 1999; Marty et al., 2010). Borcherding et al. (2006) reported size-selective feeding with small *Hemimysis* (juveniles ≤3 mm) feeding on algal material and large individuals (adults >3 mm) feeding on zooplankton. However, previous stable isotope studies in the LGL suggest opportunistic omnivory regardless of size (Marty et al., 2010). *Hemimysis,* in turn, are consumed by a variety of fish species, including alewife, round goby, yellow perch and rock bass (Borcherding et al., 2007; Arbačiauskas et al., 2010; Lantry et al., 2010; Fitzsimons et al, (2012-this issue)).

Intentional introductions of *Hemimysis* in European waterways have resulted in declines in zooplankton biomass and increases in phytoplankton biomass (Ketelaars et al., 1999; Borcherding et al., 2006), potentially reducing available food energy to higher trophic levels. However, some fish species, especially *Perca* sp., became voracious predators of *Hemimysis* following their establishment in European lakes (Borcherding et al., 2007; Arbačiauskas et al., 2010). Young-of-year *Perca fluviatilis*, sampled from a lake recently invaded by *Hemimysis*, increased their reliance on *Hemimysis* from 20% to 100% of their diet in just four months (Borcherding et al., 2007). In laboratory feeding experiments, this same perch species also experienced increased lipid content

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and supernormal growth performance when *Hemimysis* portions were increased in their diets (Borcherding et al., 2007). Borcherding et al. (2007) suspect *Hemimysis* are a higher quality food item (compared to zooplankton), and the reduction in zooplankton as a result of *Hemimysis* predation provokes a heavier fish reliance on *Hemimysis* to augment their diet. In contrast, Arbačiauskas et al. (2010) concluded no growth or production advantage was evident for European perch when comparing lakes with and without introduced mysids in Lithuanian waters. While both the Borcherding et al. (2007) and Arbačiauskas et al. (2010) studies reached different conclusions regarding the effect of *Hemimysis* on fish growth and production, both groups agree that *Hemimysis* will reduce resident zooplankton density in invaded waters.

To date, there are few studies exploring the potential ecological impacts of *Hemimysis* in the LGL. *Hemimysis* utilise a variety of prey (Marty et al., 2010; L. Rudstam, Cornell University, pers. comm.), have high production and densities in Lake Ontario (Taraborelli et al, (2012-this issue)), a relatively large body size, and high energy content (Walsh et al., 2010). For these reasons, *Hemimysis* have high potential to alter energy flow in the nearshore region through dietary transfer. Using diet analysis, Lantry et al. (2010) observed the presence of *Hemimysis* in three of nine fish species (alewife, *Alosa pseudoharengus*; yellow perch, *Perca flavescens*; rock bass *Ambloplites rupestris*) from southern Lake Ontario. They found 84% frequency of occurrence of *Hemimysis* in alewife stomachs, which accounted for 46–74.5% of their dry weight diet composition, suggesting *Hemimysis* have the potential to alter feeding preference and food web pathways. While Lantry et al. (2010) did document consumption of *Hemimysis* by select fish species, their study focused on a small portion of Lake Ontario in late summer and relied on stomach content analyses, which only provide a "snapshot" of fish diet composition. Owing to the wide seasonal and spatial variation in *Hemimysis* density (Taraborelli et al, (2012-this issue)) and fish diet (Bowen, 1996), without sampling throughout the year, it is hard to determine whether the diet composition, and ultimately growth and production, of these fish will change notably in response to the presence of *Hemimysis* as a prey item.

Stable isotopes (^{13}C and ^{15}N) are commonly used to evaluate trophic interactions and food web structure (Peterson and Fry, 1987; Post, 2002; Campbell et al., 2003). The ratio of stable isotopes of nitrogen (^{15}N:^{14}N) can be used to estimate trophic position because the $\delta^{15}N$ of a consumer is typically enriched by 3.4‰ relative to its diet (Peterson and Fry, 1987; Post, 2002). In contrast, the ratio of carbon isotopes (^{13}C:^{12}C) changes at a slower rate as carbon moves though food webs (Peterson and Fry, 1987; Post, 2002) so it can be used to determine the ultimate sources of carbon, and the energy flow through a food web. In freshwater lakes, $\delta^{13}C$ values can help differentiate between pelagic (offshore) and littoral (near shore) sources of energy (Post, 2002) as $\delta^{13}C$ of the base of the littoral food web is more enriched in ^{13}C (less negative $\delta^{13}C$) relative to the base of pelagic food webs (France, 1995).

Hemimysis is abundant in Lake Ontario, produces multiple generations (Taraborelli et al, (2012-this issue)), and has a high feeding rate known to affect zooplankton production (Ketelaars et al., 1999; Borcherding et al., 2006). It could therefore dramatically change the local food webs of invaded lakes, becoming an important link connecting higher trophic levels (fish) to primary and secondary production. Using $\delta^{13}C$ and $\delta^{15}N$, this study is the first to evaluate nearshore Great Lakes food webs across a gradient of *Hemimysis* density to determine: 1) if dominant food web pathways change seasonally, and 2) whether fish are exhibiting a dietary shift towards the consumption of *Hemimysis*.

Methods

Four locations in Lake Ontario spanning a density range of *Hemimysis* (Fig. 1) were sampled. These sites include Bronte (43º23.570′N, 79º42.348 W; 688 ± 1553 *Hemimysis*·m^{-3}), Cobourg (43º57.137′N, 78º09.872 W; 34 ± 46 *Hemimysis*·m^{-3}), Waupoos (44º00.046′N, 76º59.485 W; 7.2 ± 14 *Hemimysis*·m^{-3}), and the upper Bay of Quinte (44º09.484′N, 77º10.037 W; no *Hemimysis* detected). Each site contained a pier or harbour structure providing shore-based access to sample *Hemimysis* (Taraborelli et al, (2012-this issue)). Each site was sampled in the spring (May–Jun), summer (Jul–Aug) and fall (Sept–Oct) seasons in 2009.

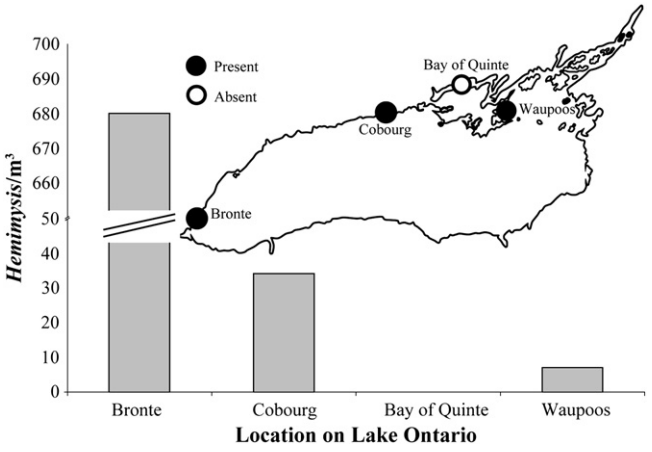

Fig. 1. Map of Lake Ontario showing the four sites selected for the current study associated with 2009 annual *Hemimysis anomala* densities (Taraborelli et al, (2012-this issue)).

Sample collection

Hemimysis were collected at night using both vertical plankton net hauls (0.75 m diameter, 400 μm mesh size) and sweep nets (250 μm mesh size) at standardized locations at each site. *Hemimysis* were transported to the lab in filtered lake water where they were separated from other taxa, rinsed in distilled water, and stored at −80 ºC prior to stable isotope analyses.

Other invertebrates known to represent common fish prey (T. Johnson, unpubl. data) were sampled in the vicinity of *Hemimysis* collections. Bulk zooplankton samples were collected using vertical tows of a 63 μm mesh net. Amphipods, chironomids, oligochaetes, and dreissenid mussels (*Dreissena bugensis* and *D. polymorpha*) were collected by scraping rocks and piers, and through the use of ponars on local sediment. Dreissenid mussels were shucked prior to analysis. All invertebrate samples were transported back to the lab on ice where they were rinsed in distilled water and stored at −80 ºC prior to stable isotope analyses.

Three common fish species representing different feeding behaviours were chosen to evaluate potential trophic shifts related to *Hemimysis*. Species included yellow perch, round goby (*Neogobius melanostomus*), and alewife. Yellow perch are native to the LGL where juveniles (<150 mm size class) feed primarily on plankton and small invertebrates in the nearshore and adults (>150 mm size class) feed on larger invertebrates and fish in near shore habitats. We suspect yellow perch will feed on *Hemimysis* at crepuscular periods when *Hemimysis* are entering and leaving the refuge provided by complex substrates. Round gobies are invasive opportunistic benthivores from the native range of *Hemimysis* and prefer rocky/complex substrates. Owing to the similarity of preferred habitat, we expect that round gobies would opportunistically feed on *Hemimysis*. Lastly, alewife are a non-native pelagic planktivore that are efficient predators of *Mysis diluviana* in the LGL, and we suspect will opportunistically feed on *Hemimysis*.

Fish were collected at each site using a variety of gears (fyke nets, gillnets, trapnets, beach seines, and electrofishing). All fish samples came from gear within 100 m of known concentrations of *Hemimysis*. Three individual small and three individual large fish were targeted for each species at each site and in each season. Stomachs were removed from the fish and preserved in 70% ethanol for diet content

analysis. A skinless, boneless, dorsal muscle sample (>3 g) was removed and stored at −80 ºC prior to stable isotope analysis.

Diet analysis

Stomachs were removed from up to 30 fish per species per size class within each site and season. Before dissecting, the stomach was placed in a graduated cylinder to determine the volume displaced by the full stomach. Stomach contents were then removed and the empty volume determined. The volume of stomach contents was determined by subtraction. Stomach contents were sorted to the lowest taxonomic level (Thorp and Covich, 2001). Once sorted, a proportion of the total gut content was estimated for each taxonomic group and multiplied by the total gut content volume to obtain a volumetric estimate of the consumed prey.

Stable isotope analyses

All samples were freeze dried in cryotubes, homogenized with a glass rod, and analysed for stable isotopes at the University of Windsor using a Delta V IRMS (Thermo Electron Corporation, Waltham, MA, USA) equipped with an elemental analyzer (Costech, Santa Clarita, CA, USA). Lipid extraction was not performed on fish tissues as the muscle C:N ratio fell below 3.5 for all samples and were consistent for the entire sample set (see Post et al., 2007). NIST Standard 8414 and red tilapia muscle, along with three glycine reference standards were analysed every 12th sample, to compensate for machine drift and for quantification of $\delta^{13}C$, $\delta^{15}N$, % C and %N; every tenth sample was run in triplicate.

Statistical analyses

Although all four sites are located within Lake Ontario, there are environmental differences between the sites which may shift the entire food web, complicating among site comparison. Gastropods and filter feeding bivalves (i.e. dreissenid mussels) integrate these inherent differences in their tissues, and thus their stable isotope values can be used to standardize the isotopic values of other organisms within each site, facilitating comparisons among sites (Post, 2002; Campbell et al., 2003). Baseline comparisons using dreissenid mussels were conducted using analysis of variance (ANOVA) to test for seasonal and site interactions as well as individual seasonal and site effects in $\delta^{15}N$ and $\delta^{13}C$ of the samples (Cabana and Rasmussen, 1996; Vander Zanden et al., 1999; Campbell et al., 2003). Effect terms were systematically removed (starting with the interaction term) and Akaike's Information Criterion (corrected for small sample sizes; AICc) was used to determine the most parsimonious model describing the data. Site and seasonal standardization was then accomplished by subtracting the isotopic values of the mussels from the isotopic values of invertebrates and fish to create $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$:

$$\Delta\delta^{15}N = \delta^{15}N_{IorF} - \delta^{15}N_M \quad (1)$$

$$\Delta\delta^{13}C = \delta^{13}C_{IorF} - \delta^{13}C_M \quad (2)$$

where $\delta^{15}N_{I\ or\ F}$ and $\delta^{13}C_{I\ or\ F}$ are the $\delta^{15}N$ and $\delta^{13}C$ values of the individual invertebrate or fish sample, $\delta^{15}N_M$ and $\delta^{13}C_M$ is the $\delta^{15}N$ and $\delta^{13}C_M$ of the mussels.

ANOVA was used to test for seasonal and site effects on *Hemimysis* $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$. The trophic enrichment of fish species consuming *Hemimysis* will be relative to the *Hemimysis* that they consume. However, tissue turnover rates of invertebrates are higher than those of fish resulting in more pronounced seasonal changes in invertebrate isotopic values (Fry and Arnold, 1982; MacAvoy et al., 2001; Suring and Wing, 2009). By pooling *Hemimysis* $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values across seasons for each site, a more generalized *Hemimysis* isotopic value was generated for each site. Fish $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ within each season was compared to the mean *Hemimysis* $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ per site. Therefore, while significant seasonal effects were detected in *Hemimysis* $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$, these were not considered when interpreting $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ of the fish species.

Analysis of covariance (ANCOVA) was used to explore body size (ontogenetic) effects on $\delta^{15}N$ and $\delta^{13}C$ within the three fish species. If ontogenetic differences were found, the size classes remained separate; otherwise data were combined prior to subsequent analysis. Three-way factorial ANOVAs were used to determine whether there were significant seasonal, site and species effects on $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$. The three-way interaction was significant, so ANOVA was used to test for seasonal differences in $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ for each fish species (large yellow perch, small yellow perch, alewife and round goby) within each site. Lastly, between site variation was tested as an effect on $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ for each fish species using type III ANOVAs.

All statistical analyses were conducted using R statistical software version 2.11.1 and its base packages (R Development Core Team, 2010) as well as the "multcomp" and "car" packages (Hothorn et al., 2008; Fox and Weisberg, 2010).

Results

Establishing baseline

We found no significant season × site interaction on $\delta^{15}N$ of the mussels ($p = 0.184$). Using AICc and systematically removing each term, the most parsimonious model describing the data excluded the season × site interaction, seasonal and site effects. There was no significant difference in the explanatory power of the original interaction model and the reduced model with all terms removed ($p = 0.232$). As a result, $\delta^{15}N$ values were pooled across the seasons and sites and averaged (7.43 ± 1.57, $n = 55$) to obtain the mussel baseline-adjusted value for $\delta^{15}N$ of *Hemimysis* and fish ($\delta^{15}N_M$ from Eq. 1).

With regard to the $\delta^{13}C$ values for the mussels, we found a significant season × site interaction ($p = 0.019$) indicating $\delta^{13}C$ values for mussels vary significantly by season across sites in which they were collected. We tested seasonal effects on $\delta^{13}C$ within each site and found significant seasonal effects at Bronte ($p = 0.002$), but not at the other sites. Tukey post-hoc comparisons revealed significant differences between spring and fall ($p = 0.026$) and between summer and fall ($p = 0.002$) in $\delta^{13}C$ of mussels from Bronte. As a result, $\delta^{13}C$ values were pooled across the seasons for the Bay of Quinte, Waupoos and Cobourg sites and pooled for the spring and summer seasons at Bronte, with the fall Bronte samples analysed separately (Table 1).

The significant seasonal effect at Bronte prompted us to examine site effects in two scenarios: 1) seasonally pooled Bay of Quinte, Waupoos, Cobourg and Bronte (Bronte spring and summer) data and 2) seasonally pooled Bay of Quinte, Waupoos, Cobourg and Bronte (Bronte fall) data. In the first scenario, we found significant site effects ($p < 0.001$) for mussel $\delta^{13}C$ values. Tukey post-hoc comparisons revealed significant differences between the Bay of Quinte and the three other sites (Waupoos, $p < 0.001$; Cobourg, $p = 0.001$; Bronte spring and summer, $p < 0.001$) and between Waupoos and Cobourg ($p = 0.008$). In the second scenario, we again found significant site effects ($p < 0.001$). Tukey post-hoc comparisons again revealed significant differences between the Bay of Quinte and the three other sites (Waupoos, Cobourg and Bronte fall; $p < 0.001$, $p = 0.004$, $p < 0.001$, respectively), and between Bronte fall and Cobourg ($p < 0.001$). Mussel baseline $\delta^{13}C$ adjustments to *Hemimysis* and fish $\delta^{13}C$ values were based on the seasonal pooling above and on a per site basis (Eq. (2)). Baseline adjustment values are summarized in Table 1.

Hemimysis

We tested seasonal and site effects on the calculated $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values for *Hemimysis*. Seasonal effects on *Hemimysis* $\Delta\delta^{15}N$

Table 1
Average $\delta^{15}N$ and $\delta^{13}C$ values for *D. polymorpha* (mean ± SD) at *Hemimysis* collection sites in Lake Ontario in 2009. Seasonal and site effects were not significant for $\delta^{15}N$ values. "All" refers to an averaged $\delta^{13}C$ value across all seasons as seasonal effects were not significant for these sites. Fall $\delta^{13}C$ of Bronte zebra mussels were found to be significantly different compared to spring and summer zebra mussels. Sample sizes are found in parentheses with the specified seasonal pooling.

		Stable isotope values (mean ± SD)	
Site	Season (n)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Bay of Quinte	All (9)	7.78 ± 2.69	−31.01 ± 1.75
Waupoos	All (18)	7.64 ± 0.63	−23.49 ± 3.44
Cobourg	All (12)	6.63 ± 2.07	−26.59 ± 1.88
Bronte	Spring and summer (10)	7.92 ± 0.34	−25.07 ± 1.11
Bronte	Fall (6)	7.06 ± 1.19	−20.13 ± 3.21

and $\Delta\delta^{13}C$ values were found to be significant ($p = 0.008$ and $p < 0.001$, respectively), however, due to differences in tissue turnover rates between invertebrates and fish, *Hemimysis* $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values were pooled within sites regardless of the season they were collected to somewhat compensate for tissue turnover rate differences (MacAvoy et al., 2001). Seasonal baseline-adjusted *Hemimysis* $\delta^{15}N$ and $\delta^{13}C$ are presented in Table 2.

Hemimysis $\Delta\delta^{15}N$ values were not significantly different between sites ($p = 0.282$), producing an averaged $\Delta\delta^{15}N$ of 3.56 ± 1.76 ($n = 113$) for all sites. *Hemimysis* $\Delta\delta^{13}C$ values were significantly different between sites ($p < 0.001$), so they were treated separately in subsequent analyses.

Within each site *Hemimysis* $\Delta\delta^{15}N$ values were significantly higher than benthos $\Delta\delta^{15}N$ values ($p < 0.001$, Fig. 2). *Hemimysis* $\Delta\delta^{15}N$ values were significantly higher than zooplankton at Bronte ($p < 0.001$), but not significantly different at Waupoos ($p = 0.12$) (Fig. 2a and Fig. 2c, respectively). Bronte *Hemimysis* $\Delta\delta^{13}C$ values were significantly depleted relative to the benthos values ($p < 0.001$) and were significantly enriched compared to zooplankton ($p < 0.001$). *Hemimysis* $\Delta\delta^{13}C$ values from Cobourg and Waupoos were not significantly different from benthos values ($p = 0.66$ and $p = 0.46$, respectively), but *Hemimysis* $\Delta\delta^{13}C$ values from Waupoos were significantly enriched compared to zooplankton ($p < 0.001$) (Figs. 2(b, c).

Table 2
Seasonal averaged $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values for *H. anomala* (mean ± SD) at Waupoos, Cobourg and Bronte, Lake Ontario in 2009. Site effect was not significant for $\Delta\delta^{15}N$ but was significant for $\Delta\delta^{13}C$ so seasonal comparisons within each site are presented in this Table. Post-hoc Tukey comparisons tested seasonal effects, which were considered significant if $p < 0.05$. Sample sizes are found in parentheses.

		Stable isotope values (mean ± SD)	
Site	Season (n)	$\Delta\delta^{15}N$ (‰)	$\Delta\delta^{13}C$ (‰)
	Spring	Insuf. material	Insuf. Material
Waupoos	Summer (9)	2.79 ± 0.86 A	2.68 ± 1.2 A
	Fall (5)	3.84 ± 0.48 B	4.32 ± 1.47 B
Cobourg	Spring (5)	3.95 ± 1.86 A	5.68 ± 0.49 A
	Summer (4)	1.66 ± 0.48 A	3.90 ± 0.95 B
	Fall (1)	2.76 A	7.34 A
Bronte	Spring (27)	4.18 ± 1.79 A	2.39 ± 0.71 A
	Summer (35)	3.18 ± 2.33 A	3.09 ± 1.75 A
	Fall (27)	3.87 ± 0.79 A	−0.68 ± 1.30 B

Fish

We found no physical evidence of *Hemimysis* in the stomachs of fishes from any of the sites: alewife (Bronte, n = 30; Cobourg, n = 71; and Waupoos, n = 19; Bay of Quinte, none collected), large yellow perch (Bronte, n = 21; Cobourg, n = 37; and Waupoos, n = 6; Bay of Quinte, n = 6), small yellow perch (Bronte, n = 5; Cobourg, n = 11; Waupoos, n = 67; Bay of Quinte, n = 17) and round gobies (Bronte, n = 51; Cobourg, n = 25; and Waupoos, n = 64; Bay of Quinte, n = 1). Although no *Hemimysis* were found in any fish stomachs, stable isotopes in fish muscle tissue represent the integration of prey items over a longer time period compared to diet analysis. We examined the stable isotopes of our fish species to determine whether patterns existed consistent with the consumption of *Hemimysis*.

ANCOVAs used to detect fish size (total length in mm) effects on ^{15}N and ^{13}C were non-significant for alewife and round goby so size classes for these two species were pooled. However, fish size was a significant effect for yellow perch ^{15}N and ^{13}C values ($p < 0.001$ for both) so the small and large size classes remained throughout the analysis for this species. We tested seasonal variation of each fish species (large and small yellow perch, alewife and round goby) within each site (Table 3). Although some seasonal effects were statistically significant, isotopic differences between the seasonal means were small (<5% of the mean for $\delta^{15}N$ and <12% of the mean for $\delta^{13}C$) and therefore unlikely to have ecological significance. We therefore pooled our samples across seasons within sites to increase sample sizes allowing for more robust testing of the effects of *Hemimysis* on the ecosystem. Sample sizes for these comparisons can be found in Table 3.

Large yellow perch (YP) $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values were significantly different between sites ($p < 0.001$ for both isotopes). Post-hoc Tukey comparisons showed all three sites containing *Hemimysis* had significantly higher $\Delta\delta^{15}N$ values compared to the Bay of Quinte, where no *Hemimysis* have been detected (Fig. 3a). Bronte, the high *Hemimysis* density site, had significantly higher $\Delta\delta^{15}N$ values compared to Cobourg and Waupoos, the medium and low *Hemimysis* density sites (respectively). $\Delta\delta^{13}C$ values at the low *Hemimysis* density site, Waupoos, were significantly higher than Cobourg, which was significantly higher than both the Bay of Quinte and Bronte (Fig. 3e).

$\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values of small YP were also significantly different between sites ($p < 0.001$ for both isotopes). Post-hoc Tukey comparisons revealed that our high *Hemimysis* density site, Bronte, had significantly higher $\Delta\delta^{15}N$ values compared to the other three sites (Fig. 3b). $\Delta\delta^{15}N$ values of small YP from Waupoos, our low *Hemimysis* density site were significantly higher than both Cobourg and the Bay of Quinte. $\Delta\delta^{13}C$ values from Cobourg, our medium *Hemimysis* density site were higher than our other three sites (Fig. 3f). Waupoos $\Delta\delta^{13}C$ values were significantly higher than both Bronte and the Bay of Quinte (Fig. 3f).

Alewife $\Delta\delta^{15}N$ values were not significantly different across sites ($p = 0.150$, Fig. 3c) but $\Delta\delta^{13}C$ values were significantly different between sites ($p < 0.001$). Post-hoc Tukey comparisons on $\Delta\delta^{13}C$ values showed Waupoos, the low *Hemimysis* density site, was significantly lower than the other three sites (Fig. 3g).

Round goby $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values were significantly different between sites ($p < 0.001$for both isotopes). Post-hoc Tukey comparisons showed Bronte, our high *Hemimysis* density site having significantly higher $\Delta\delta^{15}N$ values compared to the other three sites (Fig. 3d). Round goby $\Delta\delta^{15}N$ values from Cobourg (medium *Hemimysis* density) were significantly lower than the other three study sites (Fig. 3d). Round goby $\Delta\delta^{13}C$ values from Bronte, were significantly more depleted compared to the other three sites. While Cobourg round gobies were significantly enriched compared to Waupoos, round goby $\Delta\delta^{13}C$ values from both of these sites were not significantly different from the Bay of Quinte (*Hemimysis* not detected) (Fig. 3h). A summary of the sample sizes used in the above statistical tests can be found in Fig. 3.

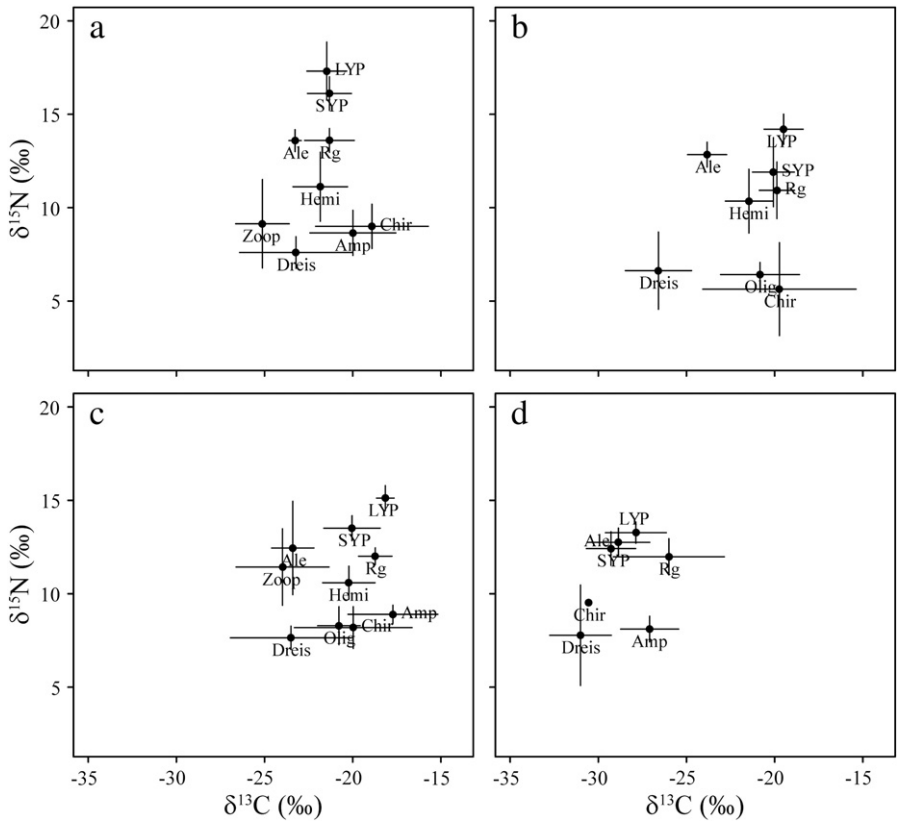

Fig. 2. Food web $\delta^{15}N$ and $\delta^{13}C$ biplots for (a) Bronte, (b) Cobourg, (c) Waupoos and (d) Bay of Quinte. Our three priority fish species (large and small yellow perch (LYP and SYP, respectively), alewife (Ale), and round goby (Rg)) are represented as well as common prey taxa (chironomids (Chir), dreissenid mussels (Dreis), amphipods (Amp) and oligochaetes (Olig)). Mean $\delta^{15}N$ and $\delta^{13}C$ values are presented with error bars representing one standard error from the mean.

Discussion

Fish isotopic values are consistent with expected isotopic shifts reflecting the consumption of *Hemimysis* with the most pronounced effects observed at Bronte, the site with the highest *Hemimysis* density. Increased fish $\Delta\delta^{15}N$ values suggest the insertion of *Hemimysis* into the food web results in an increase in food chain length. These results are most evident at the Bronte site, implying higher *Hemimysis* densities result in greater food chain lengthening. Fish $\Delta\delta^{13}C$ values are comparable to *Hemimysis* at the Bronte site, and intermediate to traditional prey and *Hemimysis* at the Cobourg and Waupoos sites where *Hemimysis* densities are lower. Our stable isotope data for yellow perch, alewife and round goby from the Bronte site are most consistent with expected isotopic shifts resulting from the consumption of *Hemimysis*.

Stable isotopes provided evidence that fish are utilising *Hemimysis* as prey while conventional visual gut content analyses did not. Previous studies (Borcherding et al., 2007; Lantry et al., 2010) and our own unpublished results for a larger data set have found *Hemimysis* in fish stomachs. However, small-bodied taxa such as *Hemimysis* digest rapidly making detection by visual means more difficult with increasing time post-ingestion (Kionka and Windell, 1972; Legler et al., 2010). Laboratory digestion rate experiments using yellow perch have shown *Hemimysis* to be fully digested within 2–4 hours post-ingestion at 14–24 ºC (T. Johnson, unpubl. data). Borcherding et al. (2007) fished their nets for only two hours, while our nets were fished overnight (~16 h) increasing time post-ingestion and reducing our ability to detect physical remains. Stable isotopes are a more integrative tool recording assimilated dietary items, and are therefore not subject to problems with differential digestion and visual detection.

Examining the isotopic values of common prey items for our three fish species helps illustrate the expected isotopic shift that would occur if *Hemimysis* were incorporated into fish diets. If fish are consuming *Hemimysis* their isotopic values should shift toward the value of *Hemimysis* (Peterson and Fry, 1987). Relative to benthos, *Hemimysis* $\Delta\delta^{15}N$ value is enriched while their $\Delta\delta^{13}C$ is comparable (Fig. 2). Therefore, if a benthivorous fish consumes *Hemimysis*, their $\Delta\delta^{13}C$ value will remain relatively unchanged but their $\Delta\delta^{15}N$ value should increase. *Hemimysis* $\Delta\delta^{15}N$ values are comparable to zooplankton, but their $\Delta\delta^{13}C$ is more enriched (Fig. 2). Thus, a planktivorous fish consuming *Hemimysis* will exhibit an increased $\Delta\delta^{13}C$ signifying a more littoral carbon source, while their $\Delta\delta^{15}N$ will be relatively unchanged (Fig. 2).

Variability in *Hemimysis* $\delta^{13}C$ values has been attributed to a trophic feeding ontogeny (Borcherding et al., 2006), but all *Hemimysis* analysed in our study were adults suggesting observed variability is a result of the variation in dietary selection and / or temporal prey source values (Marty et al., 2010). Variation observed may correspond to site-specific changes in seasonal food availability as productivity in Lake Ontario changes seasonally and can vary among sites (Schelske and Hodell, 1991). More fine-scale temporal *Hemimysis* sampling over the year is needed to determine whether seasonal variation in food sources is driving the observed variation in *Hemimysis* $\delta^{13}C$ values.

As an obligate planktivore, we expected alewife captured in the vicinity of known concentrations of *Hemimysis* to exhibit enrichment in $\Delta\delta^{13}C$ as their reliance on pelagic plankton was reduced. Such a shift was evident at the high *Hemimysis* density Bronte site, but the $\Delta\delta^{13}C$ for alewife at the Waupoos and Cobourg sites remained depleted relative to *Hemimysis* suggesting they continue to rely on pelagic zooplankton prey. Lantry et al. (2010) reported the presence of *Hemimysis* in 84% of alewife stomachs captured in southern Lake Ontario near Oswego, and a known high density of *Hemimysis*. We did not expect $\Delta\delta^{15}N$ to be very informative for alewife as zooplankton and *Hemimysis* do not differ substantially for this isotope.

Table 3
Summary of type III ANOVAs testing for seasonal effects on $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ within a species of fish (large and small yellow perch, alewife and round goby) and within a site (Bronte, Cobourg, Waupoos and Bay of Quinte). NA signifies seasons when that fish species was not caught, and the letters denote seasonal differences within a taxa and site. All differences were considered significant if $p<0.05$. Sample size is indicated by the number within parentheses.

		Stable isotope values (mean ± SD (n))					
Site	Species	$\Delta\delta^{15}N$ (‰)			$\Delta\delta^{13}C$ (‰)		
		Spring	Summer	Fall	Spring	Summer	Fall
Bronte	Lg. yellow perch	NA	10.33 ± 1.93 A(2)	9.01 A (1)	NA	3.44 ± 1.54 A (2)	−1.01 A (1)
	Sm. yellow perch	8.93 A (1)	7.91 A (1)	8.94 ± 1.29 A (2)	5.50 A (1)	2.54 A (1)	−1.45 ± 0.17 B (2)
	Round goby	6.50 ± 0.35 A (8)c	6.17 ± 0.76 A(15)	5.74 ± 0.34 A (6)	0.67 ± 0.55 A (8)	3.54 ± 1.88 A (15)	−0.57 ± 0.47 B (6)
	Alewife	5.72 ± 0.68 A (3)	6.30 ± 0.53 A (10)	NA	1.55 ± 0.40 A (3)	1.88 ± 0.32 A (10)	NA
Cobourg	Lg. yellow perch	7.00 ± 0.42 A (5)	6.76 ± 0.97 A (7)	5.67 A (1)	7.50 ± 0.65 A (5)	6.69 ± 1.32 A (7)	7.94 A (1)
	Sm. yellow perch	6.17 ± 0.15 A (5)	3.05 ± 1.22 B (5)	NA	7.31 ± 0.50 A (5)	5.86 ± 1.22 B (5)	NA
	Round goby	4.91 ± 0.41 A (6)	2.73 ± 1.05 B (7)	3.00 ± 1.81 A (6)	7.04 ± 0.81 A (6)	5.87 ± 0.80 B (7)	7.17 ± 0.93 AB (6)
	Alewife	5.86 ± 0.39 A (6)	5.48 ± 0.55 AB (9)	4.73 ± 0.63 B (5)	3.25 ± 1.05 A (6)	2.85 ± 0.45 A (9)	2.02 ± 1.75 A (5)
Waupoos	Lg. yellow perch	8.05 ± 0.71 A (13)	7.22 ± 0.33 B (8)	7.45 ± 0.41 AB (5)	5.63 ± 0.23 A (13)	5.13 ± 0.55B (8)	4.92 ± 0.51B (5)
	Sm. yellow perch	6.62 ± 0.41 A (8)	5.75 ± 0.64 B (14)	6.27 ± 0.09 AB (2)	2.29 ± 1.14 A (8)	3.83 ± 1.49 B (14)	5.47 ± 0.15 B (2)
	Round goby	4.88 ± 0.36 A (6)	4.41 ± 0.41 B (24)	4.92 ± 0.36 A (7)	4.77 ± 1.31 AB (6)	4.49 ± 0.78 A (24)	5.74 ± 0.55 B (7)
	Alewife	6.22 ± 0.44 A (9)	1.86 ± 3.25 B (4)	5.98 ± 0.30 A (2)	−0.32 ± 0.64 A (9)	1.65 ± 0.91 B (4)	−1.16 ± 0.09 A (2)
Bay of Quinte	Lg. yellow perch	6.19 AB (1)	5.39 ± 0.45 A (8)	6.25 ± 0.32 B (8)	4.30 A (1)	1.58 ± 0.66 B (8)	4.55 ± 1.09 A (8)
	Sm. yellow perch	3.91 ± 0.56 A (5)	5.27 ± 0.59 B (31)	4.45 ± 1.52 AB (6)	3.41 ± 0.36 A (5)	0.94 ± 1.20 B (31)	4.43 ± 2.56 A (6)
	Round goby	3.28 ± 0.01 A (2)	4.39 ± 0.31 B (3)	5.56 ± 0.09 C (3)	3.61 ± 0.21 A (2)	8.72 ± 0.72 B (3)	2.24 ± 0.14 A (3)
	Alewife	NA	5.32 ± 0.77(19)	NA	NA	2.15 ± 1.78(19)	NA

Yellow perch undergo a trophic ontogeny, relying on planktonic prey as juveniles and incorporating larger benthic invertebrates and eventually fish as they grow. As such, with increasing *Hemimysis* density, patterns along the $\Delta\delta^{13}C$ axis should be stronger than $\Delta\delta^{15}N$ for small YP as we suspect *Hemimysis* may replace zooplankton (^{13}C enriched vs ^{13}C depleted) in their diet. Large YP are littoral omnivores and may substitute benthic organisms for *Hemimysis* (^{15}N depleted vs ^{15}N enriched) or indirectly incorporate *Hemimysis* into their diets through prey fish. Combined isotopic values will provide the most complete interpretation for both size classes of perch. The $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values were lower for small than large yellow perch reflecting the aforementioned trophic ontogeny for this species. Large and small YP $\Delta\delta^{15}N$ were lowest in the Bay of Quinte, higher at Waupoos and Cobourg, and highest at Bronte, following a gradient in *Hemimysis* density and suggesting *Hemimysis* contribute to an overall lengthening of the food chain (Figs. 3a and b). The variability in small YP $\Delta\delta^{13}C$ suggests a high degree of omnivory in this species (Fig. 3f). Elevated $\Delta\delta^{15}N$ and overlap of $\Delta\delta^{13}C$ between small YP and *Hemimysis*, especially at Bronte and Waupoos sites suggest small YP are incorporating *Hemimysis* into their diets (Figs. 3b and f). Large YP $\Delta\delta^{15}N$ from Waupoos and Cobourg exhibited trophic enrichment close to what would be expected if feeding on *Hemimysis* (Fig. 3a), but their $\Delta\delta^{13}C$ values are enriched relative to *Hemimysis* suggesting large YP from these sites consume prey of a similar trophic position to *Hemimysis* but from a more littoral source (Fig. 3e), like round goby (*cf* Post, 2002). Large YP from Bronte have a much higher $\Delta\delta^{15}N$ than the other sites, which would be consistent with a higher level of piscivory (Grey, 2001). There is considerable overlap between $\Delta\delta^{13}C$ values for large YP and *Hemimysis* at Bronte, but also high variability in values among individuals, suggesting these perch are relying on multiple carbon sources.

Round goby are littoral benthivores and therefore we expected an increase in $\Delta\delta^{15}N$ if they increased their reliance on *Hemimysis* as prey as *Hemimysis* are elevated in $\delta^{15}N$ relative to benthic organisms. We would not expect changes in $\Delta\delta^{13}C$ as *Hemimysis* show considerable overlap with benthos. At the high *Hemimysis* density Bronte site, $\Delta\delta^{15}N$ values for round gobies was close to the expected 3.4‰ trophic enrichment (Post, 2002), but shifts at the other sites were not suggestive of predation on *Hemimysis* by round goby. Behavioural adaptations of *Hemimysis* minimise predation success for round gobies (Fitzsimons et al. (2012-this issue)), which combined with the lower *Hemimysis* density at Cobourg and Waupoos support the observation of limited isotopic shifts for round gobies at these sites.

Comparing fish $\Delta\delta^{15}N$ across sites revealed highest levels at Bronte, the site with the highest density of *Hemimysis*. Standardizing the isotopic values across our sites to a common baseline (dreissenid mussels) removes anthropogenic and environmental effects on stable isotope data (Post, 2002; Campbell et al., 2003), suggesting the observed patterns in $\Delta\delta^{15}N$ as *Hemimysis* density increases, may be a result of an increasing

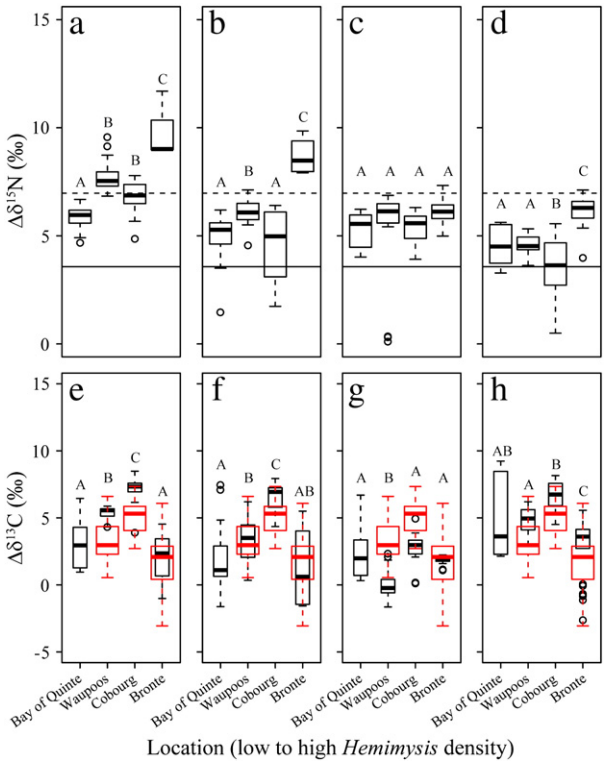

Fig. 3. $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ of large (a and e, respectively; Bay of Quinte, n = 17; Waupoos, n = 26; Cobourg, n = 13; Bronte, n = 3) and small (b and f, respectively; Bay of Quinte, n = 42; Waupoos, n = 24; Cobourg, n = 10; Bronte, n = 4) yellow perch (*P. flavescens*), alewife (*A.pseudoharengus*) (c and g, respectively; Bay of Quinte, n = 19; Waupoos, n = 15; Cobourg, n = 20; Bronte, n = 13) and round goby (*N. melanostomus*) (d and h, respectively; Bay of Quinte, n = 8; Waupoos, n = 37; Cobourg, n = 19; Bronte, n = 29) relative to the $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ of *Hemimysis anomala* (solid line and red boxplots, respectively). The dashed lines in (a), (b), (c) and (d) represent a 3.4‰ ^{15}N trophic enrichment relative to *Hemimysis*. The letters above the boxplots indicate significant differences (where $p<0.05$) between sites from post-hoc Tukey tests.

reliance on *Hemimysis* in fish diets. Piscivory is likely partially responsible for high large YP $\Delta\delta^{15}$N values, however large YP $\Delta\delta^{15}$N still increases as *Hemimysis* density increases across sites, with the highest values at Bronte. While piscivory may contribute to the elevated $\Delta\delta^{15}$N values in large YP, small YP do not rely heavily on fish in their diet and alewife and round goby rarely consume fish (Scott and Crossman, 1998; Corkum et al., 2004). Therefore, it is unlikely that piscivory is causing the elevated $\Delta\delta^{15}$N in alewife, round goby and small YP at Bronte. Regardless of the strong relationship between $\Delta\delta^{15}$N and *Hemimysis* density across sites, we cannot conclusively state that *Hemimysis* have been incorporated into fish diets. Despite intensive sampling our study could not capture every organism contributing to these four food webs, so it is possible that other organisms not captured in this study may contribute to the patterns in δ^{15}N and δ^{13}C observed in the three fish species across the *Hemimysis* gradient.

By examining the isotopic patterns of three species of fishes representing different feeding behaviours across a gradient of *Hemimysis* density we were able to provide a more robust picture of the likelihood of *Hemimysis* to alter nearshore food web pathways. Planktivorous fishes, such as alewife, that have a documented history of consuming mysids in the Great Lakes (Stewart et al., 2009) showed the greatest isotopic shift in our study consistent with the consumption of *Hemimysis*. As *Hemimysis* density increases, our isotopic data suggest *Hemimysis* are playing a larger role in supporting higher trophic levels. At sites with an intermediate density of *Hemimysis* (Cobourg and Waupoos), the observed isotopic shifts were less pronounced compared to Bronte (high *Hemimysis* density). However, as a recent invader to Lake Ontario (Kipp and Ricciardi, 2007), it is possible that fish species have not fully adapted their feeding to the presence of this new littoral food source. As *Hemimysis* populations continue to expand in both range and density, we predict they will become more important in the diets of resident fishes. While stable isotopes provide an integrative picture of feeding pathways and trophic position, additional studies using conventional diet analyses and incorporating other taxa may help solidify energy flow pathways in the food web. This will aid future studies examining potential changes in fish bioenergetics due to the incorporation of *Hemimysis* into their diets.

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