Spatial and seasonal variability in the diet of round goby (*Neogobius melanostomus*): stable isotopes indicate that stomach contents overestimate the importance of dreissenids

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Abstract: Our results provide new information that diet, carbon source and trophic position of an invasive fish species, round goby (*Neogobius melanostomus*), varies seasonally, spatially and with body size in littoral habitats of Lake Ontario. Based on stomach contents and stable isotopes, round goby fed at a higher trophic position in the cooler, less productive Kingston Basin relative to the Bay of Quinte. Bay of Quinte round goby were more reliant on terrestrial carbon, whereas littoral carbon dominated in the Kingston Basin. Although stomach contents suggested dreissenids were the dominant prey item of round goby, stable isotope mixing models estimated that dreissenids were never >39% and 11% of the diet in Bay of Quinte and Kingston Basin, respectively. Stable isotopes indicated amphipods, chironomids and cladocerans were the most important prey, and were at times common items in stomach contents, but this varied with site, season and year. Given their high abundance, the impact of round gobies on the benthic biodiversity of the Great Lakes may be more significant than indicated by stomach content analysis alone.

Résumé : Notre étude apporte de nouvelles données qui indiquent que le régime alimentaire, les sources de carbone et la position trophique de l'espèce envahissante de poissons, le gobie à taches noires (*Neogobius melanostomus*), varient en fonction de la saison, de l'espace et de la taille corporelle dans les habitats littoraux du lac Ontario. D'après les contenus stomacaux et les isotopes stables, les gobies à taches noires du bassin de Kingston, qui est plus frais et moins productif, se nourrissent à un niveau trophique plus élevé que ceux de la baie de Quinte. Les gobies à taches noires de la baie de Quinte sont plus dépendants du carbone terrestre, alors que le carbone littoral prédomine dans le bassin de Kingston. Bien que les contenus stomacaux indiquent que les dreisséniés constituent les proies principales, les modèles de mélange d'isotopes stables révèlent que les dreisséniés ne représentent jamais >39 % du régime alimentaire dans la baie de Quinte et >11 % dans le bassin de Kingston. Les isotopes stables indiquent que les amphipodes, les chironomidés et les cladocères constituent les proies prédominantes et qu'ils sont, à certains moments, fréquents dans les contenus stomacaux, mais qu'il y a une variation en fonction du site, de la saison et de l'année. Étant donné leur forte abondance, l'impact des gobies à taches noires sur la biodiversité des Grands Lacs peut être plus important que ne l'indiquent les seuls contenus stomacaux.

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Introduction

Quantifying spatial and temporal variability in food web structure and fish diet remains a challenge for ecologists (Warren 1989; Martinez et al. 1999; McCann et al. 2005). Aquatic habitats within a single lake system often differ in physical and chemical properties, such as nutrients, temperature, and depth, which can influence diet, habitat use, and trophic positions of fish across seasons and sites (McIntyre et al. 2006; Zambrano et al. 2010). Trophic interactions may also differ over ontogeny, with shifts in diet, habitat use, or trophic position of species typically accompanying an increase in fish size (Jennings et al. 2001; McIntyre et al. 2006). Consequently, single time point estimates or small-scale studies may misrepresent trophic interactions and ultimately the dynamics of food web structure (Paine 1980). It is therefore important to account for spatial and temporal factors and the influence of ontogeny when describing food web dynamics (Warren 1989; Sÿvaranta et al. 2006).

Aquatic invasive species (AIS) are a serious concern in the Laurentian Great Lakes, where the structure and biological integrity of communities have been compromised (Mills et al. 1994; Ricciardi and MacIsaac 2000). The vast majority of these introductions have been human-mediated, most commonly via ballast water transport in transoceanic vessels (Ricciardi and MacIsaac 2000). Successful AIS often have broad physiological and environmental tolerances, rapid reproduction, and occupy similar habitats in natal and introduced ecosystems (Corkum et al. 2004). Where AIS have

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successfully established and proliferated, they tend to have detrimental impacts on local food webs (Kuhns and Berg 1999; French and Jude 2001), although only a small percentage of all successful invasive species are considered a nuisance (Willamson et al. 1986).

The benthic-feeding round goby (*Neogobius melanostomus*) has been described as the fastest advancing and one of the furthest spreading of all AIS established within the Great Lakes basin (Corkum et al. 2004). Round goby likely arrived through ballast water from the Black Sea region in the early 1990s (Jude et al. 1992). This small fish (<20 cm) has been implicated in a number of ecological and economic problems, including declines in benthic invertebrate abundance (French and Jude 2001; Barton et al. 2005; Lederer et al. 2006), changes in fish community composition through predation and competition (Ghedotti et al. 1995; Balshine et al. 2005), and changes in native predator feeding behaviour (Johnson et al. 2005; Campbell et al. 2009; Taraborelli et al. 2010).

Round goby has become an integral species in Great Lakes communities, utilizing a diverse prey assemblage, having the ability to consume the very abundant invasive dreissenid mussels, and being consumed by many fish and other vertebrate predators (Johnson et al. 2005; Hebert et al. 2008; Jones et al. 2009). Many studies suggest dreissenid mussels are the predominant prey for round goby, especially for larger size fish (Ray and Corkum 1997; Corkum et al. 2004). This conclusion is based mainly on stomach content analysis, which may overestimate the contribution of this hard-shelled organism to total diet and underestimate the impact on other components of the nearshore benthic community (Barton et al. 2005).

We employed both stomach contents and stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) to assess differences in round goby diet, trophic position, and carbon sources, with respect to body size, across two littoral sites (Bay of Quinte and Kingston Basin) and three seasons (spring, summer, and fall) in the eastern basin of Lake Ontario. Within eastern Lake Ontario, the Bay of Quinte has been listed as an Area of Concern, with high summer temperatures, shallow depths, and agricultural inputs contributing to abundant *Cladophora* growth throughout the embayment. The Kingston Basin is a comparatively pristine location, with a greater depth, higher water clarity, and cool water inputs from the open lake. We predict that round goby diet choice and trophic position will vary with differences in temperature and across sites that differ in nutrient status and the influence of primary production sources (nearshore vs. open-lake processes) (McIntyre et al. 2006). We also expect round goby diet to shift from smaller, soft-bodied invertebrates to dreissenids with increasing fish size (Ray and Corkum 1997; Barton et al. 2005; Campbell et al. 2009) because of gape and required crushing force limitations at smaller body sizes.

Materials and methods

Study site and species

Round goby and benthic invertebrates were collected at two geographical locations with contrasting temperature in northeastern Lake Ontario, the Bay of Quinte (44°08.978N, 77°10.013W) and the Kingston Basin (44°00.163N, 76°59.318W) (Fig. 1) during the summer of 2009 (14 July – 9 September) and the spring (25 May – 8 June), summer (5 July – 5 August), and fall (27 September – 15 November) of 2010. The Bay of Quinte is a large, shallow, and eutrophic embayment, where summer temperatures range from 18 to 28 °C (mean 23.21 ± 0.28 °C in 2009 and 24.30 ± 0.20 °C in 2010). The Kingston Basin is a deeper, oligotrophic region that is more representative of an open-lake environment, where summer temperatures usually range from 14 to 25 °C (mean 20.71 ± 0.21 °C in 2009 and 21.32 ± 0.40 °C in 2010). Water temperature was continuously recorded at 1 m subsurface and 1 m above the bottom using loggers deployed within each site during the sample collection periods (Table 1). In 2010, daily water temperature data for the Bay of Quinte were obtained from the Belleville water treatment plant. Water temperatures obtained with loggers and at the treatment plant intake were highly correlated in 2009.

Sample collection

Round gobies were collected using a variety of methods sampling different littoral habitats (depth < 1.2 m) in each of the Bay of Quinte and Kingston Basin. All round gobies from a given location were used to provide individual replicate observations to test for spatial and temporal variation in diet and trophic position. Benthic invertebrates were collected with ponar grab samplers and dipnets in the vicinity of the round goby collections. Approximately 10–20 individual invertebrates of a given taxa were pooled into a single season- and site-specific sample to achieve sufficient material for stable isotope analysis. Quagga mussels (*Dreissena bugensis*), representing >90% of the dreissenid species, were collected to serve as a trophic baseline for stable isotope analysis of the two food webs. Typically, sessile primary consumers such as mussels or snails are used to represent the base of the food web (Post 2002) because zooplankton and motile benthic invertebrates are subject to greater temporal and spatial variability related to seasonal production dynamics and differing carbon sources among habitats (Syväranta and Jones 2009; Syväranta and Rautio 2010). Guzzo et al. (2011) found dreissenid mussels to be a more consistent baseline than zooplankton and particulate organic carbon when interpreting trophic relationships of young-of-the year yellow perch (*Perca flavescens*) and white perch (*Morone americana*) in western Lake Erie. Dreissenid mussels are especially well suited to our study, as they are abundant in both locations and are a dominant food item of round goby (French and Jude 2001; Johnson et al. 2005). Fish and invertebrate samples were immediately placed on ice and returned to the lab. All fish were weighed (±0.01 g), measured (±0.1 mm), and sexed based on external features (urogenital papilla). As round goby lack a true stomach, the entire digestive tract from the esophagus to the anus was retained for gut content analysis. A skinless, boneless dorsal muscle sample was excised from all individual fish and frozen at –80 °C until analyzed for stable isotopes. For mollusks and other shelled invertebrates, only soft tissue was retained for stable isotope analysis.

Sample analysis

Round goby were separated into small (≤80 mm) and large (>80 mm) size categories, as a size-dependent shift in diet occurs between 70 and 100 mm (French and Jude 2001; Bar-

Fig. 1. Collection sites for round goby and benthic invertebrates in Bay of Quinte and Kingston Basin, eastern Lake Ontario.

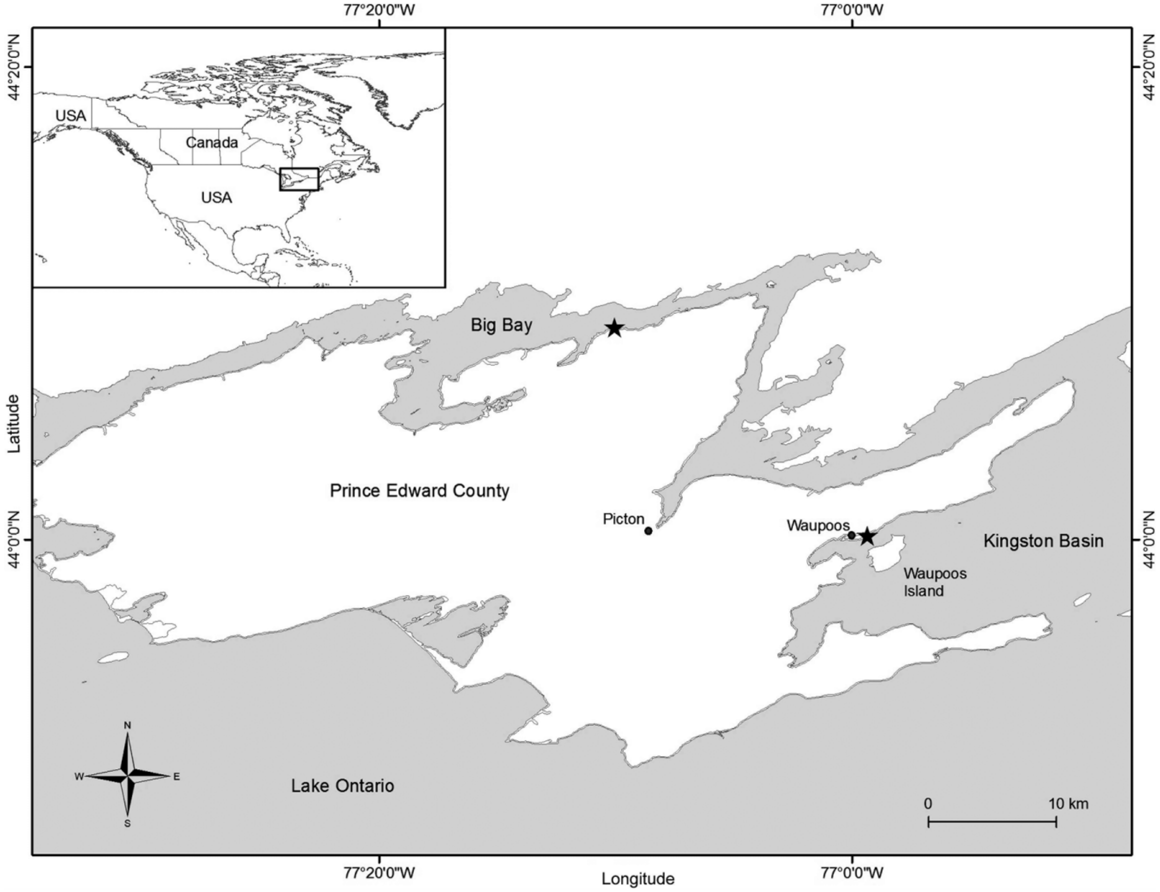

Table 1. Seasonal values of $\delta^{13}C$ and $\delta^{15}N$ (mean ± 1 standard error, SE) in round goby from the Bay of Quinte and Kingston Basin, Lake Ontario.

			Bay of Quinte			Kingston Basin		
Date	Size range (mm)		*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$
2009 Summer	55–79	Expected	22	–22.51	10.92	6	–19.54	11.33
		Observed		–25.87±0.20	11.47±0.06		–19.16±0.36	12.01±0.10
	81–126	Expected	18	–22.25	11.01	8	–21.31	11.34
		Observed		–26.35±0.19	11.30±0.11		–20.29±0.64	11.67±0.14
2010 Spring	35–80	Expected	19	–22.67	10.85	9	–20.97	13.02
		Observed		–25.62±0.23	10.81±0.09		–18.15±0.14	12.90±0.14
	81–120	Expected	10	–22.25	10.97	15	–20.99	11.55
		Observed		–26.54±0.25	11.16±0.10		–19.36±0.21	12.70±0.08
2010 Summer	42–80	Expected	11	–22.31	10.99	11	–21.40	11.36
		Observed		–23.73±0.18	10.60±0.14		–18.10±0.18	12.61±0.14
	81–104	Expected	7	–22.30	10.97	18	–21.46	11.35
		Observed		–24.70±0.19	10.97±0.19		–18.09±0.16	12.54±0.10
2010 Fall	59–80	Expected	12	–22.87	10.76	18	–19.75	11.39
		Observed		–21.98±0.34	11.64±0.19		–17.39±0.44	12.43±0.10
	81–117	Expected	14	–22.29	10.98	7	–19.55	11.36
		Observed		–21.11±0.36	11.87±0.18		–17.69±0.63	12.43±0.17

Note: Expected values are based on percent volumetric contribution of prey and their respective stable isotope values; observed values are empirical data.

ton et al. 2005). The volumes of gut contents and individual taxa were determined by water displacement, and contents were enumerated under a dissection microscope. Prey taxa were identified to the Order or Family level (Voshell 2002). Non-mollusc prey items are termed "non-shelled prey" and include the follwoing taxa: Chironomidae, Amphipoda, Copepoda, Cladocera, Trichoptera, Odonata, and Ephemeroptera. Similar prey classifications were pooled in a single category; for example, Chironomidae pupae and larvae were pooled in Chironomidae.

For $\delta^{13}C$ and $\delta^{15}N$ analysis, fish muscle and invertebrate samples were freeze-dried for 48 h and ground using a mortar and pestle. For each fish and invertebrate sample, 400–600 µg of tissue was weighed into 5 mm × 9 mm tin cups. Samples and standards were analyzed using a Delta V IRMS (Thermo Electron Corporation, Waltham, Massachusetts, USA) equipped with an elemental analyzer (Costech, Santa Clarita, California, USA) to quantify the abundances of $\delta^{13}C$ and $\delta^{15}N$. Samples were not lipid-extracted because the measured C:N ratio did not exceed 3.5 in preliminary test runs, indicating low lipid content. Lipid extraction has also been shown to affect $\delta^{15}N$ values (Post et al. 2007). The abundances of carbon and nitrogen isotopes in each sample were expressed in delta notation relative to a standard, using the following equation:

$$(1)\qquad \delta R\ (‰) = (R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1) \times 1000$$

where R is the ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. The standard reference material was Pee Dee Belemnite carbonate for CO_2 and atmospheric nitrogen for N_2. NIST standard 8414 and an internal fish muscle standard (tilapia, *Oreochromis niloticus*), along with three internal glycine reference standards, were analyzed every 12th sample, and to assess repeatability, every tenth sample was run in triplicate. Precision of analysis for standards was calculated based on the standard deviation of reference standards, which were 0.05 for $\delta^{13}C$ and 0.12 for $\delta^{15}N$ for NIST standard 8414 ($n = 207$) and 0.12 for $\delta^{13}C$ and 0.17 for $\delta^{15}N$ for an internal laboratory fish muscle standard ($n = 214$).

Data analysis

Stomach contents

To assess whether the number of stomach contents examined was sufficient to describe the dietary diversity of round goby, cumulative rarefaction prey curves from stomach contents were generated for the two sites in each season using Primer 6.0 (Primer-E Ltd., Ivybridge, United Kingdom) (Braccini et al. 2005). For both size classes of round goby, and for each season and site, percent number (%N), percent volume (%V), and percent frequency of occurrence (%O) were calculated, along with index of relative importance (IRI) and percent IRI (%IRI) (Cortés 1997) using the following equations:

$$(2)\qquad \mathrm{IRI}_x = (\%N + \%V) \times \%O$$

$$(3)\qquad \%\mathrm{IRI}_x = \left[\mathrm{IRI}_x/\sum(\mathrm{IRI})\right] \times 100$$

Stable isotopes

All stable isotope-related data ($\delta^{13}C$ and $\delta^{15}N$) were analyzed using Statistica software (Statsoft Inc., Tulsa, Oklahoma, USA), were verified for normality using a Shapiro–Wilk test, and were deemed statistically significant at a p value of less than 0.05. There was no observed effect of sex on $\delta^{13}C$ or $\delta^{15}N$ (one-factor analysis of variance, ANOVA; $p > 0.05$); therefore, male and female data were pooled. Round goby total length distributions were compared using an ANOVA between sites and seasons. Linear regression analysis was used to assess trends in $\delta^{13}C$ or $\delta^{15}N$ values with round goby size, with all seasons combined within a site. Since few significant size relationships were found (see below), size was not considered in additional analyses. A multivariate analysis of variance (MANOVA) was used to examine variation in round goby $\delta^{13}C$ and $\delta^{15}N$ with site, season, as well as the interaction. Since the null hypothesis was rejected, separate factorial ANOVAs were run on individual dependent variables ($\delta^{13}C$ or $\delta^{15}N$) with site and season as independent factors. Tukey's post hoc comparisons were used to assess differences between sites and seasons.

Comparing stomach contents and stable isotopes

To compare the stable isotope and stomach content results, we used three methods, and in all cases the data was analyzed by site and season. The first method was to convert stomach contents and stable isotope values to an estimate of consumer trophic position. For stomach contents, this was done using the equation of Vander Zanden et al. (1997):

$$(4)\qquad \text{trophic position} = \sum(V_x T_x) + 1$$

where V_x is the percent volume of prey item x, and T_x is the assigned trophic position of different prey items, based on documented feeding ecology (Vander Zanden et al. 1997). While general, the assigned trophic positions provide a reasonable guide for incorporating relative contributions of different prey taxa into a consumer trophic position estimate. To estimate trophic position from stable isotopes, $\delta^{15}N$ was used with the equation of Cabana and Rasmussen (1996):

$$(5)\qquad \text{trophic position} = (\delta^{15}N_{\mathrm{consumer}} - \delta^{15}N_{\mathrm{baseline}})/3.4 + 2$$

where $\delta^{15}N_{\mathrm{consumer}}$ is the stable nitrogen isotope value of the round goby, $\delta^{15}N_{\mathrm{baseline}}$ is the baseline organism (quagga mussels, matched to the location and season of sampling for the round goby), 3.4 is the diet tissue enrichment factor (Post 2002), and 2 refers to the trophic level of the baseline organism. An ANOVA was used to assess variation in consumer trophic position across sites and seasons.

The second method used linear mixing models to estimate expected values for $\delta^{13}C$ and $\delta^{15}N$ based on the quantified fractional contribution (%V) of different prey items in stomach contents using the following equations:

$$(6)\qquad \delta^{13}C_{\mathrm{expected}} = \left[\sum a(\%V_a) + b(\%V_b) + c(\%V_c)\ \ldots\right] + 1$$

$$(7)\qquad \delta^{15}N_{\mathrm{expected}} = \left[\sum a(\%V_a) + b(\%V_b) + c(\%V_c)\ \ldots\right] + 3.4$$

where the letters a, b, etc. represent the $\delta^{13}C$ or $\delta^{15}N$ isotope value of different prey, $\%V_x$ represents the percent volume of the designated prey item, and 1‰ and 3.4‰ are the diet tissue enrichment factors between a prey and consumer, for $\delta^{13}C$ and $\delta^{15}N$, respectively (Post 2002).

The last method estimated the proportion of different diet items based on stable isotopes using the mixing model MixSIR (Semmens and Moore 2008). MixSIR enables the user to incorporate multiple stable isotopes and numerous prey sources, and posterior probability distributions are determined for each prey source using numerical integration (Moore and

Semmens 2008). Although the Bayesian model approach enables prior information to be incorporated, uninformative priors were used so that estimates were unbiased, and prey items were assumed to be a priori equally likely to contribute to the stable isotope composition of the consumer. For δ^{13}C, a diet tissue fractionation factor of 1.0‰ ± 0.4‰ SD was used, and for δ^{15}N, 3.4‰ ± 1.1‰ was used (Post 2002), with 1 000 000 model iterations (Semmens and Moore 2008).To account for variability in the proportional contributions of prey sources, reporting the 95th percentile represents a more accurate distribution of possible solutions, rather than the 50th percentile (or median). Assumptions of mixing models are discussed in greater detail in Moore and Semmens (2008).

Results

A total of 259 round gobies, ranging in size from 35 to 126 mm, were sampled. Mean total length did not differ significantly between the Kingston Basin (81.89 ± 1.39 mm (mean ± standard error, SE), $n = 146$) and the Bay of Quinte (77.01 ± 1.75 mm, $n = 113$) (ANOVA: $F_{[1,258]} = 2.281$, $p = 0.133$) or with season ($F_{[2,257]} = 1.222$, $p = 0.297$); however, the interaction of site and season was significant (site × season: $F_{[2,257]} = 6.631$, $p = 0.0016$). Within a site, mean sizes were not significantly different between years (Student's *t* test) (Bay of Quinte: $t_{[1,1]} = 1.02$, $p = 0.31$; Kingston Basin: $t_{[1,1]} = 0.32$, $p = 0.75$).

Stomach contents

Of the 259 round goby stomachs, 9.6% ($n = 25$) were empty. Based on rarefaction cumulative prey curves, for both sites and in most seasons, an asymptotic number of prey items was observed (Supplemental Fig. S1[1]). Overall, the %IRI of stomach contents indicated that dreissenids were the dominant prey item of round goby, and in most instances dreissenid %IRI was >79% (Fig. 2). Based on %IRI, the importance of dreissenids was higher for the Bay of Quinte compared with the Kingston Basin for all seasons, increasing in importance from spring to summer at both locations, but declining with the fall collection. The contribution of other prey items was spatially and seasonally variable. Within the Kingston Basin, fish eggs were important prey items (%IRI > 50%) to round goby in the spring of 2010, and ostracods were important (%IRI > 38%) to round goby diet in the fall of 2010. Other prey items, such as Amphipoda, Trichoptera, Odonata, Ephemeroptera, Cladocera, and Copepoda, were found in stomach samples; however, based on %IRI, these often contributed less than 10% individually to the stomach contents. Larger round gobies (>80 mm) had higher %IRI for dreissenids and lower %IRI for non-shelled invertebrates (especially chironomids) compared with small gobies (≤80 mm). Round goby diets were more diverse in the Kingston Basin, in the fall, and for smaller individuals (Fig. 2).

Stable isotopes

There were large ranges in round goby δ^{13}C, ranging from –22‰ to –16‰ in the Kingston Basin and from –29‰ to –18‰ in the Bay of Quinte (Table 1). Stable isotope values of invertebrate prey items were lower in δ^{13}C and δ^{15}N in the Bay of Quinte compared with the Kingston Basin, similar to our findings of round goby isotopic composition (Table 2). When data from all seasons were pooled within a site, linear regression analysis revealed no significant trends for δ^{13}C or δ^{15}N with total length for round gobies (Bay of Quinte δ^{13}C: $R^2 = 0.02$, $F_{[1,98]} = 1.97$, $p > 0.05$; δ^{15}N: $R^2 = 0.09$, $F_{[1,98]} = 9.13$, $p > 0.05$; Kingston Basin δ^{13}C: $R^2 = 0.18$, $F_{[1,82]} = 17.58$, $p < 0.01$; δ^{15}N: $R^2 = 0.08$, $F_{[1,82]} = 6.78$, $p > 0.05$). However, there were two exceptions for specific site and season total length: δ^{13}C relationships in the summer of 2010 for the Bay of Quinte ($R^2 = 0.79$, $F_{[1,16]} = 61.03$, $p < 0.001$, $y = -20.26 - 0.050x$) and in the spring of 2010 within the Kingston Basin ($R^2 = 0.51$, $F_{[1,23]} = 23.63$, $p < 0.001$, $y = -13.98 - 0.059x$) (Fig. 3).

A MANOVA, using δ^{13}C and δ^{15}N as dependent variables, indicated that there were significant differences in round goby feeding among sites and seasons. Individual ANOVA revealed significant site and season effects on round goby δ^{13}C and δ^{15}N ($p < 0.05$; Table 3). Tukey's post hoc comparisons indicated that round goby from the Bay of Quinte had lower δ^{13}C values than those from the Kingston Basin across all seasons, and values became more enriched in δ^{13}C with a shift from spring to fall in 2010 at both sites. Values of δ^{15}N in round goby were higher in the Kingston Basin compared with the Bay of Quinte. In the Kingston Basin, δ^{15}N values generally decreased from spring to fall; however, the opposite trend was observed for the Bay of Quinte.

Comparing stable isotopes with stomach contents

Trophic position was higher for the round goby within the Kingston Basin compared with the Bay of Quinte using either stable isotopes or stomach contents (Table 4). In general, trophic position estimates using stomach contents were lower than those obtained using stable isotopes, with all estimates ranging between 2.88 and 3.60 (Table 4). Collection site and season had a significant influence on trophic position calculated using stable isotopes (ANOVA, site: $F_{[1,204]} = 6.19$, $p = 0.0137$; season: $F_{[2,203]} = 59.29$, $p < 0.001$; site × season: $F_{[2,203]} = 7.63$, $p < 0.001$). There was no significant difference in round goby trophic position between spring and summer, but trophic position in fall was significantly higher than the other two seasons in the Bay of Quinte (Tukey's honestly significant difference (HSD) < 0.05). In the Kingston Basin, there were no significant differences between trophic position across season (Tukey's HSD < 0.05).

Expected values of δ^{13}C and δ^{15}N obtained using stomach contents generally did not agree with observed values using stable isotopes in the round goby (Table 1 and Fig. 4). Round goby δ^{13}C and δ^{15}N values adjusted for diet tissue fractionation factors demonstrate that prey other than dreissenids must comprise a more significant component of the round goby diet (Fig. 5).

Based on MixSIR, the proportional contribution of dreissenids in the diet of round goby did not exceed 0.39 in the Bay of Quinte and 0.11 in the Kingston Basin, for any season or site (Table 5). In the Bay of Quinte, other items including Chironomidae, Amphipoda, and Odonata had proportions exceeding 0.20 and up to 0.72 in one instance. In the Kingston

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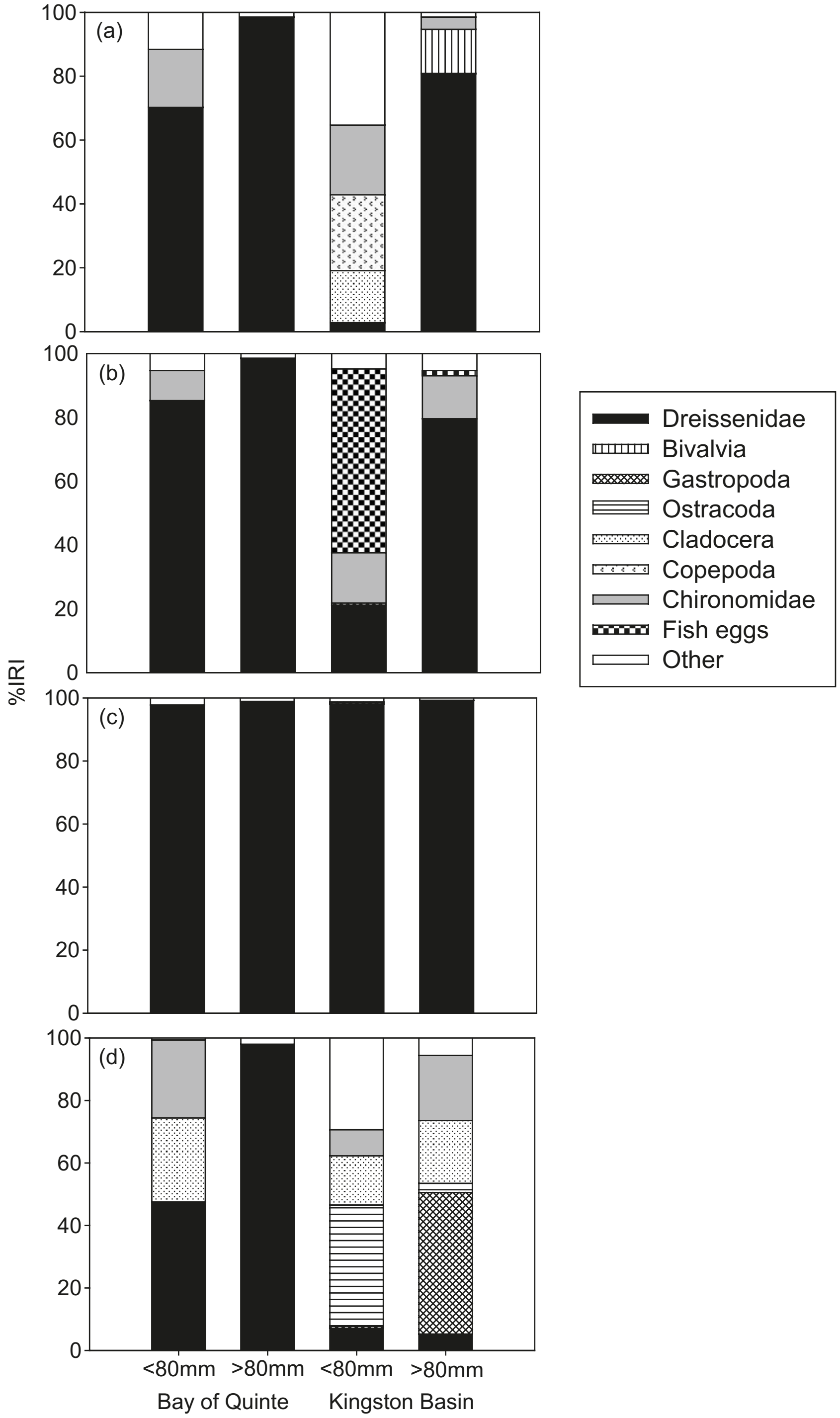
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2012-001.

Fig. 2. Stomach contents (%IRI) for small (32–80 mm) and large (81–126 mm) round goby in different seasons in the Bay of Quinte and Kingston Basin, Lake Ontario. Seasonal stomach content analysis is separated as (*a*) summer 2009; (*b*) spring 2010; (*c*) summer 2010; and (*d*) fall 2010.



Basin, the proportional contribution of Amphipoda exceeded 0.45 in three of four seasons.

Discussion

Our results provide new information that the diet, carbon source, and trophic position of the invasive round goby vary across littoral sites in eastern Lake Ontario, with season and, in two instances, body length. Stable isotope analyses revealed that dreissenid mussels were not as important to the assimilated diet of round goby as was indicated by our stomach content analysis and those from other studies (Ray and Corkum 1997; French and Jude 2001; Johnson et al. 2005). The importance of non-shelled prey has likely been underestimated in the assimilated diet of round goby. Given its hyperabundance and the stable isotope and mixing model results of this study, the round goby's predatory impact on non-dreissenid benthic invertebrate communities is likely

Table 2. Values of $\delta^{13}C$ and $\delta^{15}N$ (mean ± 1 standard error (SE), values if $n \leq 2$) for benthic invertebrates collected from the Bay of Quinte and Kingston Basin and trophic positions for prey based on those assigned in Vander Zanden et al. (1997).

	Bay of Quinte			Kingston Basin			
Taxa	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	Assigned trophic position
Dreissenidae	3	−23.24±0.24	7.61±0.10	6	−22.51±0.31	7.95±0.19	2
Chironomidae	3	−24.16±3.82	7.17±1.30	6	−19.12±0.30	7.53±0.36	2.5
Trichoptera	2	−22.76 (−18.63, −26.89)	6.79 (3.43, 10.15)	1	−18.75	7.16	2.5
Odonata	1	−23.60	7.52	1	−21.19	9.39	3
Amphipoda	2	−25.86 (−22.18,-29.53)	6.12 (5.07, 7.17)	4	−20.60±0.63	8.24±0.12	2.5
Ephemeroptera	0	—	—	1	−18.73	7.01	2.5
Cladocera	2	−31.78, −31.84	7.62, 8.57	1	−19.08	10.15	2.5
Copepoda	0	—	—	5	−24.99±1.30	12.01±0.54	2.5
Mixed zooplankton	2	−29.35, −29.87	11.71, 12.50	2	−22.21, −22.04	9.96, 10.05	2.5
Fish Eggs	0	—	—	2	−22.31 (−21.90, −22.73)	11.19 (11.02, 11.36)	3

greater than previously presumed. Higher predation rates could deplete local sources of benthic invertebrates, which are important prey items for native fishes (Balshine et al. 2005; Raby et al. 2010).

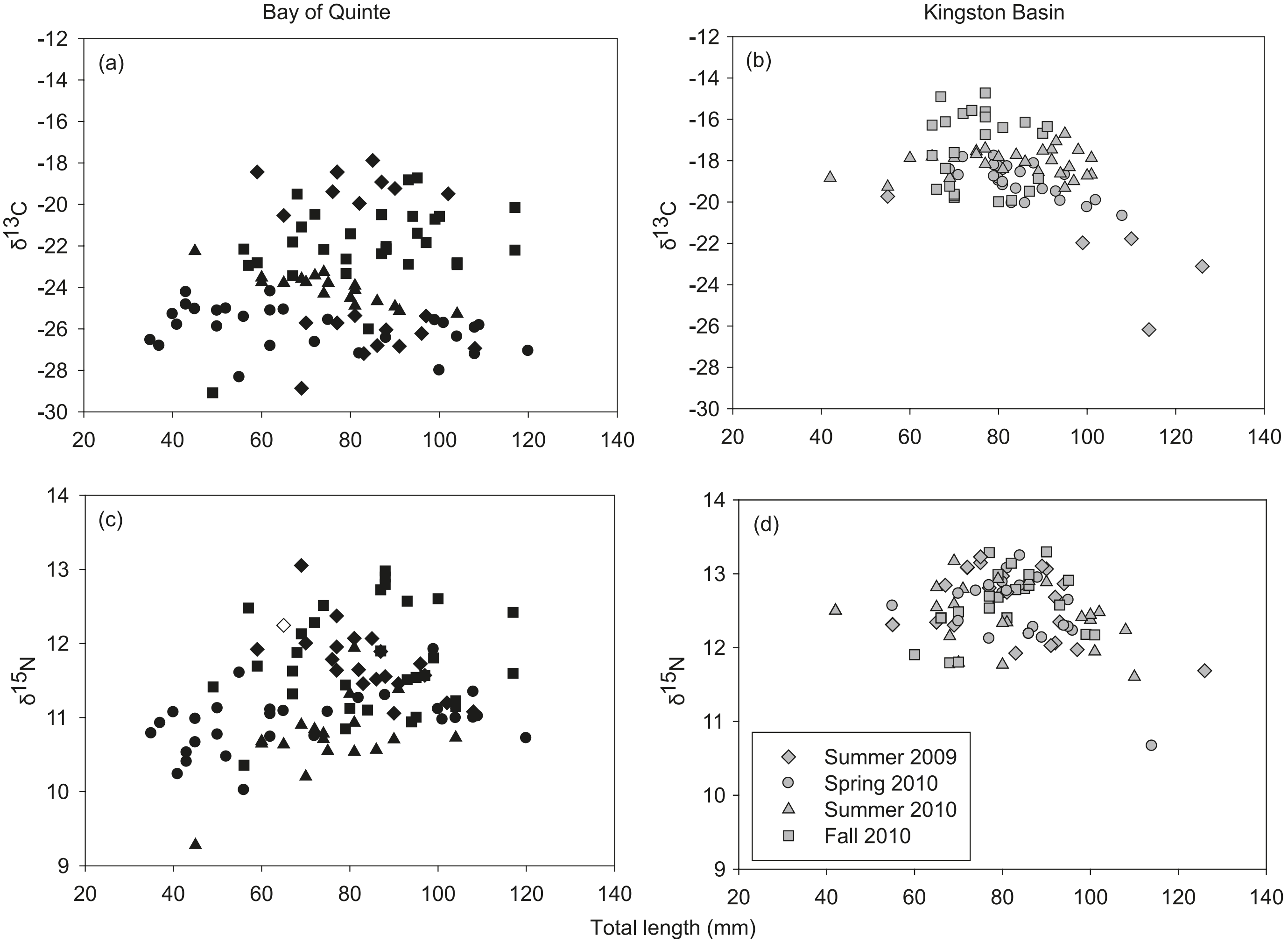
In both native and introduced ranges, the round goby is often described as an opportunistic benthivore, with smaller individuals (<80 mm) consuming a higher proportion of small invertebrates and larger gobies relying more heavily on dreissenids (Ghedotti et al. 1995; Ray and Corkum 1997; Johnson et al. 2005). The round goby's ability to exploit both dreissenid mussels and non-shelled benthic invertebrates has contributed to its invasion success (Corkum et al. 2004). While round gobies possess anatomical features facilitating the ingestion of dreissenid mussels (Charlebois et al. 1997), most non-shelled benthic invertebrates have higher energy density ($J{\cdot}g^{-1}$) than dreissenids (Johnson et al. 2005), suggesting this dietary switch is associated with lower foraging costs possibly associated with the high relative abundance of dreissenids relative to other prey. It is presumed smaller gobies consume less dreissenid prey because they lack the strength in their pharyngeal teeth to crush the shells.

While our stomach content results are generally consistent with the above perception, linear mixing models based on stomach contents generally underestimated consumer isotopic values, indicating that actual assimilation of prey items differed from those observed in stomach contents. When round goby stable isotope values were adjusted for diet tissue discrimination factors of 1‰ and 3.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (Post 2002), isotopic signatures of consumers fell between dreissenids and other invertebrate prey, suggesting both groups contribute to the diet of the gobies. Spatial and seasonal dietary proportions estimated using MixSIR suggest that non-shelled invertebrates, particularly chironomids, amphipods, and cladocerans, were more important prey items of the round goby than dreissenids.

The overestimation of dreissenids in the diet of round goby based on stomach contents is not surprising, given that mussel shells are indigestible and therefore are more easily identified in stomach contents than soft-bodied prey, which digest more rapidly (Kionka and Windell 1972). The ingestion and assimilation of different prey items are not often equal, which is a commonly identified problem when interpreting stomach content data (Barton et al. 2005; Campbell et al. 2009). Since stable isotopes are believed to reflect actual assimilation of prey items by an organism, they have seen broad application in assigning trophic pathways in aquatic and terrestrial food webs (Hecky and Hesslein 1995).

However, the precision and accuracy of stable isotopes to identify the contribution of particular prey items, including their application in mixing models, depends on obtaining samples of all potential prey items from the field, which is not always possible. Accuracy of mixing models also depends on whether diet tissue discrimination factors for a species are appropriate. The diet tissue discrimination factors of 1‰ for $\delta^{13}C$ and 3.4‰ for $\delta^{15}N$ used in this study have been widely applied for freshwater fish (Post et al. 2002), and a number of results from this study suggest confidence in these factors and the conclusions on round goby diet. For example, although the mixing models results differ from stomach contents results in some seasons, there was agreement between stomach contents and MixSIR in the fall, indicating high pro-

Fig. 3. Linear regressions of $\delta^{13}C$ or $\delta^{15}N$ and round goby total length (mm) for the Bay of Quinte (black symbols) and Kingston Basin (grey symbols) pooled for multiple seasons: Bay of Quinte length vs. $\delta^{13}C$ (*a*); Kingston Basin length vs. $\delta^{13}C$ (*b*); Bay of Quinte length vs. $\delta^{15}N$ (*c*); Kingston Basin length vs. $\delta^{15}N$ (*d*).



portions of chironomids to Bay of Quinte round goby diets and amphipods to Kingston Basin diets, and these prey items have been found in goby stomachs elsewhere in the Great Lakes (Corkum et al. 2004; Barton et al. 2005; Pennuto et al. 2010). As well, the $\delta^{13}C$ values of the round goby were similar to or greater than values for dreissenids in the Bay of Quinte and greater than values for dreissenids in the Kingston Basin. If both round goby populations were assimilating dreissenids in the proportions that stomach contents indicate, consumer $\delta^{13}C$ values would be the same. This was not observed, and unless diet discrimination factors for the round goby are different between the two locations, which would be extremely unlikely, at least one of the goby populations is assimilating far fewer dreissenids than suggested by stomach contents alone.

While some studies have reported body size relationships with $\delta^{13}C$ or $\delta^{15}N$ in round goby reflecting a size-based change in diet (Barton et al. 2005; Campbell et al. 2009), we only found evidence of such a relationship in two of eight site by season contrasts. Both dreissenids and non-shelled prey had similar $\delta^{15}N$ values, with non-shelled benthic invertebrates having slightly higher values, such that trophic ontogeny based on $\delta^{15}N$ was not evident in our data. In a similar way, all of our round gobies were collected in waters <2 m depth in both the Bay of Quinte and Kingston Basin, and therefore ontogenetic spatial differences, expressed in $\delta^{13}C$, were not evident as may be in Lake Erie studies (Barton et al. 2005; Campbell et al. 2009) that spanned depths of 2 to 10 m.

Evidence from throughout the Great Lakes basin and in their native range suggests round goby are opportunistic in their prey choice. High abundance in dense colonies and lack of mobility make dreissenids a candidate prey for round goby, although higher handling times associated with processing these shelled prey and lower energy density than many non-shelled benthic invertebrates reconcile the final choice of prey. In Lake Erie, as the number of appropriately sized mussels declined, chironomids and amphipods became more important to round goby diet (Barton et al. 2005), and where mussels were absent goby diets consisted of a broad array of benthic invertebrates (Pennuto et al. 2010). In the absence of bottom substrate that provided refuge for amphipods, round gobies preferred non-shelled prey to sessile dreissenids in the laboratory (Diggins et al. 2002).

Spatial differences in round goby diet, evident from stable isotopes and stomach contents, can be explained by differen-

Table 3. Multivariate analysis of variance (MANOVA) and analysis of variance (ANOVA) results for site and seasonal effects on consumer $\delta^{13}C$ and $\delta^{15}N$.

Factor	SS	df	MS	*F*	*p*
MANOVA $\delta^{13}C$–$\delta^{15}N$					
Site	976.95	1	976.95	412.35	<0.01
Season	122.52	2	61.26	25.86	<0.01
Site × Season	49.94	2	24.97	10.54	<0.01
Error	421.72	178	2.37		
ANOVA $\delta^{13}C$					
Site	1302.07	1	1302.07	339.80	<0.01
Season	204.90	2	102.45	26.74	<0.01
Site × Season	49.97	2	24.98	6.52	<0.01
Error	682.07	178	3.83		
ANOVA $\delta^{15}N$					
Site	65.91	1	65.91	215.22	<0.01
Season	2.26	2	1.13	3.69	0.03
Site × Season	9.52	2	4.76	15.55	<0.01
Error	54.51	178	0.31		

Tukey's post hoc comparisons: all honestly significantly difference (HSD) < 0.05.

Site	$\delta^{13}C$	Kingston Basin > Bay of Quinte
	$\delta^{15}N$	Kingston Basin > Bay of Quinte
Season	$\delta^{13}C$	Bay of Quinte: Fall > Summer > Spring
		Kingston Basin: Fall > Summer > Spring
	$\delta^{15}N$	Bay of Quinte: Fall > Summer > Spring
		Kingston Basin: Spring > (Summer = Fall)

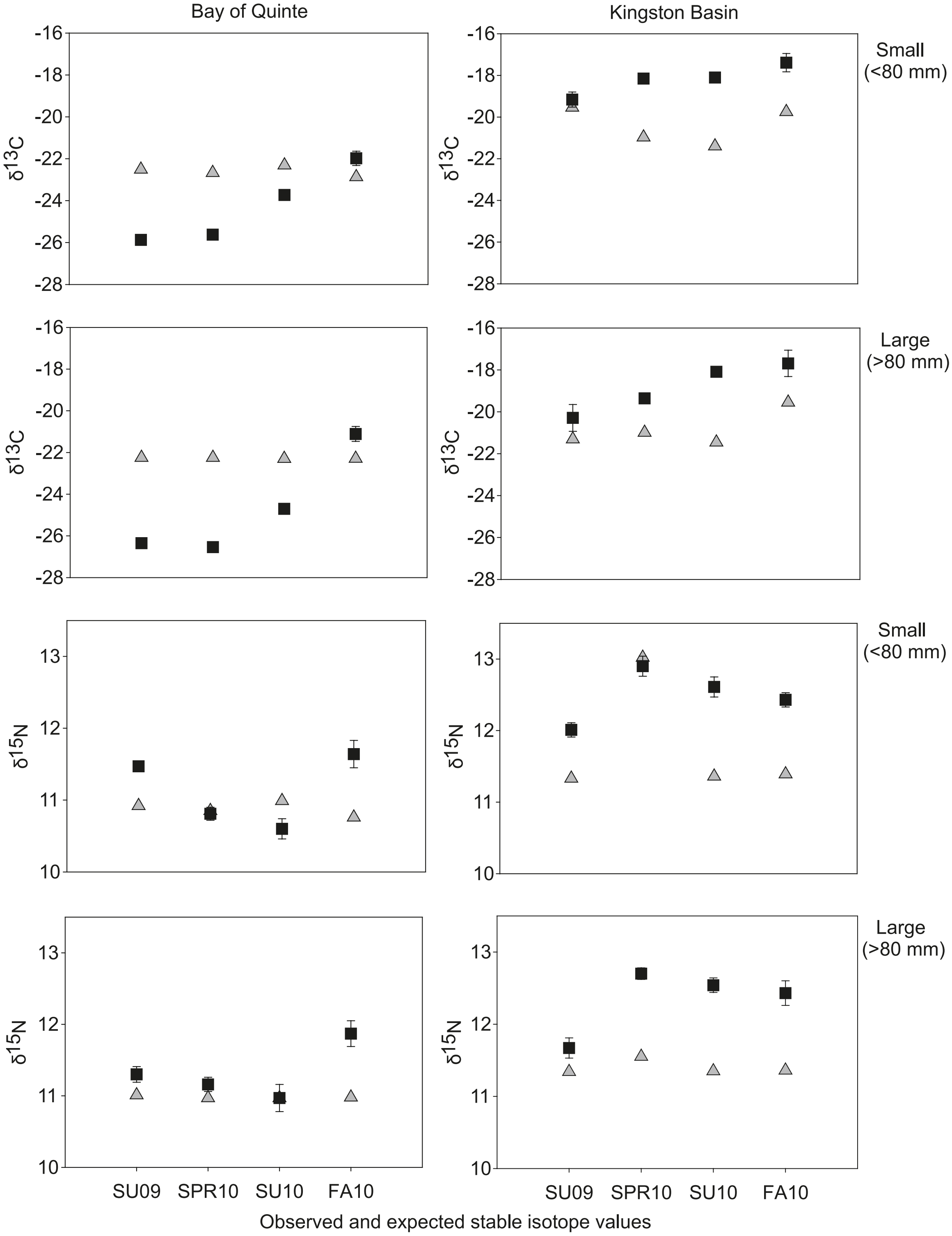
Table 4. Estimated trophic position of round goby calculated using volumetric contribution of prey items from stomach contents (SC) (Vander Zanden et al. 1997) and stable nitrogen ($\delta^{15}N$) isotopes (Cabana and Rasmussen 1996) in the Bay of Quinte and Kingston Basin, Lake Ontario.

			Bay of Quinte		Kingston Basin	
Season	Size class (mm)	Method	*n*	Trophic position	*n*	Trophic position
Summer 2009	59–79	SC	27	3.05	5	3.24
		$\delta^{15}N$	22	3.13±0.02	6	3.22±0.03
	81–126	SC	18	3.00	14	3.02
		$\delta^{15}N$	18	3.09±0.03	8	3.09±0.04
Spring 2010	35–80	SC	18	3.13	27	3.60
		$\delta^{15}N$	19	2.94±0.03	9	3.45±0.01
	81–120	SC	8	3.02	25	3.14
		$\delta^{15}N$	10	3.05±0.03	15	3.40±0.02
Summer 2010	42–80	SC	10	3.00	6	3.00
		$\delta^{15}N$	11	2.88±0.04	11	3.37±0.04
	81–104	SC	6	3.01	24	3.00
		$\delta^{15}N$	7	2.99±0.06	18	3.35±0.03
Fall 2010	59–80	SC	9	3.32	16	3.28
		$\delta^{15}N$	12	3.19±0.06	18	3.31±0.03
	81–117	SC	14	3.02	7	3.24
		$\delta^{15}N$	14	3.25±0.05	7	3.32±0.05

ces in habitat and its effect on benthic community composition. The Bay of Quinte is characterized by a muddy bottom favouring soft-bodied organisms such as chironomids, while the Kingston Basin has many more hard substrates favouring dreissenids and associated grazers such as amphipods, which colonize interstitial spaces provided by dreissenid mussel colonies (Cobb and Watzin 2002; Taraborelli et al. 2009; R. Dermott, Fisheries and Oceans Canada, 867 Lakeshore Road, Burlington, ON L7R 4A6, Canada, unpublished data), which is consistent with the stomach content and stable isotope modeling results for each location.

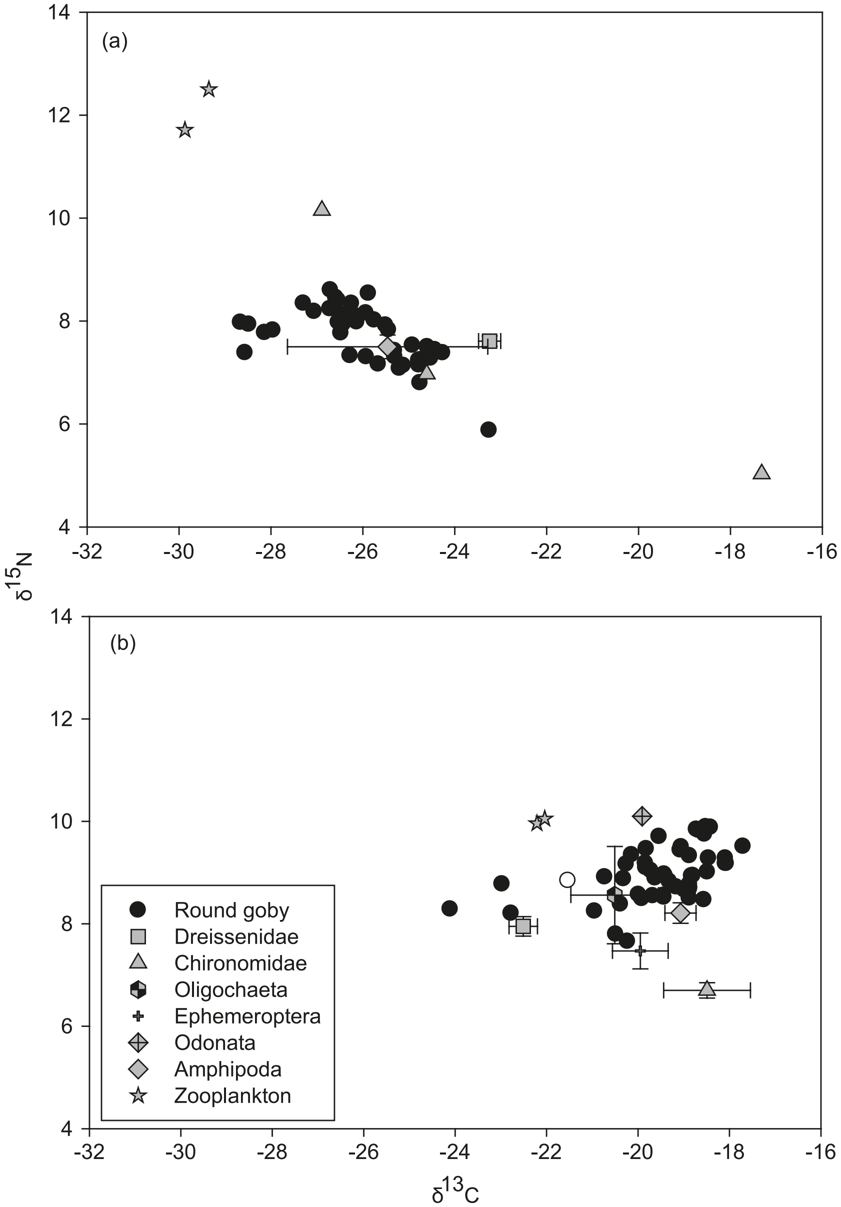
Changes in consumer isotopic values can result from shifts in diet as well as temporal variation at the base of the food web (Newsome et al. 2009). In the Kingston Basin, the seasonal increase in $\delta^{13}C$ for round goby was not observed in prey items, suggesting that goby diet changed among seasons. Such a conclusion is supported by the stomach content analysis, which showed increasing importance of certain in-

Fig. 4. Observed (circles) and expected based on linear mixing model (triangles) stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values for each season (spring, summer, and fall) for small (≤80 mm) and large (>80 mm) round gobies for the Bay of Quinte and Kingston Basin.



vertebrate species (i.e., chironomids in the Bay of Quinte and amphipods in the Kingston Basin) in the fall. Increasing $\delta^{13}C$ and $\delta^{15}N$ from spring to fall in round gobies reflected increased assimilation of more non-dreissenid prey items with higher $\delta^{13}C$ and $\delta^{15}N$. Stomach content analysis and mixing model results indicated greater importance of prey such as amphipods in the Kingston Basin and chironomids in the Bay of Quinte in the fall relative to spring and summer, which have higher $\delta^{13}C$ and $\delta^{15}N$ than dreissenids. Without knowledge of variation in specific prey abundance with season, it is difficult to assign changes in stomach contents and stable isotopes to changes in prey density over time. However, given round goby's flexible feeding strategy, seasonal isotope values may reflect round goby's ability to opportun-

Fig. 5. Comparison of all sizes of round goby and potential prey items stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values for the summer in the Bay of Quinte (*a*) and Kingston Basin (*b*). Circles represent round goby δ^{13}C and δ^{15}N adjusted for diet tissue discrimination by subtracting 1‰ for carbon and 3.4‰ for nitrogen from raw stable isotope values (following Newsome et al. 2009). Prey types include Dreissenidae, Chironomidae, Oligochaeta, Ephemeroptera, Odonata, Amphipoda, and zooplankton. All prey values are represented as mean ± 1 standard error (SE). The number of samples for each prey type can be found in Table 2.



istically exploit and assimilate prey items with variable seasonal abundances. Since stomach contents in the Bay of Quinte round goby did not change much with season, particularly for the larger individuals, the increase in δ^{13}C may also reflect diminished influence of allochthonous sources such as spring runoff, which would be reflected in lower δ^{13}C of primary producers and consumers in the spring.

Interannual variation in stable isotope values for round goby is generally consistent with stomach contents and shifts in proportional contributions of prey items determined by MixSIR. In the Bay of Quinte, round gobies relied less heavily on chironomids in 2010 relative to 2009. This was reflected in higher round goby δ^{13}C and lower δ^{15}N, consistent with the increased importance of Amphipoda and Cladocera as shown by stomach contents and mixing model results. Although stomach content analysis indicates that the non-dreissenid fraction of round goby diet was small in Kingston Basin, the lower proportional contribution of amphipods in 2010 compared with 2009 was reflected in consumer stable isotope values as they became higher in δ^{13}C and δ^{15}N. Decreased consumption of preferred prey items such as amphipods and chironomids in habitats that favour their existence from one year to the next might result from depletion of these species because of the high density of round goby.

Within Areas of Concern such as the Bay of Quinte, degradation of benthic invertebrate communities represents one of the beneficial use impairments (Grapentine 2009). Lower relative abundance of some benthic invertebrate species in

Table 5. Proportional contribution of prey items using Bayesian mixing model, MixSIR (Semmens and Moore 2008), for round gobies from the Bay of Quinte and Kingston Basin.

	Bay of Quinte			Kingston Basin			
Prey item	Summer 2009	Spring 2010	Summer 2010	Fall 2010	Summer 2009	Spring 2010	Summer 2010	Fall 2010
Dreissenidae	0.01–0.07	<0.01–0.22	<0.01–0.39	0.04–0.28	<0.01–0.11	<0.01–0.04	<0.01–0.04	<0.01–0.10
Chironomidae	0.62–0.72	0.18–0.33	0.12–0.36	0.47–0.58	<0.01–0.03	<0.01–0.05	<0.01–0.12	<0.01–0.18
Trichoptera	<0.01–0.13	<0.01–0.19	<0.01–0.33	0.03–0.16	<0.01–0.02	<0.01–0.04	<0.01–0.15	<0.01–0.14
Odonata	0.02–0.12	<0.01–0.22	<0.01–0.45	<0.01–0.05	<0.01–0.02	<0.01–0.86	<0.01–0.04	<0.01–0.20
Amphipoda	<0.01–0.06	<0.01–0.37	<0.01–0.47	<0.01–0.02	0.83–0.88	0.45–0.76	<0.01–0.07	0.47–0.82
Ephemeroptera	—	—	—	—	<0.01–0.04	<0.01–0.07	<0.01–0.21	<0.01–0.14
Cladocera	<0.01–0.06	<0.01–0.33	<0.01–0.32	<0.01–0.01	<0.01–0.06	0.20–0.43	0.69–0.88	<0.01–0.29
Mixed zooplankton	<0.01–0.14	<0.01–0.17	<0.01–0.29	<0.01–0.09	—	—	—	—

Note: Mixed zooplankton were not included in the Kingston Bay models because their $\delta^{13}C$ values exceeded reasonable values for diet sources based on a diet tissue fractionation factor of 1.0‰ ± 0.4‰. Ephemeroptera were not sampled in the Bay of Quinte and therefore not considered as a prey option.

the Bay of Quinte may be the result of degraded conditions associated with increased nutrients, high contaminant levels, and degraded sediment conditions (Miliani and Grapentine 2006). However, the densities of round goby in both the Bay of Quinte and Kingston Basin are large (~10 m^{-2}; Taraborelli et al. 2009; OMNR 2010), and especially if their predatory impact on non-shelled invertebrates is underestimated, their influence on production and biodiversity of nearshore benthic invertebrate communities may be very pronounced, as has been reported elsewhere in the Great Lakes basin (Barton et al. 2005; Lederer et al. 2008; Raby et al. 2010). Round goby may therefore be further contributing to the impaired state of the benthic community and ultimately the recovery potential of the Bay of Quinte.

Stable isotopes have provided a means to assess food web relationships and consumption patterns at different spatial and temporal scales, and while stomach contents provide insights into detailed short-term dietary trends, it is important to exercise caution in their interpretation. Conservation and management of fish populations within the Great Lakes and other aquatic systems will benefit when ecological tools are correctly combined with seasonal, spatial, and ontogenetic data to answer applied ecological questions.

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