

Food Partitioning between the Amphipods *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyaella azteca* as Revealed by Stable Isotopes

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ABSTRACT. Colonies of introduced *Dreissena* mussels provide substrate and food resources for benthic invertebrates resulting in increases in population abundance of many species including the native amphipod *Gammarus fasciatus*. Conversely, abundance of *Gammarus* is inversely associated with that of an introduced amphipod species, *Echinogammarus ischnus*. In this study, we explored carbon and nitrogen isotopic composition of *E. ischnus*, *G. fasciatus*, and *Hyaella azteca* and of *Dreissena* faeces/pseudofaeces from western Lake Erie to investigate possible exploitative competition among amphipods. Carbon isotopic composition ($\delta^{13}\text{C}$) of *H. azteca* and *G. fasciatus* were similar, indicating that they share food resources, whereas *E. ischnus* was significantly depleted indicating its use of different resources. *Dreissena* faeces/pseudofaeces may be a part of *G. fasciatus* diet as revealed by carbon isotopic signatures, explaining, in part, why its abundance is positively associated with *Dreissena*. Phytoplankton may be the primary food source for juvenile *E. ischnus* and *G. fasciatus* as they had lighter carbon isotopic signatures than adult amphipods, suggesting an ontogenetic diet shift by both species. Isotopic separation of *G. fasciatus* and *E. ischnus* suggests that the latter is replacing the former by a mechanism other than exploitative competition for food.

INDEX WORDS: Food partitioning, amphipod, stable isotopes, nonindigenous species, Lake Erie.

INTRODUCTION

Invasions by nonindigenous species (NIS) provide ecologists with unplanned opportunities to assess trophic interactions in aquatic ecosystems. NIS can have profound effects on invaded ecosystems, dramatically altering food-web structure and impoverishing native species diversity (e.g., Vander Zanden *et al.* 1999). Zebra mussels *Dreissena polymorpha* (Pallas) and quagga mussels *Dreissena rostriformis* (Desh.) are native to the Ponto-Caspian basin, but widely introduced into areas of eastern and western Europe and the Laurentian Great Lakes; these introductions have provided vivid examples of the profound effect NIS may have on novel ecosystems and their indigenous species (Ricciardi and

MacIsaac 2000, Reid and Orlova 2002, Vanderploeg *et al.* 2002). *Dreissena* mussels have dramatically altered benthic habitat and food web structure in the lower Great Lakes (Dermott *et al.* 1993, Stewart *et al.* 1998, Bially and MacIsaac 2000).

Gammarus fasciatus Say, an indigenous amphipod species in Lake Erie, increased in abundance after establishment of *Dreissena* populations, possibly because of enhanced habitat availability (Dermott *et al.* 1993, Griffiths 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Bially and MacIsaac 2000) or increased refugia from biotic and abiotic disturbances (Wisenden and Bailey 1995, Bially and MacIsaac 2000). Increased food availability from *Dreissena* faeces and/or pseudofaeces has also been reported as a possible explanation for an increase in *G. fasciatus* abundance (Wisenden and

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Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Kuhns and Berg 1999).

While elevated populations of *G. fasciatus* are correlated with *Dreissena* colonies, an introduced amphipod species, *Echinogammarus ischnus* (Stebbing), seems to have the opposite effect. This species was first reported in the Laurentian Great Lakes during 1995 (Witt *et al.* 1997), although archived samples revealed its presence in western Lake Erie in 1994 and possibly as early as 1993 (van Overdijk *et al.* 2003). *E. ischnus* appears to be displacing *G. fasciatus* on *Dreissena*-dominated habitats in some areas of the Great Lakes (Dermott *et al.* 1998, Stewart *et al.* 1998, Burkart 1999, van Overdijk *et al.* 2003). *E. ischnus* has a strong affinity for habitats encrusted with *Dreissena*, but *G. fasciatus* uses these substrates as well (van Overdijk *et al.* 2003).

Hyalella azteca (Saussure), another native amphipod species in the Great Lakes, has been detected in freshwaters clinging to vegetation and burrowing in bottom sediments (Kruschwitz 1978), though it also occurs on *Dreissena*- and *Cladophora*-encrusted rocks in Lake Erie (van Overdijk *et al.* 2003).

Stable isotope techniques have been used in ecological studies to illuminate consumer-prey relationships (Fry and Sherr 1984, Fry 1991) and can be a useful tool for detecting changes in food-web structure following perturbations, such as species invasions (Vander Zanden *et al.* 1999). Consumers often have $\delta^{13}\text{C}$ values similar to or slightly enriched (by $\sim 1\%$) relative to their food resources, whereas on average $\delta^{15}\text{N}$ displays a stepwise increment of 3.4‰ between trophic levels (Peterson and Fry 1987, Post 2002). Isotopic measurements made on body tissues provide valuable information regarding assimilation of food over long time periods, in contrast to stomach content analyses which reveal diet composition for only the most recent time interval. Furthermore, stomach content analyses may not reflect actual food assimilation.

In this study, we employed stable isotope analyses to investigate whether *E. ischnus* may compete with *G. fasciatus* and *H. azteca* for food resources. We also measured the isotopic signature of *Dreissena* faeces/pseudofaeces to determine its potential role in the diet of both *E. ischnus* and *G. fasciatus*.

METHODS

Amphipods and potential food sources were collected off the east shore of Middle Sister Island,

western Lake Erie on 1 August 2001 using SCUBA-diving and snorkelling. Ambient water temperature was 20°C during collection. A transect perpendicular to shore was fixed and at four depths, 0 m (shore), 0.5 m, 1.0 m, and 2.0 m, buoys were placed to mark sampling sites. At each site a 1×1 m quadrat was placed and a visual description of the relative coverage of different substrates was made. Three *Dreissena*-encrusted rocks of similar size were sealed underwater in polypropylene bags, brought to the surface and preserved with 10% sugar-formalin to record amphipod abundance. Amphipods for stable carbon and nitrogen isotope analyses were collected by placing three rocks from each depth into separate polypropylene bags and later dislodging amphipods by agitating in a bucket of water for 1 minute at the surface. Water from the bucket was then passed through a 500- μm mesh sieve and retained amphipods were washed into a jar and immediately placed on ice. Amphipod species were identified and separated in the laboratory, divided into males, non-gravid females, gravid females and juveniles when possible. They were kept in milli-Q water for a minimum of 1 hour to enable gut evacuation. Finally they were put into separated vials and preserved at -20°C . Adult *G. fasciatus* included both males and females since they were not separate into sexes. Prior to stable isotope analysis, amphipods were dried at 60°C for 24 hours.

Potential food sources including faeces/pseudofaeces from *Dreissena* colonies, detritus, and algae (*Cladophora*, other filamentous Chlorophyta, and associated epiphytes) and *Vallisneria americana* Michx. were collected and immediately put on ice. Faeces/pseudofaeces from mussel colonies were collected by using 30-cc syringes. Detritus, which we define as degraded material from habitats other than mussel colonies, were collected in the same way as the faeces. Live *Dreissena* was collected in the field and put in a bucket with lake water. In the laboratory, *Dreissena* were transferred to a glass jar, and after 2 days, faeces were collected with a syringe, transferred to two vials, and dried at 60°C. This was done in order to get freshly produced faeces/pseudofaeces from mussels and compare it to faeces collected in the field. In the laboratory, faeces and detritus were examined under a microscope. Fragments of mussel shells were removed from faeces and algae parts from detritus. No meiofauna was found in the collected material. Finally, all potential food sources were dried at 60°C in separate vials prior to analysis of stable isotopes.

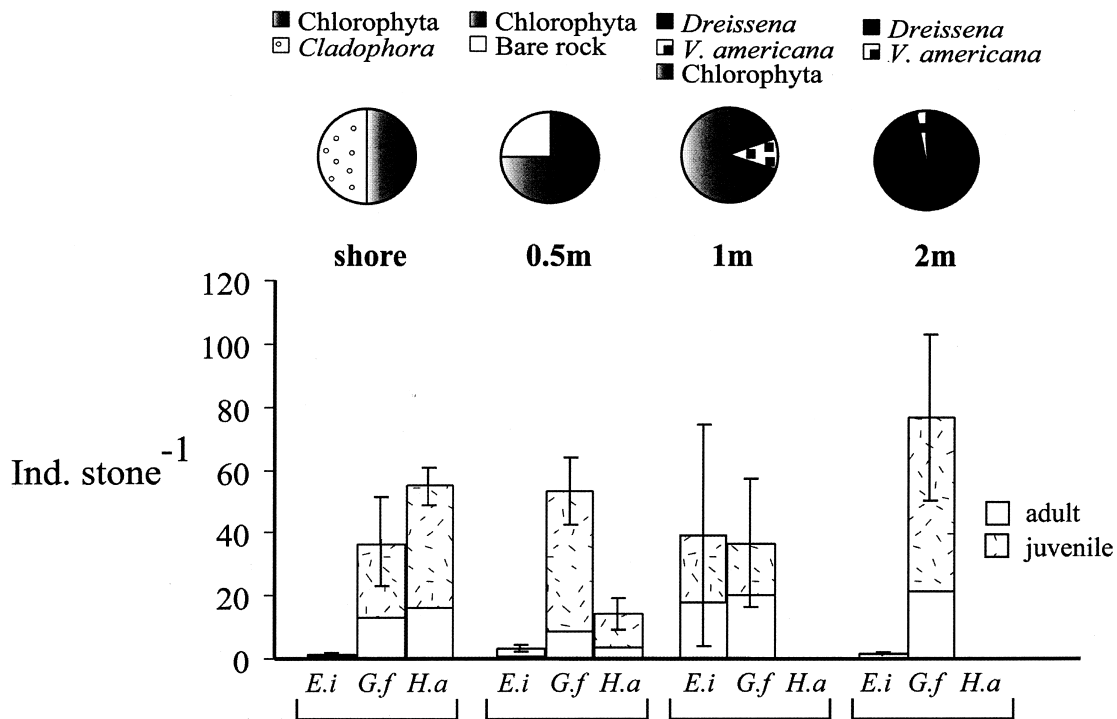


FIG. 1. Average number per stone of *Echinogammarus ischnus* (E.i.), *Gammarus fasciatus* (G.f.), and *Hyalella azteca* (H.a.) at different depths along a transect in western Lake Erie ($n = 3$). Stacked bars show the number of each species separated into adults and juveniles. Error bars represent standard error (SE). Pie charts show habitat structure at different depths. The different habitat types were Chlorophyta, Cladophora, bare rock, *Dreissena* colonies, and *Vallisneria americana*.

Stable carbon and nitrogen isotopes were analyzed using an auto-sampling elemental analyzer (Thermo Finnigan Flash 1112 series) connected to an isotope ratio mass spectrometer (Thermo Finnigan-Delta Plus) via a ConFlo III interface (ThermoQuest) in continuous flow mode. Samples were ground, weighed and wrapped in tin capsules prior to analysis and run against N_1 (IAEA-N1), N_2 (IAEA-N2), CH_6 (NIST sucrose ANV), and CH_7 (IAEA PEFI polyethylene foil) standards of known relation to the international standards Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen.

Statistics

Differences in isotopic signatures and abundance were investigated using analysis of variance (ANOVA). Prior to ANOVA, all data were $\log_{10(x+1)}$ transformed and tested for homoscedasticity using Cochran's C-test. Paired *a posteriori* comparisons were carried out with a Tukey HSD test using 95%

confidence limits. A Kruskal-Wallis non-parametric test was applied when variances were heterogeneous.

RESULTS

Habitat Structure and Amphipod Abundance

The sampling site nearest to shore was covered principally by *Cladophora* and other Chlorophyta (Fig. 1). At 0.5 m, Chlorophyta covered approximately 75% of the lake bottom with bare rocks covering the remaining area. The 1 m sampling site had the most diverse habitat including 70% coverage by Chlorophyta, 20% by *Dreissena*, and 10% by *Vallisneria americana*. The sampling site at 2 m was almost completely covered by *Dreissena* (97%), with a small area (3%) covered by *V. americana*.

Echinogammarus ischnus was most abundant at 1 m, but its abundance was very low at the other depths surveyed (Fig. 1). *Gammarus fasciatus* was abundant at all depths, and exhibited no significant

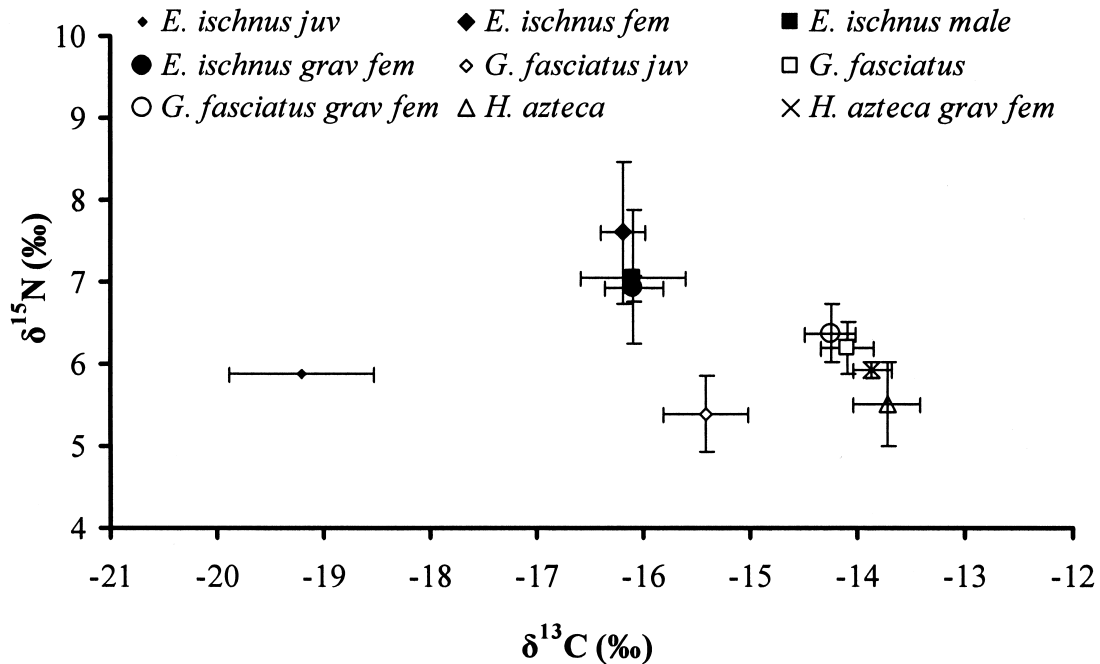


FIG. 2. Average (\pm SE) carbon and nitrogen isotopic composition of *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyalella azteca* from all depths (shore to 2 m). The isotopic composition of males ($n = 6$), females ($n = 4$), gravid females ($n = 4$), and juveniles ($n = 6$) is presented for *E. ischnus*. *G. fasciatus* ($n = 11$) and *H. azteca* ($n = 5$) were separated into adults (no separation of sexes), gravid females ($n = 9$ for *G. fasciatus* and $n = 2$ for *H. azteca*) and juveniles ($n = 10$ for *G. fasciatus*, no juvenile *H. azteca* were found).

difference among depths (Kruskal-Wallis, $p > 0.05$). *Hyalella azteca* was most abundant close to shore, less common at the 0.5 m depth, and absent from deeper sites (Tukey test, $p < 0.001$; Fig. 1). Juvenile *G. fasciatus* tended to be less abundant at the 1 m depth, but there were no significant differences among depths (ANOVA, $p > 0.05$; Fig. 1).

Stable Isotopes

E. ischnus differed from the two native species with respect to both carbon and nitrogen isotope composition. The carbon isotopic signal for *E. ischnus* was significantly lighter ($\delta^{13}\text{C} = -17.0\text{‰}$) than that for *G. fasciatus* ($\delta^{13}\text{C} = -14.6\text{‰}$) and *H. azteca* ($\delta^{13}\text{C} = -13.8\text{‰}$) (ANOVA, $p < 0.001$, Tukey test). Conversely, the nitrogen isotopic signal for *E. ischnus* was significantly heavier (7.1‰) than those of *G. fasciatus* (6.0‰) and *H. azteca* (5.6‰) (ANOVA, $p < 0.05$, Tukey test). There was, however, no difference in carbon and nitrogen isotopic composition between *G. fasciatus* and *H. azteca* (ANOVA, $p > 0.05$).

Juvenile *E. ischnus* ($\delta^{13}\text{C} = -19.3\text{‰}$) had a lighter carbon isotope signal than non-gravid females ($\delta^{13}\text{C} = -16.2\text{‰}$), gravid females ($\delta^{13}\text{C} = -16.1\text{‰}$) and males ($\delta^{13}\text{C} = -16.0\text{‰}$) (ANOVA, $p < 0.05$, Tukey test; Fig. 2). No adult stages differed with regard to carbon isotopic composition (ANOVA, $p > 0.05$). Similarly, juvenile *G. fasciatus* ($\delta^{13}\text{C} = -15.3\text{‰}$) were significantly lighter than males and non-gravid females ($\delta^{13}\text{C} = -14.1$) and gravid females ($\delta^{13}\text{C} = -14.2\text{‰}$) (ANOVA, $p < 0.05$, Tukey test; Fig. 2). Stable carbon isotopic composition of *H. azteca* adults including gravid females did not differ significantly (ANOVA, $p > 0.05$). The $\delta^{15}\text{N}$ for the various ontogenetic stages and sexes did not differ significantly among the three species (ANOVA, $p > 0.05$).

The range of carbon and nitrogen isotope signatures for potential food sources was -7.4 to -14.6‰ , and 4.1 to 6.6‰, respectively (Fig. 3). In terms of carbon isotopic composition, *Cladophora* (shore) was the most enriched potential food source ($\delta^{13}\text{C} = -7.4\text{‰}$). *Dreissena* faeces had the most de-

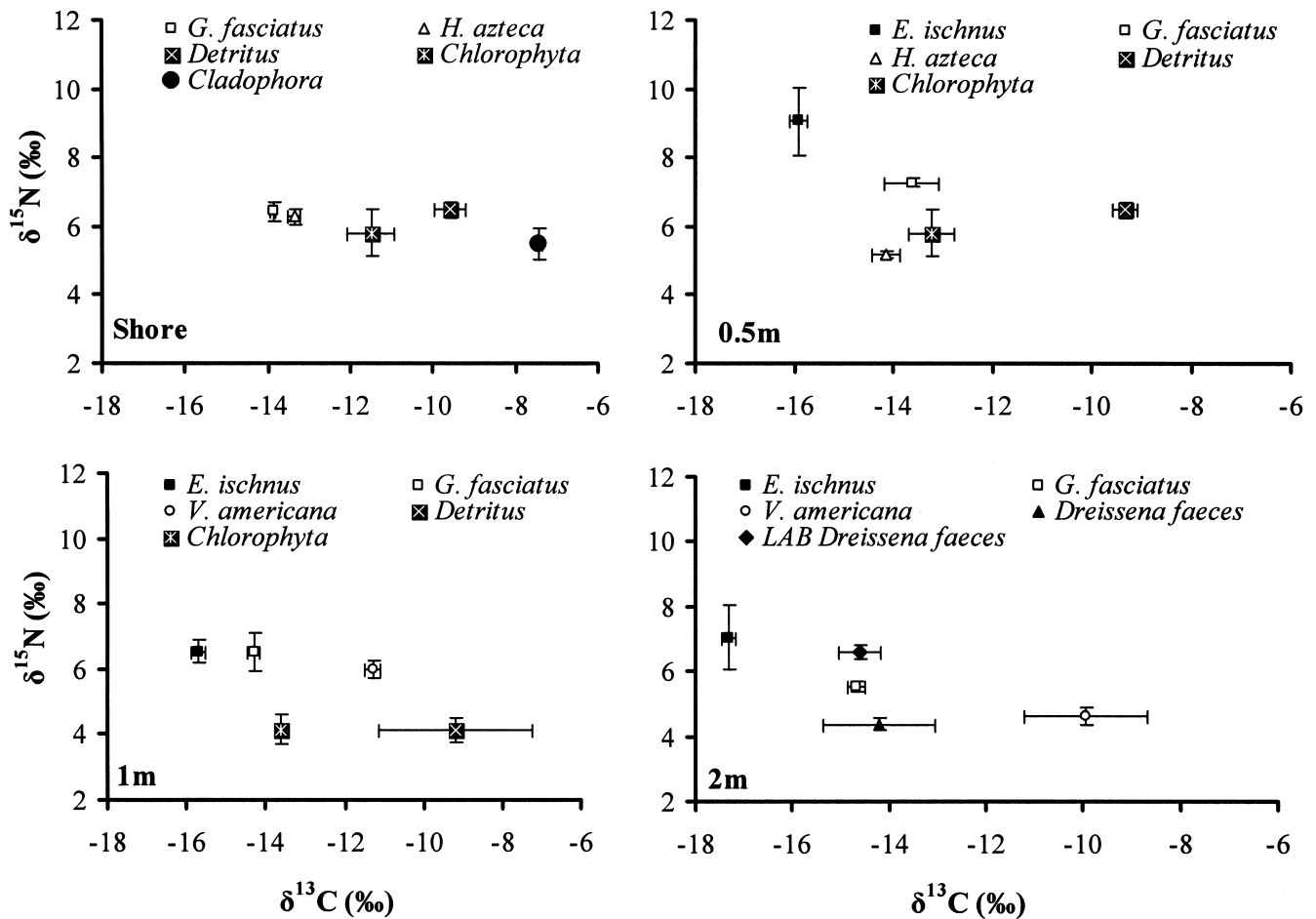


FIG. 3. Average (\pm SE) carbon and nitrogen isotopic composition of adult (males, females, and gravid females) *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyalella azteca* and potential food sources from different depths. Potential food sources shown are: detritus ($n = 2$), Chlorophyta ($n = 2$), Cladophora ($n = 2$), Vallisneria americana ($n = 2$), Dreissena faeces ($n = 4$), and LAB Dreissena faeces ($n = 2$) (see Material and Methods for details).

pleted carbon isotope signal, between -14.2 and -14.6 ‰. Faeces collected in the laboratory were more nitrogen-enriched ($\delta^{15}\text{N} = 6.6$ ‰) than those collected *in situ* ($\delta^{15}\text{N} = 4.4$ ‰; Fig. 3).

Isotope signatures demonstrated some variation according to depth from which amphipods were collected. For example, the carbon isotopic signatures of adult *E. ischnus* were more depleted at 2 m (-17.3 ‰) than at 0.5 m (-15.9 ‰) and 1 m (-15.7 ‰) (ANOVA, $p < 0.05$, Tukey test; Fig. 3). The nitrogen isotope signal of *E. ischnus* was slightly but insignificantly enriched at 0.5 m ($\delta^{15}\text{N} = 9.1$ ‰) as compared to the 1m ($\delta^{15}\text{N} = 6.5$ ‰) and 2 m ($\delta^{15}\text{N} = 7.0$ ‰) depths (ANOVA, $p = 0.1$; Fig. 3). No significant differences in isotopic signatures among depths were found for adult *G. fasciatus*

(ANOVA, $p > 0.05$). The nitrogen isotopic signature for *H. azteca* was more enriched near the shore ($\delta^{15}\text{N} = 6.2$ ‰) than at the 0.5 m depth ($\delta^{15}\text{N} = 5.1$ ‰) (ANOVA, $p < 0.05$; Fig. 3).

DISCUSSION

Our results indicate that faeces/pseudofaeces do not constitute a large part of the diet of *Echinogammarus ischnus*, as the carbon isotopic composition differed from what would be predicted from typical fractionation between a consumer and its food resource. This does not support the hypothesis that *Dreissena* may facilitate establishment and dispersal of *E. ischnus* through provision of food associated with its production of faeces and pseudofaeces

(Köhn and Waterstraat 1990, Burkart 1999, van Overdijk *et al.* 2003). The positive effect of *Dreissena* colonies on *E. ischnus* is thus probably the result of increased substrate complexity, which could function as a refuge from fish predators (see van Overdijk *et al.* 2003).

In contrast, the carbon isotopic composition indicate that mussel faeces/pseudofaeces may constitute a part of *Gammarus fasciatus* diet, possibly explaining why it has increased in abundance subsequent to establishment of *Dreissena* in Lake Erie, and why it was relatively abundant at 2 m depth (Fig. 1). The nitrogen isotopic composition of *G. fasciatus* was enriched by only 1‰ relative to *Dreissena* faeces, indicating that it also relies on other food sources. Faeces/pseudofaeces collected from mussels in the laboratory were more nitrogen-enriched compared to the faeces collected *in situ*. One explanation for the relatively lighter faecal material from the field could be that it is more degraded and thus composed of bacteria to a larger extent compared to freshly produced faeces from the laboratory. This indicates that amphipods do not select for freshly produced faeces but rather degraded organic matter produced within mussel colonies. Further studies are required to establish the importance of faeces/pseudofaeces in the diet of *G. fasciatus*.

Hyalella azteca and *G. fasciatus* had similar carbon isotopic signatures, indicating common food resources. Amphipods in general were carbon-depleted relative to detritus, algae and the macrophyte in this study, and juvenile *G. fasciatus* and *E. ischnus* had a lighter carbon isotope signatures than adults. Phytoplankton have a lighter carbon isotopic signal than benthic algae (Hecky and Hesslein 1995, France 1995), and may be the primary food source for young amphipods. None of the amphipods were clearly dependent on the food sources sampled in this survey, thus any discussion about the potential importance of faeces/pseudofaeces or phytoplankton remains speculative. In future studies, settling phytoplankton should be sampled and macrophytic algae with epiphytes could be further partitioned separating algal species from each other.

E. ischnus appears to be displacing or substituting for *G. fasciatus* in some areas (Ratti and Barton 2003, van Overdijk *et al.* 2003). This pattern could result from exploitative competition for food. While our study is limited to only a single transect in the western basin of the lake, the different isotopic signatures of these species indicate that they are likely exploiting different foods and not competing for

this resource. The carbon isotopic composition of *E. ischnus* was always more depleted than that of the two native species, indicating that it occupies a different food niche. Our results are based on data from one sampling occasion in early August and we cannot exclude that food competition could occur during other times of the year.

Nitrogen isotopic signatures suggest that *E. ischnus* is more carnivorous than either *G. fasciatus* or *H. azteca*. Laboratory studies have demonstrated some propensity for *E. ischnus* and *G. fasciatus* to prey upon each other when kept at low densities, although the primary interaction between these species appeared to be based on aggression by the former toward the latter (van Overdijk *et al.* 2003). However, carbon isotope signatures of *E. ischnus* were depleted (about 2‰) compared to the two other amphipod species and does not support the hypothesis that the two amphipods contribute significantly to the diet of *E. ischnus*. Therefore, it is more likely that *E. ischnus* consumes a mixture of food resources, possibly including a small fraction of amphipods. Small invertebrates, i.e. meiofauna, could constitute part of the diet of *E. ischnus*, as they are an important food source for amphipods in other aquatic habitats (e.g., Hwan Yu *et al.* 2003). Overall, the carbon isotopic signature of *E. ischnus* varied among depths, indicating that it is able to consume a variety of food items.

Two other hypotheses that may account for partial substitution of amphipod species are differential use of substrates and substrate-mediated vulnerability to predation. Previous work demonstrated that *E. ischnus* exhibited greater affinity for *Dreissena*-substrates, whereas *G. fasciatus* preferred both *Dreissena*- and *Cladophora*-encrusted habitats (van Overdijk *et al.* 2003). Areas with large *Dreissena* colonies would thus be expected to favour *E. ischnus*, while mixed substrates and those dominated by *Cladophora* or *Dreissena* should favour *G. fasciatus*. Field data from this study provide only partial support for these expectations. *G. fasciatus* was abundant in mixed habitats as well as in *Dreissena*-dominated ones, however, *E. ischnus* was most abundant at the 1 m depth in mixed-substrate habitats rather than at 2 m, where *Dreissena* dominated. Differential exposure to predators could also influence relative abundances of different amphipod species. Round gobies (*Neogobius melanostomus* (Pallas)) are very abundant throughout much of western Lake Erie, and as juveniles feed extensively on amphipods (Kuhns and Berg 1999). If exposure to fish predators varies as a function of the

substrate utilized by amphipods, it could affect relative species abundances.

Our field survey revealed that the overall abundance of *Gammarus fasciatus* was greater than that of *Echinogammarus ischnus* at our study site in western Lake Erie. This indicates that *G. fasciatus* is continuing to thrive in Lake Erie, is in agreement with a survey conducted at the eastern end of the lake during the same year (Ratti and Barton 2003). Prolific growth of *Cladophora* in the eastern basin may account for this trend, as *G. fasciatus* utilizes this substrate more extensively than does *E. ischnus* (van Overdijk *et al.* 2003). Our study showed that *Cladophora* was not as abundant at the study site, and thus cannot account for the high relative abundance of *G. fasciatus* here. For example, at our 2 m site the lake bottom was largely covered by *Dreissena* colonies, and abundance of *G. fasciatus* was high whereas that of *E. ischnus* was low. *E. ischnus* was abundant at the 1 m depth, where the lake bottom was covered by a mixture of algae and *Dreissena*.

In conclusion, isotopic signatures indicate that *E. ischnus* does not compete for food with *G. fasciatus* and *H. azteca*, although the latter species may exploit common resources. Changes in isotopic signatures among depths suggest a wide range of food items for *E. ischnus*. Carbon isotope signatures of juvenile and adult *E. ischnus* and *G. fasciatus* differed, suggesting an ontogenetic diet shift by both species.

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