Effects of Food Type, Habitat, and Fish Predation on the Relative Abundance of Two Amphipod Species, *Gammarus fasciatus* and *Echinogammarus ischnus*

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**ABSTRACT.** We evaluated the abundance patterns of *Gammarus fasciatus* and *Echinogammarus ischnus* in dreissenid and macrophyte areas in Hatchery Bay, Lake Erie before (1997) and after round goby (2001, 2002) invaded the area. Total amphipod abundance was higher before round goby invasion in both habitats. In mussel beds, *E. ischnus* abundance was similar or significantly higher than *G. fasciatus*. In macrophytes, *G. fasciatus* was significantly more abundant than *E. ischnus*. In laboratory experiments, we compared amphipod survivorship and growth when fed mussel feces and pseudofeces (F+P) or macrophytes with epiphytes (M+E). *Gammarus fasciatus* survivorship and growth were higher when fed F+P than M+E. *Echinogammarus ischnus* showed similar survivorship under both diets, but significantly higher growth when fed M+E than F+P. Therefore inter-habitat differences in food resources cannot explain the abundance patterns observed in the lake. We also estimated the relative vulnerability of *G. fasciatus* and *E. ischnus* to yellow perch (*Perca flavescens*) and round goby (*Neogobius melanostomus*) predation in laboratory feeding trials using mussel colonies or macrophyte beds as substrate. Both fish strongly preferred *E. ischnus* in macrophytes, but consumed relatively more *G. fasciatus* than *E. ischnus* in dreissenid habitats. Our results suggest that dreissenid establishment may have facilitated the invasion of *E. ischnus*. However, habitat-specific differences in vulnerability to fish predation may mediate the coexistence of *G. fasciatus* and *E. ischnus* by minimizing expansion of *E. ischnus* to macrophyte areas. Our results also suggest that round goby invasion can alter amphipod abundance patterns in Lake Erie.

**INDEX WORDS:** Amphipods, *Dreissena* spp., macrophytes, round goby, yellow perch, species coexistence.

**INTRODUCTION**

The success of biological invasions depends upon physical and biotic conditions in the target community (Elton 1958, Simberloff 1986). However, once an exotic species is established, it can modify abiotic and biotic conditions and facilitate the colonization success of future invaders (Aplet 1990). Introduced species can increase resource availability (Vitousek et al. 1987, Vitousek and Walker 1989), which can facilitate invasibility by other exotic species (Vitousek 1990, Aplet 1990). Furthermore, if invaders can increase resource heterogeneity they may increase the number of species that can coexist (MacArthur et al. 1972, Huston 1994). The success of an invader, however, may be constrained by predation risk (Robinson and Wellborn 1988). Predators can often decrease success of invaders by selectively consuming an exotic prey (Orians 1986). Conversely, predators can also enhance invasibility by selectively consuming a competitively superior native prey, therefore reducing interspecific competition and allowing coexistence of competitors (Lodge 1993).

Habitat heterogeneity can be an important factor mediating predator-prey interactions among native and exotic species (Crowder and Cooper 1982). Differences in refuge availability among habitats can mediate interspecific competition and lead to differences in the distribution of potential competitor species (Sih 1987, Duffy and Hay 1991). Predator-prey interactions also are dependent on differences in prey vulnerability to predation, which
are determined by the size, coloration and behavior of prey in relation to the habitat (see Heck and Crowder 1991 for a review).

The Great Lakes have been drastically affected by exotic species. The remarkable abundance of the exotic zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels have greatly modified littoral habitats and energy flow in the Great Lakes. Habitat complexity is greater in *Dreissena* clusters compared to bare rocks (González and Downing 1999). Dreissenids filter seston from the water column and subsequently deposit feces and pseudofeces (seson that is filtered, coated with mucous, then ejected without being ingested) at the lake bottom. Their high filtering capacity has led to increased water clarity (Leach 1992, Budd et al. 2001) and increased light penetration has led to an increase in near-shore macrophytes abundance (Stuckey and Moore 1995, Skubinna et al. 1995) and periphyton (Lowe and Pillsbury 1995). Thus, the dreissenid invasion has diversified littoral habitats due to increased habitat complexity in mussel colonies and increased macrophytes abundance. Mussel colonies and macrophytes may provide macroinvertebrates with different food resources and refuge from predation.

The effects of dreissenid invasion on macroinvertebrates on rocky substrates have been extensively studied in the last decade, while the role of increased macrophytes resulting from the dreissenid invasion is not well understood. Benthic invertebrate abundance on rocky substrates increased dramatically following the dreissenid invasion (Dermott et al. 1992, Stewart and Haynes 1994). In particular *Gammarus fasciatus*, a widely distributed amphipod species in North America (Clemens 1950), became one of the most abundant macroinvertebrates associated with dreissenid colonies (Dermott et al. 1992, Stewart and Haynes 1994, Ricciardi et al. 1997). Higher amphipod abundance on mussels is related to increased habitat complexity (Ricciardi et al. 1997, Stewart et al. 1998, González and Downing 1999). Macrophytes also increased the littoral habitat complexity and are utilized by benthic invertebrates (Gilinsky 1984). Information about amphipod populations in macrophytes in the Great Lakes is scarce, although amphipods can utilize such habitat (Clemens 1950, Dermott et al. 1998, Kashian and Burton 2000).

Recently two species from the Ponto-Caspian region have invaded the Great Lakes: the amphipod, *Echinogammarus ischnus* (Witt et al. 1997) and a fish, the round goby, *Neogobius melanostomus* (Jude et al. 1992). *Echinogammarus ischnus*, commonly associated with dreissenid colonies (Köhn and Waterstraat 1990), invaded Lake Erie in 1994 (Witt et al. 1997). Dermott et al. (1998) documented a higher abundance of *E. ischnus* than *G. fasciatus* on mussel colonies in several areas in the Great Lakes and suggested that *E. ischnus* had displaced *G. fasciatus* from mussel colonies. *Echinogammarus ischnus*, however, was scarce in macrophyte beds in Lake St. Clair and Lake Ontario (Witt et al. 1997, Dermott et al. 1998). In Lake Michigan, *E. ischnus* was abundant in sites with dreissenid colonies but was not present in sites with submerged vegetation (Nalepa et al. 2001). Round goby, a benthivorous fish species associated with riprap, vegetated areas and dreissenid colonies (Jude and DeBoe 1996), invaded Lake Erie in 1996 (Charlebois et al. 1997). Round gobies can feed on soft benthic invertebrates, including amphipods, but also prey on dreissenids (Charlebois et al. 1997, Ghedotti et al. 1995, Jude et al. 1995).

These two exotic species are likely to interact with *G. fasciatus* and native fish species such as yellow perch (*Perca flavescens*). Yellow perch is an important component of the commercial and sport fisheries in the Great Lakes, especially Lake Erie and Lake Michigan (Francis et al. 1995). Perch undergo three ontogenetic niche shifts (Wu and Culver 1991). Larval perch are pelagic and feed predominantly on zooplankton. Juveniles (30–200 mm) shift to become more littoral in their habitat and feed mainly macroinvertebrates. Perch spend several years at this feeding stage until they are large enough to become piscivorous (Hayes and Taylor 1990). In Lake Erie and Lake Michigan, benthic invertebrates such as amphipods are a major component of juvenile yellow perch diet, particularly after *Dreissena* spp. invasion (Robillard et al. 1999, Tyson and Knight, 2001). Yellow perch also consume *Dreissena* spp. (Morrison et al. 1997).

Food resources vary between mussel colonies and macrophytes beds. Biodeposition of organic matter, mainly in the form of feces and pseudofeces, is higher in the presence than in the absence of mussels (Klers et al. 1996, Stewart et al. 1998). Feces and pseudofeces are consumed by amphipods (Fisher et al. 1992), although the implications for amphipod fitness are not well understood. Amphipods can also consume macrophytes and associated epiphytes (Clemens 1950, Newman 1991, Delong et al. 1993). Therefore, dreissenid establishment may facilitate the invasion of *E. ischnus* by
providing increased food resources. In addition, differences in food resources between dreissenid and macrophyte-dominated habitats may determine spatial distributions of *E. ischnus* and *G. fasciatus*.

Differences between the type of refuge from fish predation provided by mussel and macrophytes may also mediate the distribution of native and exotic amphipods, although the value of the refuge provided by each habitat may depend on predator species. Similar benthic invertebrate biomass was observed in experimental ponds colonized by zebra mussels, with and without yellow perch (Thayer et al. 1997). Kuhns and Berg (1999) reported higher total invertebrate densities in colonization cages with zebra mussel colonies when round gobies were excluded. Therefore, yellow perch and round goby have the potential to affect amphipod abundance patterns.

Here we document differences in the distribution of *G. fasciatus* and *E. ischnus* in mussel colonies and macrophyte beds during late summer in 1996, 2001, and 2002. In 1996, sample sites were chosen at random within habitats dominated by dreissenids (100–80% dreissenid; 0–20% macrophytes) or macrophytes (100–80% macrophytes; 0–20% dreissenids) in Hatchery Bay (Peach Point and Gibraltar Island). We collected three samples from each habitat type (*Dreissena* spp. and macrophytes). In each habitat, a bucket (30-cm diameter) with a 90-µm sieve attached to the bottom was placed upside-down and buried 2 cm into the substrate. A thin metal sheet, attached to the bucket using bungee cords, was slid between the bucket and the substrate, and the bucket was carefully lifted from the sediment and placed into a pillowcase. Pillowcases were transported to the laboratory inside coolers in less than 2 hours. Substrates were agitated in a bucket with lake water for at least 25 min to remove amphipods. Amphipods samples were preserved with a 10% formalin solution and identified to species using a dissecting microscope.

In 2001 and 2002 (after round goby establishment), amphipod densities were considerably lower than in 1996 and we modified our sampling methodology. A 1 m² quadrat was randomly placed on the substrate and four samples from each quadrat were taken using the bucket sieve method described above. Samples from each quadrat were pooled. In 2001, we only collected samples from six randomly placed quadrats in areas dominated by dreissenids (100% dreissenids). In 2002, we collected samples from 14 quadrats chosen at random along two 50-m transects (Peach Point and near Perry’s Monument, seven quadrats in each transect). However, one quadrat sample from Perry’s Monument was not included in the analysis because no amphipods were present in the sample. The habitat composition (% dreissenids and % macrophytes) in the quadrats was more variable in 2002, so samples were categorized into three groups according to mussel cover (100–70%, n = 3; <70–30%, n = 4; and < 30–0%, n = 6). Macrophytes occupied substrate without dreissenids, except in one quadrat, where the macrophyte cover was 30% and the remaining 70% was bare rock. In both surveys, amphipods were removed from the substrate similarly to 1996, but amphipods were identified and counted immediately without preservation.

The percentage of juvenile amphipods that could not be identified was high only in 2001, so we did not include these individuals in our statistical analysis. In 1996 and 2002, we tested for differences in amphipod abundance among habitats using fixed-effects multivariate analysis of variance (MANOVA: treating the abundance of the two amphipod species as dependent variables, SAS Institute 1990). Since significant treatment effects were detected in the MANOVA, we performed interhabitat comparisons (mussel vs. macrophytes) for each species and inter-species comparisons (*G. fasciatus* vs. *E. ischnus*) within each habitat using t-tests. In 2001, we performed inter-specific comparisons in dreissenid-dominated habitat using a Hotelling t-test. All data were log-transformed to meet assumptions of variance homogeneity (Sokal and Rohlf 1988).

**Effect of Diet on Amphipod Survivorship and Growth**

We determined the effect of diet on survivorship and growth of *G. fasciatus* and *E. ischnus* by rear-
Amphipod abundance patterns in macrophyte and Dreissenid habitats

Amphipods were randomly arranged in six rows, with 27 containing 250 mL of filtered lake water and a live amphipod per cup for our experiments. Each amphipod was placed in a 300-mL plastic cup used one amphipod per cup for our experiments. Live amphipods within a few hours. Therefore we sent, we filtered lake water used in the experiment but had 33 replicates. Replicate numbers for E. ischnus treatments were lower because we obtained fewer offspring from ovigerous E. ischnus than from G. fasciatus. The F+P, M+E and no food treatments for E. ischnus had 24, 19, and 20 replicates respectively. Number of amphipods in E. ischnus treatments was chosen based on preliminary data that suggested amphipod growth was more variable in F+P treatments than in M+E and no food treatments.

Amphipod survivorship was measured weekly. Following the recommendations of Pyke and Thompson (1986), survivorship was analyzed using a non-parametric test for estimating survival distributions when not all individuals under treatment conditions are followed until death (LIFETEST procedure, SAS Institute 1990). We performed intraspecific comparisons among food treatments (M+E vs. F+P) and interspecific comparisons (G. fasciatus vs. E. ischnus) within each food treatment.

To quantify growth, we measured head length weekly by gently pouring an individual onto a 100 µm sieve and measuring from the rostrum tip to the posterior margin of the head using a microscope with an ocular micrometer. Following measurement, the amphipod was placed in a clean cup containing filtered lake water and fresh food. The measurement of head length instead of body length minimized the time that amphipods were under the microscope. Previous studies have shown a positive correlation between amphipod head length and total body length (Cooper 1965, Delong et al. 1993, Morrison et al. 1997). To verify this relationship we collected amphipods from Lake Erie and regressed total body length (TL) against head length (HL) for both amphipods. The results of the statistical analysis were similar using either head length or body length estimates. Here we present the results from the analysis using head length.

We calculated weekly growth (head length$_{\text{week } n}$ – head length$_{\text{week } n-1}$) for each treatment using amphipods that survived to the end of each week. We tested for intraspecific differences in growth among treatments using a repeated measures ANOVA (SAS Institute 1990). We tested for differences only...
between the F+P and M+E because after the first week there were not enough survivors in the no-food treatment to satisfy ANOVA assumptions.

We evaluated interspecific differences in mean growth using a two-way ANOVA to test for diet (F+P vs. M+E) and species (G. fasciatus vs. E. ischnus) effects. Because we detected a strong species*diet interaction (see results) we compared treatment means using a Tukey-Kramer test (Sokal and Rohlf 1988). All data were log-transformed to meet assumptions of variance homogeneity (Sokal and Rohlf 1988).

Fish Predation Experiments

We conducted laboratory experiments to estimate the relative vulnerability of G. fasciatus and E. ischnus to predation by yellow perch and round goby in two simulated habitats, mussel colonies and macrophyte beds.

Experiments were conducted in 80-L aerated aquaria containing either cobbles with dreissenid colonies or macrophytes in a 0.0625 m² area. Macrophyte habitats consisted of 17 shoots of V. americana (shoot density, 272 shoots/m²) cut to the height of the aquarium (30 cm) and weighted down by metal nuts. Mussel habitats consisted of three pieces of cobble (cobble density, 48/m²) colonized by mussels (mean # mussels/m² = 1,203 ± 44SD). Mean # of mussels/tank was never significantly different among tanks (p > 0.9). Shoot and mussel densities used in the trials were within the range observed in the lake during early August (215–312 shoots/m², 906–2,172 mussels/m²). Aquarium walls were covered with black plastic material to minimize disturbance of fish and to ensure that fish were not influenced by activity in neighboring tanks. Laboratory temperature during the fish experiments was 23–24°C.

Yellow perch and round goby were collected in Hatchery Bay by seining or cast netting. Fish were acclimated in the laboratory for two weeks during which they were fed both amphipod species. Fish were starved for 48 hours prior to an experiment. In all experiments we removed the fish after 24 hours, and the remaining amphipods were counted by species. Fish were measured and weighed at the end of each experiment.

Yellow Perch Experiments

We estimated yellow perch predation rates in August 1997 and June 2001. In both experiments we added 100 G. fasciatus and 100 E. ischnus to each aquarium and allowed them to acclimate for 12 hours. We then added three fish to each aquarium. In 1997 there were three replicates per habitat, while in 2001 there were four replicates per habitat. A two-way ANOVA (date and habitat effects) indicated significant differences in total fish length and biomass between dates. Because consumption rates can depend on fish size (Kitchell et al. 1977), we analyzed each experiment independently.

Round Goby Experiments

We estimated round goby predation rates in August 2000 and 2001. We had difficulty collecting E. ischnus during summer 2000, therefore we only added 65 G. fasciatus and 65 E. ischnus to each aquarium. We added only two fish per tank due to the lower amphipod number. Fish mortality in two tanks (one dreissenid and one macrophyte habitat) reduced the number of replicates in both treatments to only two. In 2001 there were four replicates per habitat. Similar to the yellow perch experiments, we added 100 G. fasciatus and 100 E. ischnus and three round gobies to each tank. A two-way ANOVA detected significant differences in fish biomass/tank between dates. Due to the differences in fish biomass and amphipod density we decided to analyze each experiment independently.

In all experiments, fish consumption rates (total number of amphipods consumed/g fish biomass/day) and the ratio of the number of G. fasciatus and E. ischnus consumed (G:E) were analyzed using t-tests (SAS Institute 1990) to assess differences in fish predation between mussel and macrophyte habitats. Data were log-transformed to meet assumptions of variance homogeneity (Sokal and Rohlf 1988). We also tested if the Gammarus: Echinogammarus ratio consumed in each habitat was different from one using a two-tailed t-test. Ratios > 1 indicated a higher vulnerability of G. fasciatus to fish predation, while ratios < 1 indicated a higher vulnerability of E. ischnus to fish predation.

RESULTS

Amphipod Abundance Patterns

In 1996, we detected significant differences in amphipod abundance patterns between habitats (Wilk’s lambda value = 0.148, F_{1,4} = 22.94, p = 0.009). Inter-habitat comparisons showed that G. fasciatus abundance was significantly higher in macrophytes than in dreissenid colonies (Fig. 1a,
abundance tended to be slightly higher than *G. fasciatus*, although this trend was not statistically significant ($t_{0.05,4} = 1.73, p = 0.15$).

In 2001 and 2002, total amphipod abundance was ten-fold lower than in 1996. *Echinogammarus ischnus* abundance was significantly higher than *G. fasciatus* abundance in dreissenid colonies in 2001 (Fig. 1b; Hotelling-Law value = 172.5, $F_{2,3} = 258.8$, $p = 0.0004$).

In 2002, we also detected significant differences in amphipod abundance patterns between habitats (Wilk’s lambda value = 0.153, $F_{2,10} = 27.6$, $p < 0.001$). Inter-habitat abundance patterns differed from those found in 1996. *Gammarus fasciatus* abundance was similar among habitats ($F_{2,10} = 4.74$, $p = 0.09$), while *E. ischnus* abundance was significantly higher in dreissenid dominated habitat (100-70%) than in habitats with <70% dreissenid cover (Fig. 1.c, $F_{2,10} = 77.75$, $p < 0.001$). As in 1996, inter-species comparisons showed that *G. fasciatus* was significantly more abundant than *E. ischnus* in habitats with a <70% dreissenid cover ($F_{1,6} = 8.36$, $p = 0.03$ in <70–30% and $F_{1,10} = 230$, $p < 0.0001$ in 0 – <30%). *Echinogammarus ischnus* abundance also tended to be higher in dreissenid dominated habitat, but the trend was not statistically significant ($F_{1,4} = 6.07, p = 0.06$).

**Effect of Diet on Amphipod Survivorship and Growth**

Survivorship of both amphipod species was significantly lower in the no food treatment than in the food treatments (*G. fasciatus*: $X^2_{1,0.05} = 19.7$ for F+P and 34.2 for M+E; *E. ischnus*: $X^2_{1,0.05} = 23.3$ for F+P and 19.02 for M+E; $p = 0.0001$; Fig. 2). Survivorship of *G. fasciatus* fed F+P was significantly higher than those fed M+E ($X^2_{1,0.05} = 5.5$; $p = 0.02$; Fig. 2a), but *E. ischnus* showed similar survivorship when fed either F+P or M+E ($X^2_{1,0.05} = 0.18; p = 0.6$; Fig. 2b).

Interspecific comparisons showed that *E. ischnus* survivorship was significantly higher than *G. fasciatus* survivorship when fed M+E ($X^2_{1,0.05} = 5.80; p = 0.02$; Fig. 2). However, there were no significant differences between the two species when raised on F+P ($X^2_{1,0.05} = 0.09; p = 0.8$; Fig. 2).

We found a strong correlation between total body length and head length for *G. fasciatus* (TL (mm) = 10.768 (HL) – 1.460; $r^2 = 0.91$ n = 64) and *E. ischnus* (TL (mm) = 9.554 (HL) - 0.871; $r^2 = 0.86$ n = 123). Both amphipod species showed an increase in mean body length over the eight-week period (Fig. 2b).
Intraspecific comparisons detected significant date effects for both species ($F_{8,296} = 115.2$ for *G. fasciatus* and $F_{8,296} = 58.56$ for *E. ischnus*; $p < 0.0001$) and a significant diet effect only for *G. fasciatus* ($F_{1,395} = 27.2$, $p < 0.001$). However the date *diet interactions were significant for both species ($F_{8,395} = 2.64$, $p < 0.02$ for *G. fasciatus* and $F_{8,296} = 5.46$, $p < 0.0001$ for *E. ischnus*), mainly because differences in growth between treatments varied with time. In 5 out of 8 weeks, *G. fasciatus* grew more when fed F+P than when fed M+E, while in the other 3 weeks growth was similar on both diets (Fig. 3a). *Echinogammarus ischnus* grew more when fed M+E than when fed F+E only during the last 2 weeks of the experiments (Fig. 3b).

Interspecific comparisons of mean growth at the end of the experiment showed significant species effects ($F_{1,65} = 171.6$, $p < 0.0001$), but a species*diet interaction ($F_{1,65} = 25.5$, $p < 0.0001$). *Gammarus fasciatus* grew more when fed F+P than when fed M+E, whereas *E. ischnus* showed the opposite pattern (Fig. 4).

### FIG. 2. Weekly survivorship of (a) *G. fasciatus* and (b) *E. ischnus* in the feces and pseudofeces (F+P), macrophytes (M+E) and no food (NF) treatments over an 8-week period.

### FIG. 3. Weekly mean body length ($± 1$ SE) of (a) *G. fasciatus* and (b) *E. ischnus* in the feces and pseudofeces (F+P), macrophytes (M+E), and no food (NF) treatments over an 8-week period. Error bars that are not apparent are smaller than the symbols.

### FIG. 4. Mean growth ($± 1$ SE) of (a) *G. fasciatus* and (b) *E. ischnus* fed feces and pseudofeces (F+P) or macrophytes (M+E). Letters indicate that growth was different at a 0.05 significance level (Tukey-Kramer).
Amphipod Abundance Patterns in Macrophyte and Dreissenid Habitats

Fish Predation Experiments

Yellow Perch Experiments

Yellow perch consumption rate was higher in the 1997 than in the 2001 experiments, probably because yellow perch individuals were smaller in 1997 than in 2001. We observed significant differences in total fish length (6.6 cm ± 0.1 TL in 1997 and 14.0 cm ± 0.2 in 2001; \( F_{1,10} = 329.7, p < 0.0001 \)) and biomass (14 g ± 0.4 in 1997 and 87g ± 4.2 in 2001; \( F_{1,10} = 856.7, p < 0.0001 \)) between dates. However no significant habitat effects or date*habitat interactions were observed in total fish length and fish biomass/tank.

In both experiments, yellow perch consumption rates were similar between habitat treatments (Fig. 5a and b). However, G:E ratios were significantly lower in the macrophyte than in the mussel treatments (\( t_{0.05,4} = 8.63, p = 0.04 \) in 1997; \( t_{0.05,6} = 2.94, p = 0.03 \) in 2001; Fig. 5c and d). G:E ratios were significantly less than 1 in macrophyte treatments indicating a higher vulnerability of *E. ischnus* to yellow perch predation in this habitat (\( t_{0.05,2} = 18.58, p = 0.001 \) in 1997; \( t_{0.05,3} = 4.57, p = 0.01 \) in 2001). In mussel treatments the G:E ratios were not significantly different than 1, indicating similar vulnerability of *G. fasciatus* and *E. ischnus* to yellow perch predation.

Round Goby Experiments

No significant differences in size (9.7 cm ± 0.2 TL in 2000 and 9.8 cm ± 0.2 in 2001) were detected between dates. However, the fish biomass/tank was significantly lower in 2000 that in 2001 (27.1 g ± 0.2 in 2000 and 38.6 g ± 0.5 in 2001, \( F_{1,8} = 58.1, p < 0.001 \)). No significant habitat effects or date*habitat interactions were observed in total fish length and fish biomass/tank.

Round goby consumption rates were significantly

![Bar chart](chart.png)

**FIG. 5.** (a,b) Mean consumption rates (amphipod/g/d ± 1 SE) and (c, d) mean consumed G. fasciatus:E. ischnus ratios in mussel and macrophyte habitats after three yellow perch were allowed to feed for 24 hours. Error bars that are not apparent are smaller than the symbols.
higher in macrophyte treatments than in mussel treatments in both experiments ($t_{0.95,2} = 7.18$, $p = 0.02$ in 2000; $t_{0.95,6} = 4.34$, $p = 0.005$ in 2001, Fig. 6a and b). The G:E ratio was significantly lower in the macrophyte treatment than in the mussel treatment only in 2001 ($t_{0.95,6} = 2.87$, $p = 0.02$, Fig. 6c and d). In macrophyte treatments the G:E ratio was significantly less than 1 only in 2001 ($t_{0.95,3} = 7.47$, $p = 0.002$), indicating a higher vulnerability of *E. ischnus* to round goby predation. In mussel treatments, the G:E ratios were not significantly different from 1 indicating similar vulnerability of *G. fasciatus* and *E. ischnus* to round goby predation in this habitat.

**DISCUSSION**

Our survey results showed inter-habitat differences in the abundance of both amphipod species. *Gammarus fasciatus* abundance was consistently higher in macrophyte treatments than in dreissenid colonies, while *E. ischnus* abundance tended to be higher in dreissenid colonies. Previous studies have also reported higher abundance of *E. ischnus* in mussel colonies than in vegetation dominated areas (Witt et al. 1997, Dermott et al. 1998, Nalepa et al. 2001).

Our results support previous work that suggests the exotic *E. ischnus* may be displacing *G. fasciatus* on rocky substrate areas in the Great Lakes-St. Lawrence system (Dermott et al. 1998). An earlier study suggested that *G. fasciatus* was equally abundant in macrophyte beds and rocky substrates (Clemens 1950) in Hatchery Bay before the invasion of *Dreissena* sp. and *E. ischnus*. Prior to the invasion of *E. ischnus*, *G. fasciatus* was the dominant amphipod in mussel colonies, in terms of numbers and biomass, in Lake Erie including Hatchery Bay (Dermott et al. 1992, Dermott et al. 1998). However, the higher abundance of *G. fasciatus* in macrophyte beds suggests that the presence...
of macrophytes may allow *G. fasciatus* to coexist with the exotic species.

The drastic decrease in amphipods between 1996 and 2000-2001 cannot be attributed to differences in methodology because a similar decrease was observed in the average number of amphipods colonizing experimental cages placed in dreissenid colonies in 2001 (92 ± 15 (SE) individuals/cage; González unpublished) compared to 1995–1996 (1630 ± 275 (SE) individuals/cage; González and Downing 1999). The drastic decrease in the total number of amphipods in both habitats may be related to the invasion of round goby in the study area during 1998. Our experimental cages in those experiments excluded predators. However, regular observations by SCUBA divers observed no round gobies located around the cages in 1995 and 1996, while the average number of round gobies located around the cages was 4.45 ± 0.9(SE)/cage in 2001 (González unpublished). Kuhns and Berg (1999) reported lower benthic invertebrate abundance in colonization cages where round gobies was allowed to feed compared to cages excluding round gobies.

Food (Klerks et al. 1996, Stewart et al. 1998) and shelter (Ricciardi et al. 1997, González and Downing 1999) for benthic invertebrates have increased since the invasion of *Dreissena* sp. Although many researchers have speculated about the potential importance of feces and pseudofeces in the diet of benthic invertebrates (Klerks et al. 1996, Griffiths et al. 1992, Fisher et al. 1992), ours is the first study to document the effects of this food on amphipod survivorship and growth. The higher survivorship and growth of *G. fasciatus* when fed dreissenid egestion products provide evidence that the drastic increase of this amphipod after the *Dreissena* sp. invasion was related to increased in food availability in addition to increased habitat complexity.

Our survivorship and growth experiments, however, suggest that differences in the relative abundance of *G. fasciatus* and *E. ischnus* cannot be explained by differences in food quality associated with each habitat. Based on our intraspecific and interspecific comparisons we would expect the relative abundance of *G. fasciatus* to be higher in mussel colonies than in macrophyte beds, because growth and survivorship of *G. fasciatus* was significantly greater when fed F+P than when fed M+E. Although survivorship of both amphipods was similar under F+P diet, *G. fasciatus* net growth was higher than *E. ischnus*. Results for *E. ischnus* are more complex. Based on the intraspecific comparisons we would expect similar *E. ischnus* abundance in both habitats. The growth and survivorship of *E. ischnus* was similar when fed F+P or M+E. Our interspecific comparison, however, suggest that *E. ischnus* exhibited greater survivorship and growth than *G. fasciatus* under M+E diet.

Predation risk is an important factor constraining the spatial distribution of marine and freshwater organisms (Werner et al. 1983, Duffy and Hay 1991, González and Tessier 1997). Our results suggest that differential vulnerability to fish predation between habitats may explain differences in relative abundance of *G. fasciatus* and *E. ischnus* in mussel colonies and macrophyte beds. The lower relative abundance of *E. ischnus* in macrophytes may be caused by higher vulnerability of this amphipod to fish predation in this habitat. The G:E ratios were significantly lower in macrophyte than mussel habitats in three out of four experiments (Figs. 5 and 6) indicating fish preference for *E. ischnus* in this habitat. Also G:E ratios were significantly < 1 in the same three experiments indicating higher vulnerability of *E. ischnus* to fish predation than *G. fasciatus*. In the mussel habitat fish tended to consume more *G. fasciatus* than *E. ischnus*, but G:E ratios were never significantly > 1 indicating similar vulnerability of the two amphipod species to fish predation in this habitat. The lack of statistically significant results in the 2000 round goby experiment was probably related to low statistical power due to the loss of some replicates. However it is important emphasize that G:E ratio tend to be lower in macrophyte than mussel habitats, as in the other three experiments.

The similar trends in consumption patterns between yellow perch and round goby suggest that predator preferences were related to prey-specific characteristics mediated by habitat. Differences in coloration, size, and behavior between *G. fasciatus* and *E. ischnus* may lead to variability in their susceptibility to fish predators between habitats. In macrophytes the light greenish-gray color and clinging behavior (“C-shaped posture”) of *G. fasciatus* (Clemens 1950) may be better camouflage, whereas the relatively dark reddish color and more active behavior of *E. ischnus* (Burkart 1999) may make it more visible to predators in macrophyte beds. Active swimming behavior has been documented in *E. ischnus* (reviewed by Nalepa et al. 2001). Behavioral differences (movement) among *Crangonyx pseudogracilis*, *G. duebebeni*, and *G. pulex* was an important factor determining the feeding preference of brown trout on these three amphipod species (MacNeil et al. 1999). *Crangonyx*...
was preferentially consumed by brown trout. The most common escape response exhibited by *C. pseudograsicilis* was to swim away, while both *Gammarus* species usually adopted a “C-shaped posture” that make handling by trout difficult.

The lower overall amphipod consumption in mussel colonies in both round goby experiments may be related to mussel consumption by round goby. Stomach content analyses have showed that round gobies > 7 cm TL rely more on dreissenids, compared to round gobies < 7 cm TL (Jude et al. 1993, Ray and Corkum 1997, French and Jude 2001). The mean size of round goby in our experiments was 9.8 cm and we observed fragments of mussel shell in several tanks after the feeding trials.

The similarity in prey preference exhibited by both fish species, and the drastic decrease in benthic invertebrates after round goby invasion, suggest potential competition between round goby and yellow perch. Under intense competition for resources during the benthivorous feeding stage, round goby can create a bottleneck in yellow perch growth and delay the ontogenetic shift of perch to piscivory (Olson 1996, Heath and Roff 1996). Hence yellow perch may be vulnerable to predation by piscivores for a longer period of time, and high predator-induced mortality on young yellow perch may cause poor recruitment (Hartman and Magraf 1993). However, competition may depend on fish size. In our experiments small yellow perch (6.6 cm TL) show overall higher consumption rates than round gobies (9.8 cm TL), while larger yellow perch (14 cm TL) consumption was considerably lower than round goby. Studies investigating competition between yellow perch and round goby should consider size structure of populations.

Intraguild predation has been identified as an important factor determining the establishment of exotic amphipods in streams in Ireland and England (Dick et al. 1993, 1999). Intraguild predation between *G. fasciatus* and *E. ischnus* has recently been evaluated under laboratory conditions (Kozac 2001). *Gammarus fasciatus* prey more often on *E. ischnus* than vice versa, regardless of whether amphipods are fed M+E or F+P. Based on these findings we would expect *G. fasciatus* to be the dominant amphipod in both habitats. Fish predation may mediate the importance of intraguild predation on *E. ischnus* populations differently in mussel and macrophyte habitats. In mussel colonies higher fish predation on *G. fasciatus* may release *E. ischnus* from intraguild predation and competition by *G. fasciatus*. In macrophyte beds a strong vulnerability to fish predation and intraguild predation may limit the abundance of *E. ischnus*. Future studies should focus on how fish and intraguild predation mediate amphipod population distributions in mussel colonies and macrophyte beds.

In summary, we found differences in the relative abundance of *G. fasciatus* and *E. ischnus* between mussel and macrophyte beds. Amphipod species were differentially affected by food resources and fish predation pressure associated with mussel colonies and macrophyte beds. However, habitat-specific differences in amphipod relative abundance seem to be related to differential vulnerability to fish predation between amphipod species rather than differences in food availability between habitats. Our results suggest that diversification of the benthic habitat caused by dreissenid invasion (establishment of mussel colonies and proliferation of macrophytes) as well as habitat-specific differences in vulnerability to fish predation seem to mediate the coexistence of *G. fasciatus* and *E. ischnus* in Lake Erie by allowing the displacement of *G. fasciatus* by *E. ischnus* in mussel colonies and minimizing the expansion of *E. ischnus* into macrophyte areas. This study also suggests that the establishment of round goby may expand the overall predation pressure on amphipod populations in macrophytes and mussel colonies causing substantial changes in benthic invertebrates communities in the Great Lakes. Furthermore, due to the dietary overlap between round goby and yellow perch, the drastic decreases in benthic invertebrate abundance observed in this study after the round goby invasion may cause a bottleneck effect on growth rate of benthic yellow perch.

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