

# Microhabitat selection by the invasive amphipod *Echinogammarus ischnus* and native *Gammarus fasciatus* in laboratory experiments and in Lake Erie

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## SUMMARY

1. The amphipod *Echinogammarus ischnus* was first reported in the Laurentian Great Lakes during 1995. However, analysis of archived samples revealed the presence of the species from western Lake Erie in 1994 and possibly as early as 1993.
2. Surveys conducted in Lake Erie between 1995 and 1998 revealed that *Echinogammarus* was the dominant amphipod on rocks covered by *Dreissena* molluscs compared with those fouled by the filamentous alga *Cladophora*, while *Gammarus fasciatus* used both *Dreissena* and *Cladophora* substrata extensively.
3. In laboratory habitat selection studies, *Echinogammarus* chose *Dreissena*- over *Cladophora*-encrusted rocks and bare rocks, while *Gammarus* occupied the more complex substrata equally.
4. Field colonisation experiments demonstrated that the densities of *Echinogammarus* and *Gammarus* were positively correlated when the total density of the species was low, in contrast to the large-scale natural distribution of the species that revealed a strong inverse relationship.
5. The on-going replacement of *Gammarus* by *Echinogammarus* in the Laurentian Great Lakes may be related to the stronger affinity of the latter for substrata fouled by *Dreissena*, a genus with which it co-evolved.

*Keywords:* amphipods, competitive displacement, exotic species, habitat selection, Lake Erie

## Introduction

The North American Great Lakes are among the most highly invaded aquatic ecosystems, largely as a consequence of commercial shipping activities (Mills *et al.*, 1993; Ricciardi, 2001). The Ponto-Caspian basin (i.e. Black Sea, Azov Sea and Caspian Lake) has been the donor region for many of the non-indigenous species that have established in the Great Lakes in recent years (Ricciardi & MacIsaac, 2000; Reid & Orlova, 2002; Vanderploeg *et al.*, 2002). Prominent Ponto-Caspian species established in the Great Lakes

include zebra mussels *Dreissena polymorpha* (Pallas), quagga mussels *Dreissena bugensis* (Andrusov), round gobies *Neogobius melanostomus* (Pallas) and fishhook waterfleas *Cercopagis pengoi* (Ostroumov). *Echinogammarus ischnus* (Stebbing), an amphipod native to the Ponto-Caspian basin, was discovered at a single site in the lower Detroit River in 1995 (Witt, Hebert & Morton, 1997). Its range has since expanded dramatically, now encompassing all of the Great Lakes and the St Lawrence River (Dermott *et al.*, 1998; Nalepa *et al.*, 2001; Grigorovich *et al.*, 2003). Previously, the species spread throughout Europe dispersing *via* rivers, new canal systems and commercial ships (Jażdżewski, 1980; Bij de Vaate *et al.*, 2002).

The amphipod *Gammarus fasciatus* Say is a numerically dominant member of benthic communities in

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many areas of the Great Lakes with large *Dreissena* populations. For example, *Gammarus* densities increased significantly in Lakes St Clair, Erie and Ontario after the *Dreissena* invasion, apparently owing to enhanced habitat availability (Dermott *et al.*, 1993; Griffiths, 1993; Stewart & Haynes, 1994; Wisenden & Bailey, 1995; Botts, Patterson & Schlosser, 1996; Ricciardi, Whoriskey & Rasmussen, 1997; Bially & MacIsaac, 2000). The amphipod lives in interstitial spaces between *Dreissena* shells, where it is afforded refuge from predators and abiotic disturbances (Wisenden & Bailey, 1995; Bially & MacIsaac, 2000). It may also benefit from an enhanced food supply associated with the production of faeces and pseudo-faeces by *Dreissena* (Wisenden & Bailey, 1995; Botts *et al.*, 1996; Ricciardi *et al.*, 1997; Kuhns & Berg, 1999).

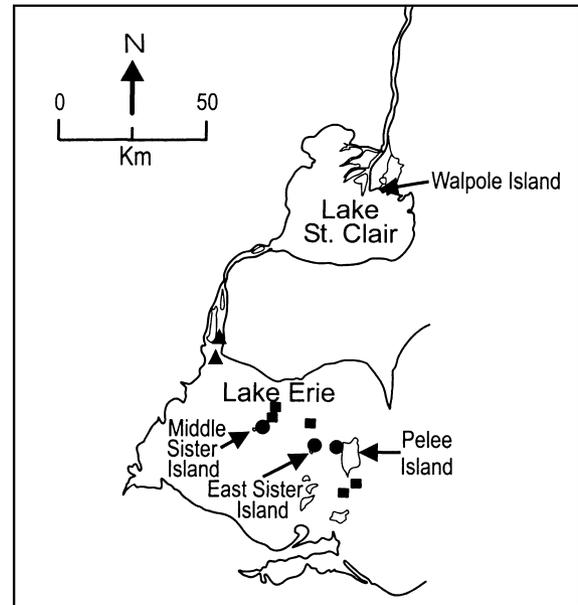
Dermott *et al.* (1998) speculated that *Echinogammarus* was replacing *Gammarus* at sites surveyed in western Lake Erie. While the establishment and range expansion of *Echinogammarus* may be related to facilitation by the co-evolved *Dreissena* (see Ricciardi, 2001), to date no mechanistic or *in situ* studies have been conducted to assess habitat preferences of the invading *Echinogammarus* or its potential effects on *Gammarus* in the Great Lakes.

In this study, we assess the possible date of establishment of *Echinogammarus* and examine temporal changes in the density of *Echinogammarus ischnus* and *G. fasciatus* in western Lake Erie. Further, we examine habitat preferences of these amphipods using laboratory and field manipulation experiments, and determine whether *Gammarus* is adversely affected by *Echinogammarus*.

## Methods

### Temporal amphipod survey

Invertebrate samples were collected in western Lake Erie during June 1994 (see Fig. 1) using a petite Ponar grab, and sieved through a 600- $\mu$ m mesh. In addition, epilithic invertebrates or those associated with *Dreissena* were collected from nearshore rocks at Pelee, Middle Sister and East Sister Islands (Fig. 1). Animals were initially fixed in 5% Kahle's solution, passed through a series of sieves (1-mm, 500- $\mu$ m and 250- $\mu$ m), sorted by order and stored in 70% ethanol. Identity of amphipods was determined using descriptions from Witt *et al.* (1997). *Echinogammarus* and *Gammarus* total



**Fig. 1** Location of sites sampled in western Lake Erie during 1994. Triangles represent sites where *Gammarus fasciatus* and *Hyalella azteca* were collected, squares where only *G. fasciatus* were collected, and circles where *Echinogammarus ischnus* and *G. fasciatus* were collected. Surveys were also conducted during 1995–98 at Middle Sister Island, as was an amphipod colonisation experiment during 1998. Animals for laboratory habitat preference experiments were collected during 1998 near Middle Sister and Walpole Islands.

body length (i.e. tip of rostrum to end of telson) was assessed using a Leica Wild M8 dissecting microscope (Leica, Heerbrugg, Switzerland), with output of images obtained from a Hitachi VK-C370 video camera (Hitachi Ltd., Tokyo, Japan) to an image analysis system (OPTIMAS, Version 6.2, Optimas Corp., Bothell, WA, USA).

Samples for amphipod species composition were collected from 1995 to 1998 near Middle Sister Island, western Lake Erie (see Fig. 1). Investigators and collection methods varied between years, thus statistical analyses are limited to 1995 and 1998 (i.e. years with consistent methods). In all cases, transects were fixed perpendicular to shore on the west and east sides of the island. Four and three transects were used in June 1995 and 1996, respectively. Six rocks, encrusted with *Dreissena*, were collected by self contained underwater breathing apparatus (SCUBA) at each of five different depths. Rocks were sealed underwater in polypropylene bags, brought to the surface and fixed with 5% Kahle's solution. Depths sampled in 1995 included 0.9, 1.5, 1.8, 2.7 and 3.6 m.

During 1996 and 1997 only three transects were surveyed in the littoral zone (<3 m depth), and exact depths from which rocks were collected were not recorded. During 1997 and 1998, rocks were collected in August (late summer) rather than June (early summer) along the same transects used in 1996. During 1997 and 1998, five *Dreissena*-encrusted rocks and five *Cladophora*-encrusted rocks were randomly collected at each of five depths. Depths sampled during 1998 included 0.5, 1.0, 1.5, 2.0 and 2.5 m. Samples collected during 1996–98 were fixed in 5% sugar–formalin.

In the laboratory, all rocks were scraped clean and animals placed in separate jars and preserved in 70% ethanol (1995) or 5% sugar–formalin solution (1996–98). Amphipods were identified using Witt *et al.* (1997) and counted. In 1995 and 1996, rock surface area was measured from the mass of aluminium foil required to cover the rock. Volume of rocks was assessed by water displacement in 1997 and 1998, and then converted to area (cm<sup>2</sup>) from a surface area–rock volume relationship (MacIsaac, 1996; unpublished data).

*Dreissena* samples were cleaned by removing shell fragments and byssal threads, blotted dry, and their wet mass recorded on an AND FX-200 electronic balance (Tokyo, Japan). *Cladophora* wet weight was determined on the balance after filaments were compressed between paper towels to remove excess water.

The number of amphipods collected was converted to density (nos cm<sup>-2</sup>) on the rocks from which they were collected, and densities  $\log(x + 1)$  transformed prior to statistical analysis (SYSTAT, Version 8.0, Systan Inc., Evanston, IL, USA). In 1995, densities of *Echinogammarus* and *Gammarus* on rocks fouled by *Dreissena* were analysed separately in relation to lake depth using one-way ANOVA. If significant differences were detected, Bonferroni's test ( $\alpha = 0.05$ ) was used to explore the differences. For 1998, the density of these species was analysed using two-way ANOVA (depth and substratum), with interaction. Substrata included *Dreissena*- and *Cladophora*-encrusted rocks. A *t*-test was used to explore species differences in mean body length for amphipods collected as part of the 1998 field survey.

#### Laboratory experiment of habitat preference

A replicated experiment in laboratory aquaria was conducted to determine amphipod habitat choice over

a 24-h period from 17 to 18 July and 13–14 August 1998. Experiments were conducted in a controlled environment chamber (21 °C and constant light) using aerated, 40-L aquaria filled with 20-L of filtered Detroit River water (Watergroup sand filter (Regina, SK, Canada) AMG-FDXT). A block of four experimental treatments, each replicated five times, was designed to assess amphipod habitat selection and interspecific interactions. Experimental treatments consisted of 50 *Echinogammarus*, 50 *Gammarus*, 25 each of *Echinogammarus* and *Gammarus* (low density), and 50 of each species (high density). Three equal-sized 'habitat' substrata randomly placed within each aquarium included: bare rocks from Middle Sister Island, *Cladophora*-encrusted rocks and *Dreissena*-encrusted rocks. The latter two-substratum types were collected at Middle Sister Island approximately 24 h before the experiment. These rocks with encrusted *Cladophora* or *Dreissena* were agitated in a bucket of water for 5 min to remove existing animals, and then transferred to experimental aquaria 24 h prior to the experiment along with the bare rock.

Study amphipods were collected at Middle Sister Island approximately 72 h before the experiment. Rocks encrusted with either *Cladophora* or *Dreissena* were agitated in a bucket of lake water for approximately 1 min to dislodge amphipods. The water in the bucket was then passed through a 1-mm sieve and amphipods retained were placed in a cooler containing lake water for transport to the laboratory. *Echinogammarus ischnus* and *G. fasciatus* were identified, sorted and held in separate aerated aquaria containing filtered Detroit River water with *Elodea canadensis* Michaux as a food source. Owing to the low density of *G. fasciatus* at the collection site, additional amphipods were collected near Walpole Island, Lake St Clair (Fig. 1) *via* repeated hauls of a benthic sled dredge, approximately 48 h before the experiment. The amphipods collected were retained on a 1-mm sieve, identified, separated and placed into their respective holding aquaria.

Healthy, mature amphipods of varying size and sex were randomly selected from holding tanks, counted and placed into separate 1-L mason jars filled with filtered Detroit River water, following which one block of each of the four treatments was initiated by decanting amphipods into experimental aquaria. This process was repeated four more times, and aquaria walls shrouded to prevent human disturbance during

the experiment and reclamation procedure. After 24-h, plastic dividers with a silicone gasket base were inserted into each aquarium to separate the rocky substrata, thereby preventing amphipods from relocating during recovery. All amphipods were thus associated with a substratum at the end of each experiment. Rocks were removed, one at a time from each aquarium, rinsed with filtered Detroit River water, and amphipods collected on a 40- $\mu$ m-mesh sieve. Animals were placed in vials and preserved in 5% sugar-formalin. Amphipods that detached from a substratum while being removed were captured with a net and preserved with the others from that substratum. Amphipods were identified and counted, and the substratum upon which they settled recorded. Surface area of experimental rocks, and the biomass of encrusted *Dreissena* and *Cladophora*, was quantified as described above.

The number of amphipods retrieved from the three substrata in each aquarium was summed and the proportion of the total on each substratum determined. Some amphipods were lost during recapture or possibly because of predation or cannibalism (Dediu, 1980). The number of individuals lost did not differ across species or density treatments and ranged from 0 to 4%. In these cases, the number of amphipods retrieved was used to calculate species proportions on different habitats. Values were arcsine (square root)-transformed prior to statistical analysis. Habitat choices of, and interspecific interactions between, amphipod species were analysed using a three-way ANOVA for each amphipod species with habitat, treatment and block as main effects, and with a treatment  $\times$  habitat interaction. In one instance when this interaction term proved significant (i.e. *Echinogammarus* experiment in August), we used its mean square error term to test main effects. Separate tests were conducted for experiments run during July and August because conditions changed between periods (i.e. there was an interaction between date and habitat).

#### Field colonisation experiment

Replicated field experiments were conducted off the east shore of Middle Sister Island between 28 and 31 July and 18–21 August 1998. Thirty rocks, encrusted with *Cladophora*, *Dreissena*, or *Dreissena* with attached *Cladophora* (*Dreissena* + *Cladophora*), were collected

at the study site from 0.5, 2.5 and 2.0 m depths, respectively, using SCUBA. Rocks were sealed in polypropylene bags underwater and brought to the surface. Rocks were agitated in a bucket of lake water for 2 min to dislodge existing amphipods, following which five rocks of each substratum type were randomly selected and preserved to determine amphipod density before transplantation (control).

A transect perpendicular to the shore was established, and depths of 0.5, 1.0, 1.5, 2.0 and 2.5 m were marked with buoys. The site consisted mainly of bedrock and cobble encrusted with *Cladophora* and/or *Dreissena*. Four rocks of each substratum type, and four similarly sized bare rocks brought to the site, were randomly selected from the group of shaken rocks, sealed in polypropylene bags, and brought to the marked depths. All rocks were positioned on bedrock in a Latin square design, using SCUBA. Fluorescent painted rocks were placed at each depth on two sides of the square to aid in reclamation. After 72 h, rocks were placed into marked polypropylene bags, sealed, returned to the surface and preserved in 5% sugar-formalin. In the laboratory, all rocks (including control) underwent the same sample processing as described above.

Some control rocks contained individuals of both amphipod species before the rocks were used in experiments. Mean amphipod density from control rocks from each habitat type was subtracted from the final density on rocks of each habitat type. These amphipod densities were then adjusted for rock area and  $\log(x + 1)$ -transformed prior to statistical analysis.

Separate two-way ANOVAs, with interaction, were conducted to determine the effects of habitat and depth on densities of *Echinogammarus* and *Gammarus*. Separate tests were conducted for the July and August experiments because conditions changed between periods. In cases where the interaction was significant, we employed the mean square error term in the denominator of ANOVA tests on main effects.

## Results

### Temporal amphipod survey

Analysis of archived samples revealed that *Echinogammarus* was present in western Lake Erie at least a year prior to its reported discovery in 1995 by Witt

et al. (1997; Fig. 1). *Echinogammarus* was detected in 5% of the Ponar grab samples from 1994 ( $n = 33$ ) and always at low density ( $0.02 \text{ cm}^{-2}$ ). However, it was commonly found on rock samples (74%;  $n = 19$ ) retrieved from each of Middle Sister, East Sister and Pelee Islands during June 1994, at a mean density of 36 per rock. *Echinogammarus* density was lower than that of *Gammarus* at all sites, and it was most abundant (average of 57 per rock) at East Sister Island. More importantly, *Echinogammarus* was represented by all size classes during June 1994 (Fig. 2). Mean rock area across all sampled years was equivalent to  $515 (\pm 9.2 \text{ SE}) \text{ cm}^{-2}$ .

Densities of both *Echinogammarus* and *Gammarus* on *Dreissena*-encrusted rocks in surveys conducted at Middle Sister Island in 1995 were significantly related to site depth (ANOVAS,  $P = 0.01$ ). *Echinogammarus* density was lower in the shallowest water (Bonferroni test; Fig. 3). By contrast, density of *Gammarus* declined slightly from shallow to deeper sites (Fig. 3). In 1998, *Echinogammarus* density was affected by both depth ( $F_{4,140} = 2.91$ ,  $P = 0.02$ ) and habitat ( $F_{1,140} = 40.3$ ,  $P < 0.0001$ ), and was consistently higher on rocks encrusted with *Dreissena* than on those fouled by *Cladophora* (Fig. 3). *Gammarus* abundance in 1998 was related to neither site depth nor habitat (two-way ANOVA,  $P > 0.10$ ; Fig. 3). Abundance patterns of both amphipods during surveys conducted in 1996 and 1997 generally paralleled patterns in other years: *Echinogammarus* abundance was usually higher than that of *Gammarus*, was lowest at nearshore locations,

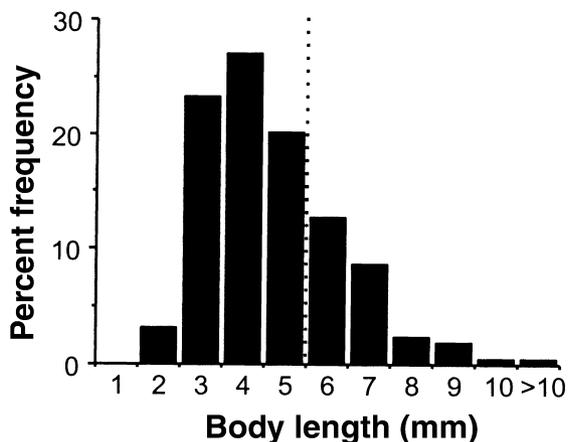


Fig. 2 Body length size distributions of *Echinogammarus ischnus* collected near East Sister Island in western Lake Erie during June 1994. Dotted line separates juveniles from adults ( $n = 219$ ).

and was highest on *Dreissena* substrata (Fig. 3). The overall pattern that emerged during the 4 years of field surveys was of progressive dominance of the amphipod community by *Echinogammarus* at the expense of *Gammarus*. Indeed, the species exhibited an inverse pattern of density, with one species always present at low density whenever the other was present at high density (see Fig. 4a). The maximum density of *Echinogammarus* during 1995 was  $4.4 \text{ cm}^{-2}$ , on a *Dreissena*-encrusted rock without *Gammarus*.

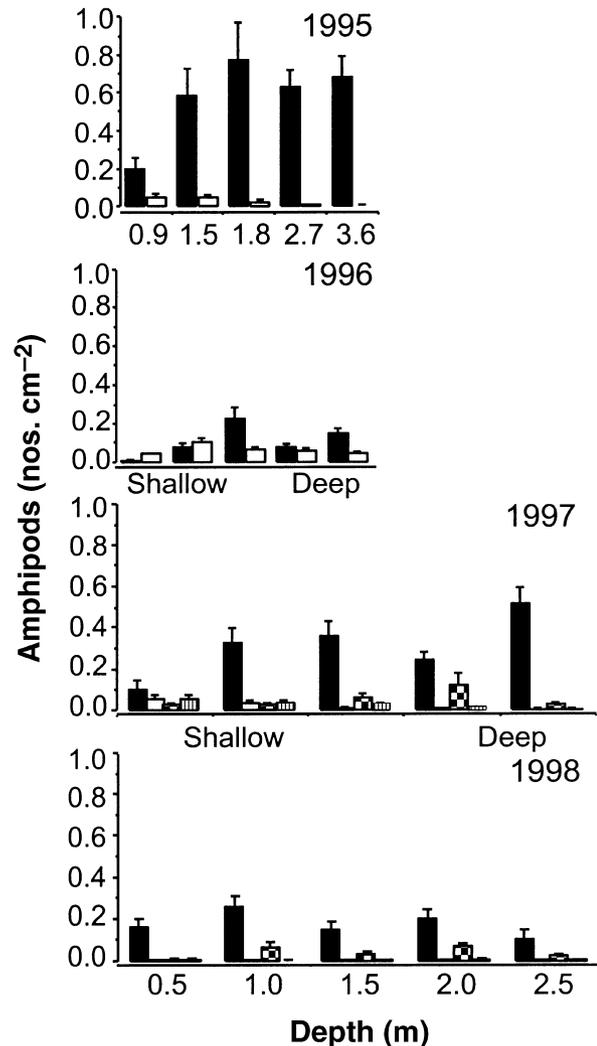


Fig. 3 Mean density ( $\pm$ SE) of *Echinogammarus ischnus* and *Gammarus fasciatus* near Middle Sister Island during 1995–98. Black and white bars represent *Echinogammarus* and *Gammarus* density on *Dreissena*-encrusted rocks, respectively. Checkered bars and shaded bars represent densities of these amphipods on *Cladophora*-encrusted rocks, respectively. Depth is measured in metres during 1995 and 1998, but is only arranged from shallowest to deepest during 1996 and 1997.

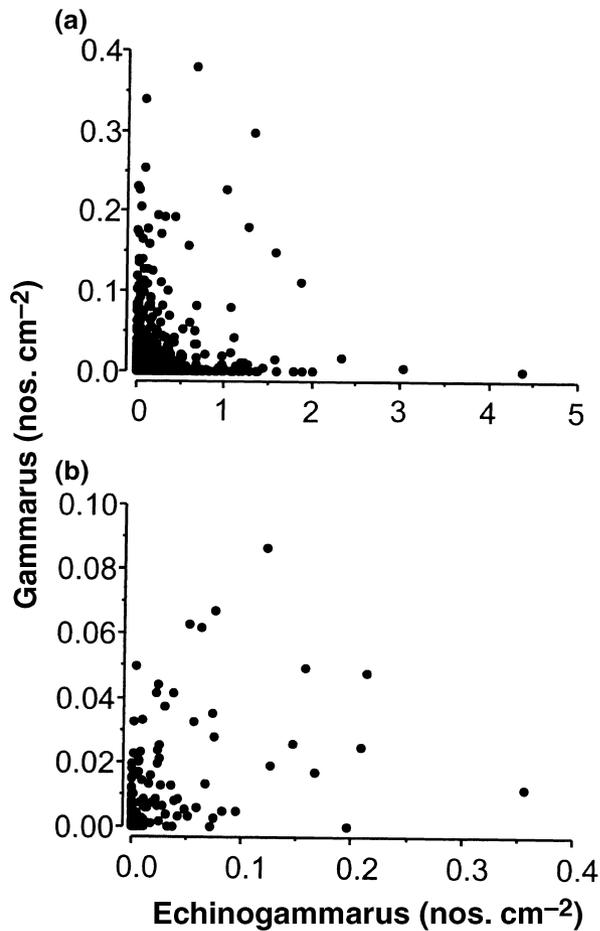


Fig. 4 Densities of *Echinogammarus ischnus* and *Gammarus fasciatus* from (a) the 1995–98 amphipod surveys, and (b) the colonisation experiment at Middle Sister Island. Note differences in scales.

Differences in the density of *Echinogammarus* and *Gammarus* were unrelated to body size, as mean body length of *Echinogammarus* (6.5 cm) and *Gammarus* (6.2 cm) did not differ statistically ( $t_{19} = 0.7$ ,  $P = 0.472$ ). *Hyalella azteca* (Saussure) was also detected in a small fraction (<0.03%) of samples, although always at very low density ( $0.002 \text{ cm}^{-2}$ ).

#### Laboratory experiment of habitat choice

In laboratory experiments to determine amphipod habitat choice, *D. polymorpha* and *D. bugensis* accounted for an average of 97 and 3% of encountered dreissenid molluscs, respectively. Rocks contained an average of 124 and 74  $\text{mg cm}^{-2}$  of *Dreissena*, and 6 and 1  $\text{mg cm}^{-2}$  of *Cladophora*, during July and August

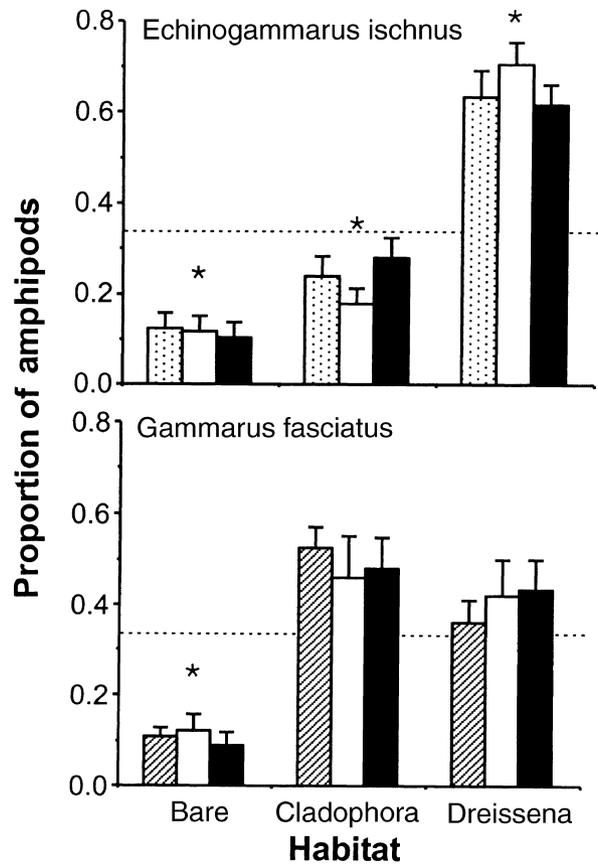


Fig. 5 Mean ( $\pm$ SE) proportion of *Echinogammarus ischnus* and *Gammarus fasciatus* on bare, *Cladophora*- and *Dreissena*-encrusted rocks in the laboratory experiment of habitat preference. Stippled bars represent treatments with 50 *Echinogammarus*, diagonal bars those with 50 *Gammarus*, while white and black bars represent treatments with 25 and 50 individuals of each species, respectively. Neutral habitat selection is indicated by the dotted line. Habitats that differed significantly (Bonferroni,  $\alpha = 0.05$ ) with respect to proportion of amphipods are indicated with an asterisk.

experiments, respectively. The decline of *Cladophora* on rocks during August appeared to be related to senescence. Mean rock area during both experiments was equivalent to 512 ( $\pm 6.65 \text{ SE}$ )  $\text{cm}^{-2}$ . *Echinogammarus* had highly significant habitat preferences (ANOVA,  $P = 0.0001$ ) that were unaffected by animal density, by species composition treatment, or by experimental blocks ( $P > 0.1000$ ; Fig. 5). For example, *Echinogammarus* always chose *Dreissena*-encrusted substrata over those fouled by *Cladophora* which, in turn, were chosen over bare substrata.

*Gammarus* also had strong habitat preferences (ANOVA,  $P = 0.0001$ ) that were unaffected by animal density, by species composition treatment, or by

experimental block ( $P > 0.1000$ ; Fig. 5). *Gammarus* chose rocks with *Cladophora* and *Dreissena* over bare substrata. Overall selection of *Cladophora*-fouled rocks was much higher for *Gammarus* (46–53%) than *Echinogammarus* (18–28%; see Fig. 5).

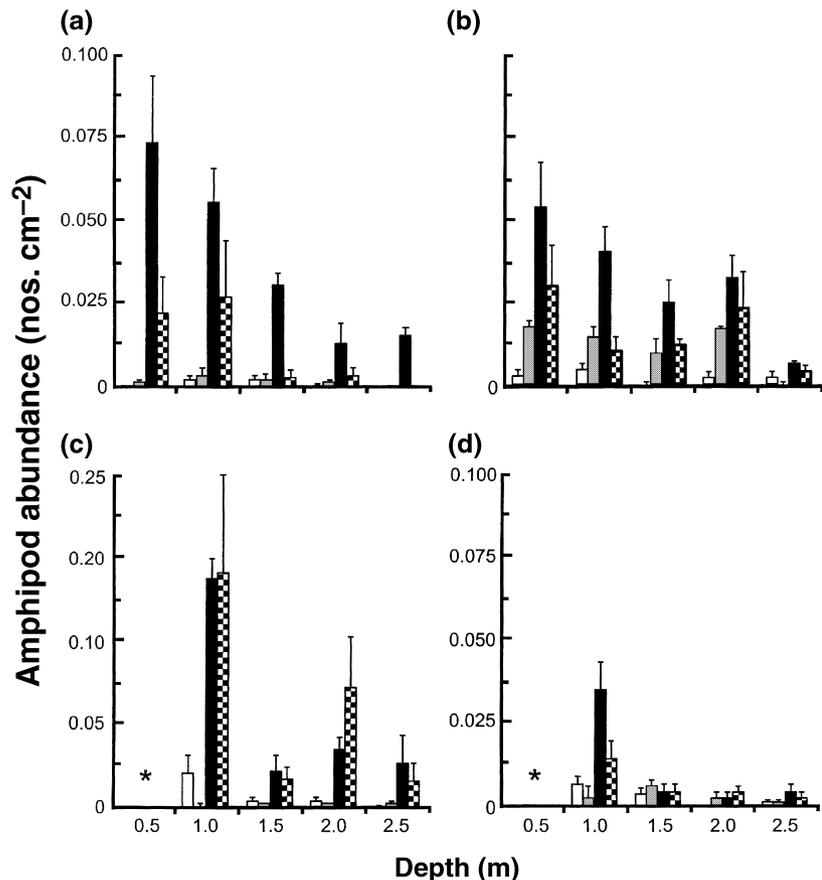
#### Field colonisation experiment

Although we attempted to standardise rock size in the field colonisation experiments conducted near Middle Sister Island, rocks encrusted with *Dreissena* and *Dreissena* + *Cladophora* were smaller than bare rocks, and rocks were, on average, smaller in August than in July. Moreover, mean mussel biomass was lower ( $89 \text{ mg cm}^{-2}$ ) on rocks encrusted with *Dreissena* and *Cladophora* than on those with only *Dreissena* ( $130 \text{ mg cm}^{-2}$ ), and was also lower in August ( $93 \text{ mg cm}^{-2}$ ) than in July ( $124 \text{ mg cm}^{-2}$ ). Species composition on rocks with mussels was 95% *D. polymorpha* and 5% *D. bugensis*. Mean *Cladophora* biomass was lower on rocks encrusted with *Dreissena* and *Cladophora* ( $2 \text{ mg cm}^{-2}$ ) than on those encrusted

only with *Cladophora* ( $3 \text{ mg cm}^{-2}$ ), and was lower during August ( $1 \text{ mg cm}^{-2}$ ) than in July ( $3 \text{ mg cm}^{-2}$ ). Mean rock area during both experiments was  $475 (\pm 3.91 \text{ SE}) \text{ cm}^{-2}$ .

Colonisation of experimental rocks in Lake Erie by *Echinogammarus* during both July and August was affected by habitat ( $P < 0.05$ ) and by an interaction between habitat and depth ( $P < 0.005$ ), but not by depth itself ( $P > 0.05$ ; two-way ANOVA; Fig. 6). For example, colonisation by *Echinogammarus* was always greatest on rocks fouled by *Dreissena* with or without attached *Cladophora*, and was usually lowest on bare or *Cladophora*-fouled rocks (Fig. 6). Total density of *Echinogammarus* was much higher during the August experiment ( $0.043 \text{ cm}^{-2}$ ) than the one conducted in July ( $0.021 \text{ cm}^{-2}$ ), increasing by an average of 205%. Overall density of *Echinogammarus* on experimental rocks was always higher than that of *Gammarus*, except on rocks fouled only by *Cladophora* (Fig. 6).

*Gammarus* colonisation during the July experiment was affected by both habitat ( $F_{3,58} = 20.4$ ,  $P < 0.0001$ )



**Fig. 6** Mean density ( $\pm$ SE) of colonizing *Echinogammarus ischnus* (a, c) and *Gammarus fasciatus* (b, d) amphipods on bare (open), *Cladophora*- (light stipple), *Dreissena*- (black), and *Dreissena* + *Cladophora*-encrusted rocks (checked) near Middle Sister Island during July (a, b) and August (c, d). \*Represents habitats in which storm events destroyed experimental units. Note different scales on (c).

and depth ( $F_{4,58} = 7.7$ ,  $P < 0.001$ ), although the interaction between factors was non-significant ( $F_{12,58} = 1.7$ ,  $P > 0.05$ ). *Gammarus* colonisation was typically greatest on rocks containing only *Dreissena*, followed sequentially by those containing *Dreissena* + *Cladophora*, *Cladophora*, and by bare rock (Fig. 6). Colonisation was greater in shallow than in deeper waters and decreased 45% between July ( $0.013 \text{ cm}^{-2}$ ) and August ( $0.007 \text{ cm}^{-2}$ ). During August, the effect of depth on colonisation was affected by habitat type ( $F_{9,48} = 5.6$ ,  $P < 0.0001$ ). Neither treatment nor depth effects affected *Gammarus* colonisation during August (two-way ANOVA,  $P > 0.10$ ).

In contrast to observed natural distribution patterns of amphipods on rocks (Fig. 4a), the colonisation study revealed that densities of *Echinogammarus* and *Gammarus* were weakly although positively correlated ( $r = 0.38$ ,  $P < 0.001$ ; Fig. 4b). Overall amphipod density was, however, approximately 92% lower in the short-term colonisation studies ( $9.3 \text{ cm}^{-2}$ ) than natural densities observed near Middle Sister Island ( $120 \text{ cm}^{-2}$ ).

## Discussion

Samples collected during June 1994 in western Lake Erie revealed that *Echinogammarus* was present in western Lake Erie at least a year prior to its initial discovery in the Detroit River (Witt *et al.*, 1997). Dermott *et al.* (1998) suggested that this amphipod was present in the western approaches of Lake Erie during 1994, a speculation confirmed in this study. Populations surveyed during June 1994 included adults and juveniles. Previous work on this species illustrated that reproduction may be confined to specific periods, or may occur year-round (see Dediú, 1980). Konopacka & Jesionowska (1995) determined that *E. ischnus* in Licheńskie Lake, Poland, had two distinctive reproductive peaks, one in spring when wintering adults bred, and the other in late summer when that year's spring cohort reproduced. Likewise, Mitskevich & Savateeva (1985) determined that adult (6.1–10 mm) *Echinogammarus* (= *Chaetogammarus*) *ischnus* present in the lower Dnieper River, Ukraine, during May 1984 were produced during late autumn 1983. Thus, if the same pattern of reproduction applies to Lake Erie, then co-occurring adults that had overwintered in the previous year would have produced juveniles present in June 1994. Yemelianova (1994)

reported that gammarid amphipods must acclimatise to new surroundings after initial invasion before initiating reproduction. Thus, while it is not possible to ascertain with certainty the year that *Echinogammarus* invaded the Great Lakes, available evidence is consistent with inoculation and establishment no later than 1994, and possibly as early as 1993.

*Echinogammarus* had a very patchy distribution during 1994 and 1995 (this study), but was detected at only a single site in the Detroit River during 1995 (Witt *et al.*, 1997). Ten Ponar grab samples taken in the same vicinity during 1994 failed to detect it. Its presence in the Detroit River is, however, consistent with its classification as a lithophilous species that prefers large rivers (Jażdżewski, 1980).

*Echinogammarus* was most abundant on East Sister, Pelee and Middle Sister Islands, respectively, during 1994 (see Fig. 1). Owing to its absence from the Detroit River, it is possible that this species invaded island sites in the western basin of Lake Erie *via* the Pelee Passage from the central basin. This pattern of invasion would be consistent with its rapid dispersal in Europe (Jażdżewski 1980; Jażdżewski & Konopacka, 1993).

Ours is the first study to examine the specific habitat preferences of *Echinogammarus* and *Gammarus*. Habitat preference experiments conducted in the laboratory and in western Lake Erie revealed that both amphipod species chose complex substrata to bare rock, but that these preferences differed between species, and were subject to seasonal and depth effects. For example, *Echinogammarus* strongly chose *Dreissena*- over *Cladophora*-encrusted rocks and bare rocks in laboratory experiments (Fig. 5), and had significantly higher densities on all substrata with *Dreissena* in field colonisation experiments (Fig. 6). By contrast, *Gammarus* occupied *Dreissena* and *Cladophora* substrata equally in laboratory experiments, and exhibited temporally variable selection in field colonisation trials (Fig. 6). In these experiments, *Gammarus* densities were lower on rocks containing *Dreissena* and *Cladophora* than on those encrusted only with *Dreissena*. However, the magnitude of this difference declined as lake depth increased. *Gammarus* density also decreased on *Cladophora*-encrusted rocks during August, possibly because of a diminution of *Cladophora* on the rocks associated with seasonal senescence (Bocsor & Judd, 1972; Shear & Konasewich, 1975). Thus, seasonal senescence of *Cladophora* appeared to

influence habitat suitability for *Gammarus*. Our findings support González & Downing's (1999) contention that amphipods preferred complex habitats in Lake Erie, although they reported a 'combined response' for the species and did not include *Cladophora*-encrusted habitats in their study. González & Downing (1999) also reported that amphipods preferred complex substrata to bare rocks only in late summer, a conclusion opposite to that reported here.

The strong association of *Echinogammarus* with *Dreissena* has been established by other researchers (Köhn & Waterstraat, 1990; Pinkster, 1993; Konopacka & Jesionowska, 1995; Stewart, Miner & Lowe, 1998a,b,c, 1999; González & Downing, 1999; Burkart, 1999; Bially & MacIsaac 2000). Köhn & Waterstraat (1990) suggested that *Echinogammarus* exploited ostracods that occur in abundance within *Dreissena* colonies. All fauna were removed from rocks prior to laboratory and field experiments, thus this reason cannot account for the strong choice for *Dreissena* revealed here. It is more likely that *Echinogammarus* benefits from *Dreissena* either by reduced vulnerability to fish predators (Pinkster, 1993; Konopacka & Jesionowska, 1995; González & Downing, 1999; Burkart, 1999; Stewart *et al.*, 1999) or enhanced food supply associated with *Dreissena* faeces and pseudo-faeces (Köhn & Waterstraat, 1990; Burkart, 1999; C. van Overdijk, unpubl. data). Invasion and dispersal of *Echinogammarus* in the Great Lakes appears to have been facilitated by prior invasion and establishment of *Dreissena*, consistent with the 'invasional meltdown' hypothesis (Ricciardi 2001).

Many previous studies have demonstrated a high density of *Gammarus* amongst *Dreissena* colonies (Dusoge, 1966; Dermott *et al.*, 1993; Griffiths, 1993; Bruner, Fisher & Landrum, 1994; Stewart & Haynes, 1994; Wisenden & Bailey, 1995; Botts *et al.*, 1996; Ricciardi *et al.*, 1997; Strayer, Smith & Hunter, 1998; Burkart, 1999; Bially & MacIsaac 2000). As with *Echinogammarus*, *Gammarus* may benefit from *Dreissena* because of enhanced food supply, a reduced risk of fish predation, or reduced abiotic stress (Dermott *et al.*, 1993; Kuhns & Berg, 1999).

*Gammarus* occupied *Cladophora*-encrusted rocks in both laboratory and field experiments, consistent with reports from previous studies (Clemens, 1950; Bocsor & Judd, 1972; Barton & Hynes, 1976; DeLong, Summers & Thorp, 1993; Stewart & Haynes, 1994; Summers *et al.*, 1997; Dermott *et al.*, 1998). *Cladophora*

provides *Gammarus* with refuge from predators and abiotic stresses, as well as a food source, particularly if the growth of the alga is prolific (Clemens, 1950).

#### *Amphipod community changes*

Our temporal study illustrates that the amphipod community in western Lake Erie has changed dramatically with the introduction of *Echinogammarus* (Fig. 3), and that the density of *Gammarus* is lower than the density (33.2 cm<sup>-2</sup>) reported by Stewart *et al.* (1998a) in August after the *Dreissena* invasion. The density of *Echinogammarus* was almost always higher than that of *Gammarus* in the field survey, except during 1994. Previous studies have predicted (Witt *et al.*, 1997) or demonstrated (Dermott *et al.*, 1998; Stewart *et al.*, 1998c; Burkart, 1999) replacement of *Gammarus* by *Echinogammarus* on *Dreissena* substrata. Our laboratory experiment and field colonisation experiments failed to detect interspecific competition, while long-term census data at Middle Sister Island provides weak evidence in support of it. These seemingly contradictory results may be reconciled by considering amphipod densities in each of the studies. Laboratory and field colonisation studies involved amphipod densities up to 10 times lower than those reported from surveys at Middle Sister Island. If interspecific interactions were density-dependent, then competitive interactions might require densities higher than those observed in our laboratory and short-term colonisation experiments (e.g. Fig. 4b). It is not yet clear if replacement of *Gammarus* by *Echinogammarus* is occurring *via* exploitative competition for habitat, interference competition, or some other mechanism. Mature *Echinogammarus* are at least as large as mature *Gammarus*, and appear more active and aggressive (C. van Overdijk, pers. observ.). Thus, behavioural differences may accentuate, or be the source of, habitat preferences. Incubation of amphipods in single- and mixed-species cultures in small vials resulted in greater cannibalism by *Gammarus* than by *Echinogammarus*, and each species preyed on the other at low frequency (I. Grigorovich, unpubl. data). Consequently, the temporal pattern of species replacement ongoing in the Great Lakes may be attributable to competition for preferred substrata, but not to predation by other amphipods.

*Gammarus* and *Echinogammarus* densities tended to be higher at nearshore than more offshore sites in the

colonisation experiment (Fig. 6), and during the temporal survey in 1998. This pattern may reflect the short-term (72 h) nature of the colonisation experiment, or may be a by-product of spatial variation in vulnerability to fish predation. Kuhns & Berg (1999) reported that round gobies (*N. melanostomus*) in Lake Michigan decreased the abundance of non-mussel invertebrates, including gammarid amphipods, by 44%. Other researchers in the Great Lakes and Europe have reported consumption of amphipods by round gobies (Shorygin, 1952; Jude & Deboe, 1996; Dubs & Corkum, 1996), small-mouth bass (*Micropterus dolomieu* (Lecepede)) and rock bass (*Ambloplites rupestris* (Rafinesque)) (Stewart *et al.*, 1999). Moreover, Diggins *et al.* (2002) detected in laboratory tank studies that round gobies prefer amphipods and that their consumption rate decreased amongst bare rocks. It is not clear, however, whether fish predation regulates amphipod abundance or species composition on complex substrata in the Great Lakes.

In summary, *E. ischnus* was present in western Lake Erie in 1994, a year before its reported discovery. Based on the size distribution of the population present during June 1994, it seems likely that the species invaded Lake Erie as early as 1993. *Echinogammarus* has a very strong affinity for *Dreissena*-encrusted rocks, and has largely displaced *G. fasciatus*, which has a weaker preference for this substratum. A colonisation experiment suggested that densities of the two species are weakly, but positively, correlated when amphipod densities are low, although long-term field patterns revealed an inverse pattern of abundances at higher densities. Finally, establishment and dispersal of *Echinogammarus* in the Great Lakes may have been facilitated by *Dreissena*, consistent with the 'invasional meltdown' hypothesis of Ricciardi (2001).

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