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RELATIONSHIPS OF HABITAT CHARACTERISTICS TO THE RELATIVE ABUNDANCE OF NATIVE AND INVASIVE AMPHIPODS IN WESTERN LAKE ERIE

by

James P. Duggan

Thesis

Submitted to the Department of Biology

Eastern Michigan University

In partial fulfillment of the requirements

for the degree of

MASTER OF SCIENCE

in

Biology

Thesis Committee:

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ABSTRACT

The invasive amphipod, *Echinogammarus ischnus,* has displaced the native amphipod, *Gammarus fasciatus*, at some locations within the Great Lakes. This study examined the relationship between amphipod community structure and habitat characteristics under natural conditions. Amphipod and algal samples were collected from four sites in western Lake Erie, during July, August, and September, 2004. Three distinct patterns in amphipod communities were observed. At a site dominated by invasive *Dreissena* mussels, only *Echinogammarus* was present; however, at sites with rich filamentous algal communities, either *Echinogammarus* and *Gammarus* co-existed or only *Gammarus* was present. A strong correlation existed between *Gammarus* relative abundance and filamentous algal relative abundance. *Gammarus* appears to be better equipped to inhabit filamentous algae, whereas *Echinogammarus* seems better adapted for areas dominated by *Dreissena*. Habitat characteristics, combined with niche differentiation and differential fish predation, may promote co-existence between *Gammarus* and *Echinogammarus* within the Great Lakes.

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INTRODUCTION

Beginning with the fur trade, large port cities developed throughout the Great Lakes, exporting grain, ore, lumber, and other products to locations worldwide (Mills, Leach et al. 1993). The building of canals began in the 18th century, culminating with the completion of the St. Lawrence Seaway System in 1959. Increased shipping through the St. Lawrence has led to an increase of invasive species within the Laurentian Lakes, predominantly arriving via ship ballast water (Mills, Leach et al. 1993, Ricciardi 2001).

Many exotic species now thriving in the Great Lakes Basin originated from the Ponto-Caspian basin; that is, the Black, Azov, and Caspian Seas (Vanderploeg et al. 2002). These include *Dreissena polymorpha* (the zebra mussel), *Dreissena bugensis* (the quagga mussel), and the amphipod *Echinogammarus ischnus*. *D. polymorpha* was first sighted in Lake St. Clair in June 1988 (Hebert et al. 1989). *D. bugensis* was first reported to be colonizing eastern Lake Erie in 1989 and colonizing Lake Ontario and western Lake Erie by 1993 (Mills, Dermott et al. 1993, Mills, Chrisman et al. 1999); it was collected in the Straits of Mackinac in 1997 and in Lake Michigan in 2000 (Nalepa et al. 2001). By the close of the 1990s, Dreissenid mussels were established throughout all the lower Great Lakes, largely because of the migration of their planktonic larva (Vanderploeg et al. 2002).

Echinogammarus ischnus was first discovered in the lower Detroit River in 1995 (Witt et al. 1997). Analysis of archived samples revealed that *Echinogammarus* was present in western Lake Erie in 1994, with introduction possibly as early as 1993 (Van Overdijk et al. 2003). *Echinogammarus* has since expanded its range, inhabiting all of the Great Lakes and the St. Lawrence River (Dermott et al. 1998, Nalepa et al. 2001, Vanderploeg et al. 2002). *Echinogammarus* may possibly displace the native amphipod *Gammarus fasciatus*, which dominates the littoral benthos and is a vital food source for fish (Dermott et al. 1998, Nalepa et al. 2001).

Both the native amphipod *Gammarus* and the Ponto-Caspian *Echinogammarus* have benefited from the successful colonization of the Great Lakes by Dreissenid mussels, owing to enhanced habitat availability (Dermott et al. 1993, Wisenden and Bailey 1995, Nalepa et al. 2001, Vanderploeg et al. 2002). The amphipods live in the interstitial spaces between *Dreissena* shells, where, in addition to shelter from disturbances and predation (Stewart and Haynes 1994, Stewart et al. 1998a, Bially and MacIsaac 2000), they may benefit from enhanced food supplied from *Dreissena* faeces and pseudo-faeces (Wisenden and Bailey 1995, Vanderploeg et al. 2002), along with periphytic growth on *Dreissena* shells and the surrounding substratum (see Hargrave 1970). *Echinogammarus* and *Dreissena* co-occur in their native Ponto-Caspian habitat (Vanderploeg et al. 2002), suggesting that *Echinogammarus* may be better adapted than *Gammarus* to inhabit substrata encrusted by *Dreissena* (Dermott et al. 1998). Thus, the distribution of *Dreissena* within the Great Lakes may also facilitate the expansion of *Echinogammarus's* range and the possible decline of *Gammarus* (Dermott et al. 1998, Nalepa et al. 2001).

Cladophora is a macroscopic, filamentous, green alga native to the Great Lakes, usually found attached to hard substrata (rocks, cobble, logs, etc.) and common to many freshwater environments, especially eutrophic habitats (Prescott 1982, John 2003). *Cladophora,* along with other filamentous and macro-colonial (e.g., *Hydrodictyon*) green algae that lack mucilaginous sheaths, often support taxonomically diverse, intricate micro-algal epiphytic assemblages (Lowe et al. 1982, Stevenson and Stoermer 1982, Marks and Power 2001, Wehr and Sheath 2003). Filamentous and macro-colonial green algae, and especially the associated micro-algal epiphytes, are an important food source

for amphipods and other primary grazers (Hargrave 1970) and may also provide refuge from predation and physical disturbance (Clemons 1950).

Two habitat-preference experiments (laboratory and field) indicated that both amphipods, *Gammarus* and *Echinogammarus*, have a high affinity for substrata consisting of *Dreissena* colonies (Van Overdijk et al. 2003). In the lab experiment, substrata consisted of *Cladophora*-covered rocks, *Dreissena*-encrusted rocks, and bare rocks. *Echinogammarus* had a significant habitat preference, choosing *Dreissena*-encrusted substrata over *Cladophora*-covered substrata and both of these substrata over bare rocks. *Gammarus* inhabited *Cladophora*-covered rocks and *Dreissena*-encrusted rocks equally but preferred these two substrata over bare rocks. Overall selection of *Cladophora*-covered rocks was higher for *Gammarus* (46-53%) than for *Echinogammarus* (18-28%) (Van Overdijk et al. 2003). In the field experiment, the substrata were *Dreissena*-encrusted rocks, *Cladophora*-covered rocks, *Dreissena* + *Cladophora* rocks, and bare rocks. Colonization by *Echinogammarus* was always greatest on rocks encrusted by *Dreissena* (with or without *Cladophora*) and was usually lowest on bare rocks or rocks covered with only *Cladophora*. Overall, *Echinogammarus* density on experimental field substrata was always greater than that of *Gammarus* except on rocks covered only by *Cladophora*. *Gammarus* colonization was greatest on rocks containing only *Dreissena*, followed sequentially by those containing *Dreissena* with attached *Cladophora*, *Cladophora*-covered rocks, and then by bare rocks. Furthermore, the densities of both amphipods varied temporally and spatially. Overall abundance was higher for *Echinogammarus* than *Gammarus*, with greater densities on *Dreissena*-encrusted substrata and in shallow water (Van Overdijk et al. 2003). In summary,

Gammarus displayed a higher affinity for *Cladophora* and other submerged vegetative substrata relative to *Echinogammarus* (Van Overdijk et al. 2003). Other studies have also indicated a higher affinity of *Gammarus* for submerged vegetation (Dermott et al. 1998, Palmer and Ricciardi 2004). *Gammarus fasciatus* has claws at the terminus of each its fourteen pereopods, and these claws are well developed in the first and second pereopods, which better enables them to cling to vegetation (Clemens 1950). This adaptation may allow *Gammarus* to continue to predominate in habitats consisting of submerged vegetation, whereas *Echinogammarus*, which lacks these claws, may predominate on *Dreissena* and other hard substrata.

This study examined the possible relationship between the amphipods *Gammarus* and *Echinogammarus* and their habitat choice under natural conditions. Relative abundance of both amphipods was observed at four sites in western Lake Erie in an attempt to (1) determine whether *Gammarus* were more commonly associated with benthic substrata covered by filamentous and macro-colonial green algae and whether *Echinogammarus* were more common on substrata with *Dreissenia*, and (2) document spatial and temporal patterns in the relative abundance of *Gammarus* and *Echinogammarus*.

METHODS

Four study sites were selected along a 30-km stretch of Michigan's Lake Erie shoreline: (1) Pointe Mouilee, Wayne County; (2) Pointe Aux Peaux, Monroe County; (3) DTE Fossil Fuel Plant, Monroe County; and (4) Luna Pier, Monroe County, hereafter referred to as sites 1 through 4 respectively (Fig. 1). At sites 1, 2, and 4, benthic algal and amphipod communities were sampled at 2-3-m intervals along a 50-m transect line (20-m at site 2) parallel to the shoreline (depth range 0.25m-0.5m). Sampling consisted of removing rocks with their associated algae and invertebrates from the lake and depositing them into a plastic bucket. If rocks were too large for removal, then algae and invertebrates were scraped off and deposited into the sampling bucket. All subsamples from a particular transect line were combined into one plastic bucket, along with additional lake water, and transported back to the lab. Samples from site 3 consisted of amphipods and algae inhabiting *Dreissena*-encrusted cement blocks suspended from the pier at a depth of 1 m. A 4-m horizontal distance separated each set of cement blocks. Mussels, along with their algae and amphipods, were scraped off the cement blocks and placed into a plastic bucket, along with additional lake water, and transported back to the lab. Samples taken were from rotated sets of sampling blocks in order to allow four weeks between sampling of individual blocks, thereby allowing sufficient time for re-growth of mussels. At all sites, samples were taken every two weeks from July through September 2004.

From sites 1, 2, and 4, amphipods were removed from samples by vigorously agitating the sample rocks in a bucket containing ca. Eight liters of lake water and then filtering the water through a 400-μm screen to remove amphipods. Sample rocks were

then scraped, and any remaining amphipods were removed manually by separating the algal filaments in a shallow dissecting pan and picking up any amphipods with fine-tipped forceps. From site 3, amphipods were removed from *Dreissena*-encrusted substrata by spreading *Dreissena* clusters on a No.16-size screen lying on top of a clean bucket and then rinsing with lake water. Amphipods fell freely into the bucket along with the water, which was then filtered to remove amphipods; this process was repeated three times. Visual inspection confirmed that further manual removal of amphipods was not required. All amphipods collected were preserved in 90% EtOH and examined under a 20X dissecting scope for enumeration and identification. Pennak's (2001) taxonomic key was used to identify specimens to genus. The total number of amphipods collected during the sampling period equaled 2270. The number of amphipods collected per date varied: Site 1, 60-271; Site 2, 5-320; Site 3, 58-413; and Site 4, 27-88. Any individual amphipod not positively identified as either *Gammarus* or *Echinogammarus* was classified as an unknown. The number of unknown amphipods at any site over all sampling dates varied between 0 and 49 and comprised approximately 10% of the total number of amphipods collected.

On each sampling date, a *Cladophora*-covered rock from Sites 1, 2, and 4 or a *Dreissena* cluster from Site 3 was randomly selected to make algal slurries. Algal slurries were made by scraping and brushing off all the algal growth on the substratum surface (rock or mussel cluster) and then blending the scraped material with a hand-held mixer. This mixture was further emulsified with a mortar and pestle. Algal slurries were preserved in 5% glutaraldehyde for identification and enumeration at 400X, viewed with a bright field microscope (Patrick and Reimer 1996, Prescott 1982, Taft and Taft 1990,

Dillard 1999). Algae were identified to genus where possible, and the number of algal cells enumerated in each sample ranged from 300 to 14255.

The relative abundance of each algal and amphipod taxon in the algal and amphipod communities was calculated for each sample. Spearman's rank correlation was used to examine the relationship between total filamentous and macro-colonial green algal relative abundance (i.e., the summed relative abundance of *Cladophora, Stigeoclonium,* and *Hydrodictyon*) and the relative abundance of *Gammarus*. Patterns in algal community composition were summarized with a principle component analysis (PCA) of the relative abundance of algal genera. Preliminary analyses indicated that a linear multivariate model (e.g., PCA) would be more appropriate for these data than a unimodal model (e.g., detrended correspondence analysis) because of the short gradient length (2.5 SD units) recovered by the unimodal model (see ter Braak 1995, ter Braak and Smilauer 1998). Principal components were computed from sample correlations (i.e., centered and standardized PCA), which resulted in an equal weighting of all algal taxa regardless of relative abundance. Site scores and selected species vectors were combined into biplots to aid interpretation of algal community structure. All multivariate analyses were calculated with CANOCO 4.0.

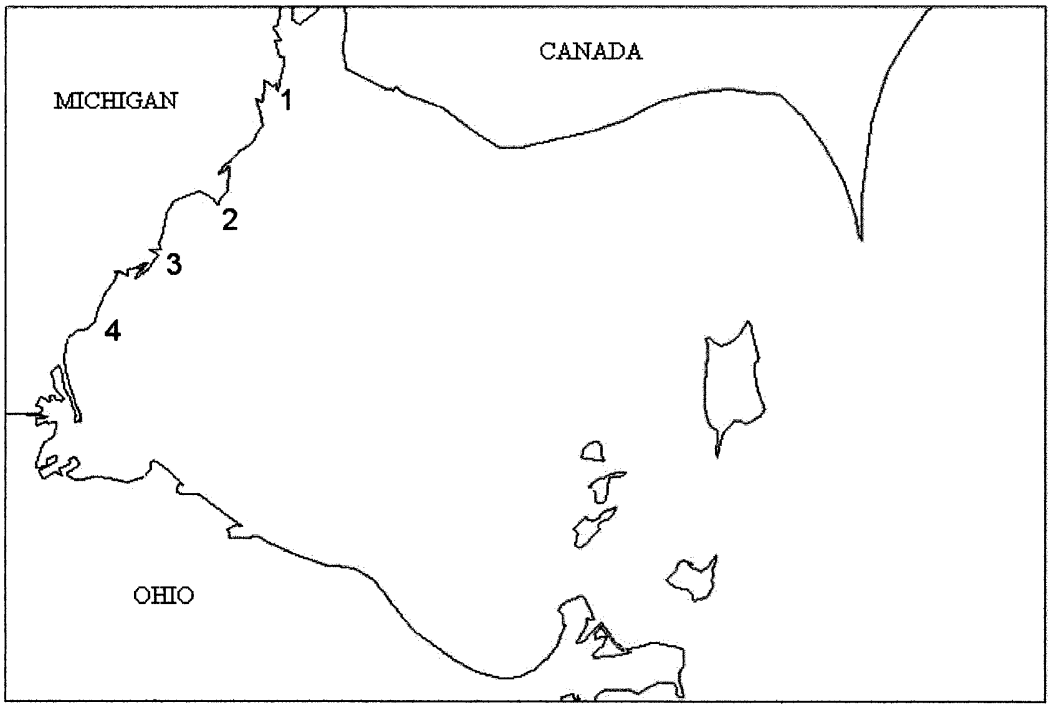

Fig. 1 Western Lake Erie sampling sites. (1) Pt. Mouilee, (2) Pt. Aux Peaux, (3) DTE, and (4) Luna Pier

RESULTS

The substrata at Site 1 consisted of broken concrete slabs and boulders covered with mats of *Cladophora* and its epiphytes. Sixteen algal taxa were identified during the summer collection period. *Cocconeis* was the most common alga (29.7%), followed by Naviculoid diatoms (10.7%), *Melosira* (9.8%), *Synedra* (9.2%), *Rhoicosphenia curvata* (8.9%), *Nitzschia* (7.4%), Cymbelloid diatoms (7.2%), and the filamentous green alga *Cladophora* (7.0 %) (Table 1).

The substrata at Site 2 consisted of a sandy bottom with small cobble and broken concrete slabs. Twenty-one algal taxa were identified during the sampling period. *Fragilaria* (sensu Patrick and Reimer 1966) (28.4%) was the most common taxon, followed by *Scenedesmus* (10.7%), *Coelosphaerium* (7.0%), *Pediastrum* (6.3%), *Melosira* (5.5%), *Cocconeis* (5.1%), *Merismopedia* (4.5%), Naviculoid diatoms (4.3%), and the colonial green alga *Hydrodictyon* (6.1%) and filamentous green alga *Cladophora* (5.5%) (Table 1).

Concrete blocks covered with zebra mussels constituted the substrata at Site 3. The zebra mussels were covered with silt, detritus, and micro-algal communities. Twenty-two algal taxa were identified during the summer collection period. *Melosira* (16.0%) was the dominant taxon, followed by Naviculoid diatoms (15.2%), *Oscillatoria* (11.7%), *Pandorina* (10.5%), *Fragilaria* (9.7%), *Synedra* (7.9%), *Pediastrum* (5.2%), and *Scenedesmus* (3.7%). No filamentous green algae were found during the sampling period (Table 1).

The substrata at Site 4 were composed of a sandy bottom with small cobble and medium-to-large rocks. Twenty-eight algal taxa were identified throughout the summer

sampling period. The dominant taxon was *R. curvata* (22.1%), followed by Naviculoid diatoms (15.7%), *Fragilaria* (11.8%), *Cladophora* (6.4%), *Merismopedia* (4.4%), Cymbelloid diatoms (3.9%), *Cocconeis* (3.7%), *Synedra* (3.7%), and *Melosira* (3.4%). The filamentous green alga *Stigeoclonium* was also present on 3 of the 5 sampling dates, representing 2.3% of the total relative abundance (Table 1).

At Site 1, both *Gammarus* and *Echinogammarus* were present during the summer sampling period. The initial relative abundance of *Echinogammarus* was 86.0% and steadily decreased to zero by the end of sampling, whereas *Gammarus* relative abundance increased during the sampling period (Fig. 2). Both Site 2 and Site 3 were inhabited by a single amphipod taxon during the entire study. *Gammarus* occupied Site 2, whereas *Echinogammarus* inhabited Site 3 (Figs. 3 and 4). Both species of amphipods co-occurred at Site 4. *Echinogammarus* relative abundance started at 75%, declined to 21.4%, and then steadily increased, ending the sampling period at 86%, whereas *Gammarus* relative abundance experienced opposite fluctuations (Fig. 5).

The PCA of algal communities by sampling date (Fig. 6) reflected the overall algal relative abundances at each site (Table 1). Forty percent of the sample variance was collected by the first two PCA axes (21.9% & 18.1%, respectively). Distinct algal communities were observed at Site 2 and Site 3, each of which was inhabited by only one species of amphipod, *Gammarus* and *Echinogammarus*, respectively. Algal communities from Site 1 and Site 4 were similar within each site, and these two communities were also in close proximity in PCA space, indicating that these two sites had relatively similar algal communities during this study.

Table 1. Mean relative abundance (%) of algal taxa sampled at each site, ranges in parentheses. Total algal taxa enumerated = 35, n = 6 samples per site

Taxon	Site 1	Site 2	Site 3	Site 4
Chlorophyta				
Filamentous and Macro-Colonial				
Cladophora	6.98 (5.6-8.4)	5.50 (0.0-15.5)	0.00	6.42 (2.7-8.7)
Hydrodictyon	0.00	6.10 (0.0-17.1)	0.00	0.00
Stigeoclonium	0.00	0.00	0.00	2.32 (0.0-8.0)
Other Chlorophytes				
Ankistrodesmus	0.00	0.00	0.35 (0.0-2.1)	0.00
Closterium	0.00	0.00	0.00	0.04 (0.0-0.2)
Cosmarium	0.05 (0.0-0.3)	2.76 (0.3-6.9)	0.00	2.82 (0.0-6.7)
Dimorphococcus	0.00	0.00	1.31 (0.0-7.9)	0.00
Oocystis	0.00	0.00	1.19 (0.04.7)	0.00
Pandorina	0.00	0.48 (0.0-2.4)	10.55 (0.0-27.8)	0.60 (0.0-3.5)
Pediastrum	0.00	6.27 (0.0-15.8)	5.24 (0.0-14.9)	0.77 (0.0-2.7)
Scenedesmus	0.38 (0.0-1.2)	10.75 (8.0-14.0)	3.67 (0.0-7.8)	1.25 (0.1-3.1)
Cyanobacteria				
Anabaena	0.00	0.00	3.29 (0.0-13.3)	0.04 (0.0-0.3)
Chroococcus	0.23 (0.0-1.4)	1.83 (0.0-5.1)	0.41 (0.0-2.5)	0.50 (0.0-1.3)
Coelosphaerium	0.00	7.04 (0.0-23.2)	0.00	0.46 (0.0-1.6)
Merismopedia	0.00	4.45 (0.0-8.0)	2.34 (0.0-10.2)	4.37 (0.0-9.2)
Oscillatoria	3.24 (0.0-6.5)	1.60 (0.0-6.6)	11.74 (0.0-37.0)	6.30 (0.0-26.5)
Spirulina	0.00	0.61 (0.0-3.1)	0.00	0.00
Diatoms				
Achnanthidium	2.74 (0.2-4.8)	0.00	0.00	2.47 (1.2-6.0)
Amphora	0.00	0.00	0.00	0.20 (0.0-0.7)
Cocconeis	29.67 (25.1-36.3)	5.09 (2.8-8.6)	0.16 (0.0-0.9)	3.75 (0.9-8.4)
Cyclotella	0.00	0.00	3.16 (2.1-4.3)	0.09 (0.0-0.3)
Cymbelloid	7.22 (5.5-10.6)	2.97 (1.6-5.3)	1.41 (0.0-2.8)	3.94 (2.5-6.2)
Diatoma	3.23 (0.0-5.0)	0.00	0.00	2.78 (0.0-9.2)
Eunotia	0.00	0.00	0.00	0.01 (0.0-0.04)
Fragilaria	0.32 (0.0-1.7)	28.36 (18.1-39.1)	9.75 (0.0-26.9)	11.80 (3.5-17.6)
Gomphonema	0.00	0.00	0.14 (0.0-0.9)	0.00
Gyrosigma	0.02 (0.0-0.1)	0.08 (0.0-0.2)	1.39 (0.0-3.5)	0.07 (0.0-0.3)
Melosira	9.76 (5.9-14.4)	5.52 (2.2-15.3)	15.97 (7.3-24.5)	3.44 (0.5-6.0)
Naviculoid	10.70 (4.4-17.2)	4.28 (3.4-7.2)	15.22 (8.5-22.6)	15.75 (12.8-24.8)
Nitzschia	7.37 (2.9-10.9)	0.90 (0.0-1.4)	1.55 (0.0-4.8)	3.73 (1.1-7.9)
R. curvata	8.93 (4.5-15.2)	3.48 (1.4-5.9)	0.00	22.13 (7.2-34.2)
Rhopalodia	0.00	0.32 (0.20.6)	0.00	0.07 (0.0-0.3)
Surirella	0.00	0.00	2.13 (1.3-4.8)	0.22 (0.0-0.7)
Synedra	9.49 (4.1-12.0)	1.40 (0.3-3.4)	7.10 (3.5-17.9)	4.30 (2.3-5.0)
Euglenoids				
Trachelomonas	0.00	0.00	1.08 (0.0-2.6)	0.00

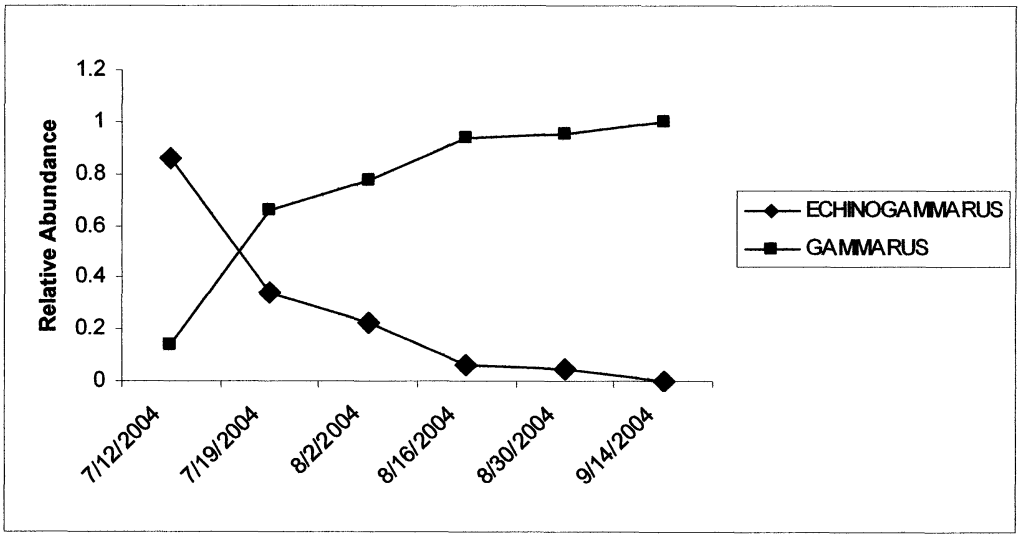

Fig. 2 Site 1, Pt. Mouilee. Relative abundances of *Echinogammarus* and *Gammarus*

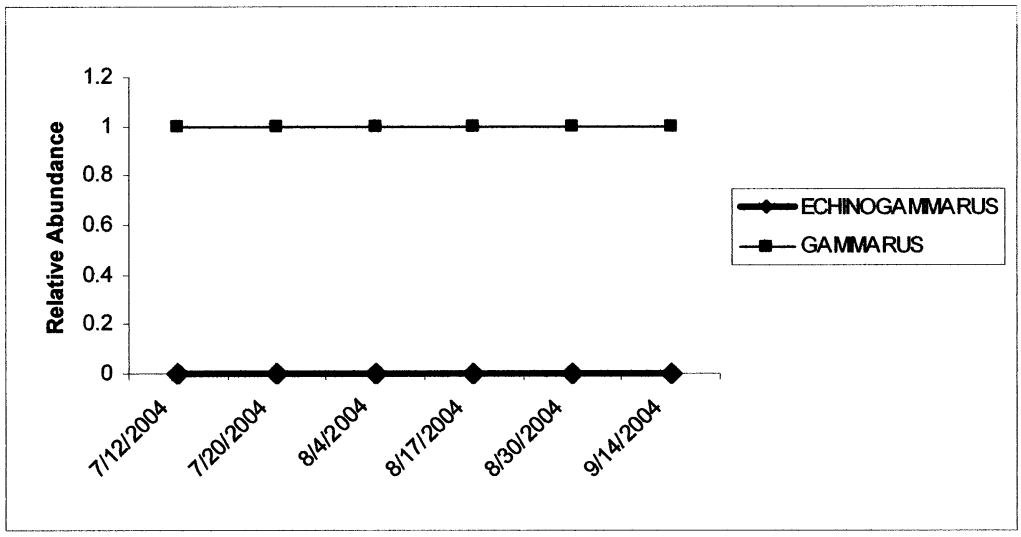

Fig. 3 Site 2, Pt. Aux Peaux. Relative abundances of *Echinogammarus* and *Gammarus*

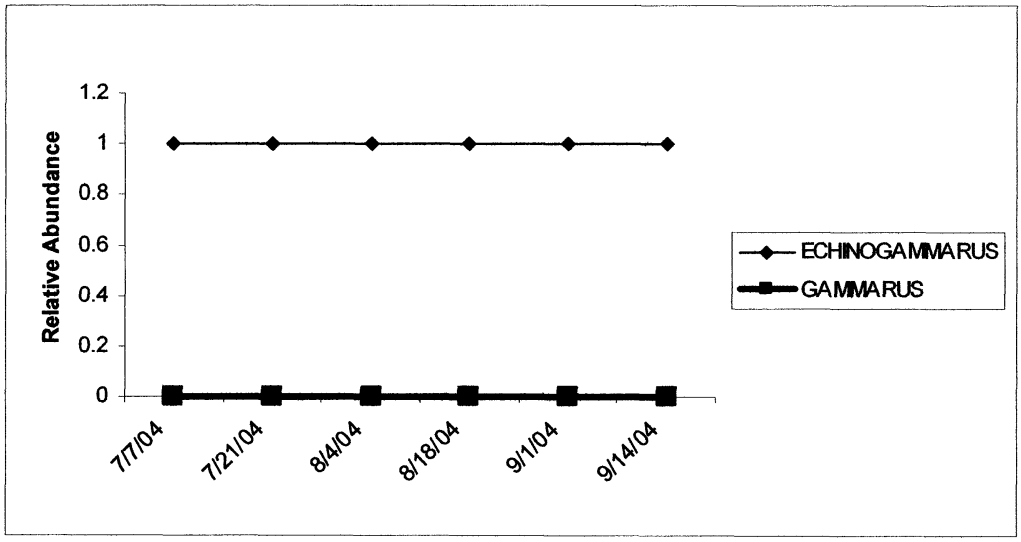

Fig. 4 Site 3, DTE. Relative abundances of *Echinogammarus* and *Gammarus*

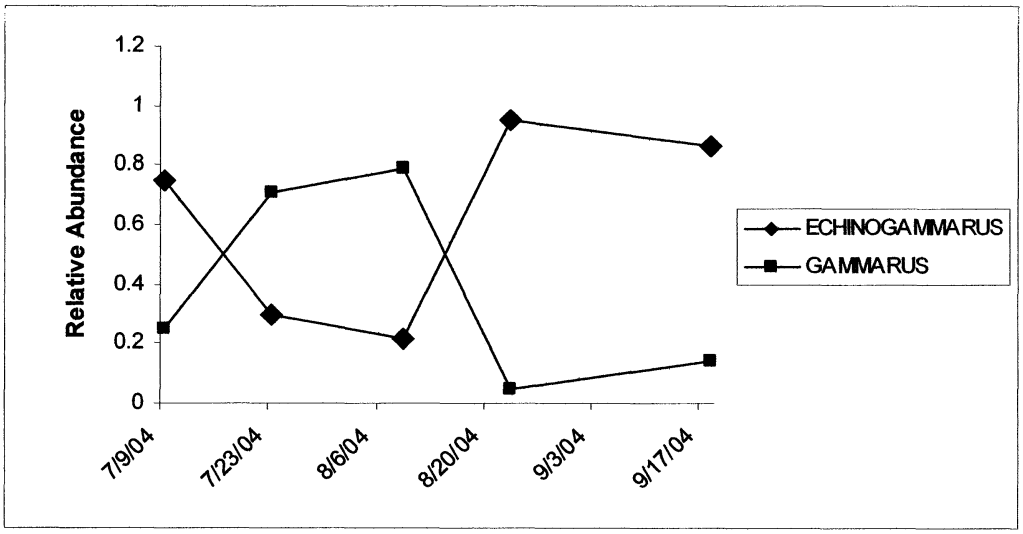

Fig. 5 Site 4, Luna Pier. Relative abundances of *Echinogammarus* and *Gammarus*

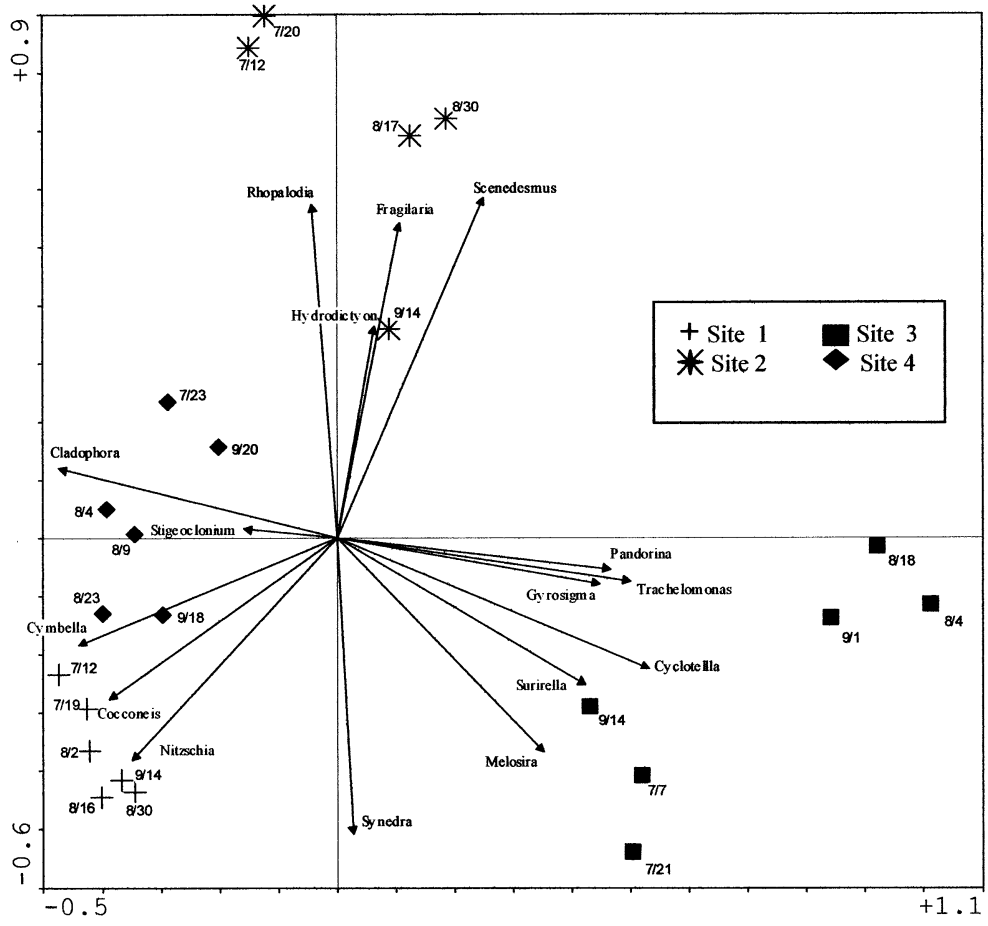

Fig. 6 PCA biplot of algal communities. Date of collection is shown next to each site symbol for each individual sample. Selected taxa vectors are included to aid in interpretation of algal community composition

Both Site 1 and Site 4 sustained abundant populations of filamentous green algae (Table 1, Fig. 6) and also exhibited co-habitation of the amphipods *Gammarus* and *Echinogammarus* during the summer sampling period (Figs. 2 and 5). At Site 1, *Echinogammarus* dominated at the beginning of sampling period, but by mid-July, *Gammarus* and *Echinogammarus* relative abundance nearly equaled each other at approximately 60% and 40%, respectively. Thereafter, *Echinogammarus* relative abundance steadily declined to zero, whereas *Gammarus* relative abundance increased (Fig. 2). Site 4, which also demonstrated co-habitation of both amphipod taxa, saw *Echinogammarus* dominance oscillate, allowing *Gammarus* to dominate for approximately 1/3 of the sampling season (Fig. 5).

Site 2 maintained prolific growths of filamentous and macro-colonial green algae (Table 1, Fig. 6) but did not exhibit any co-habitation of *Echinogammarus* and *Gammarus*. Instead, *Gammarus* was the sole amphipod inhabiting these substrata during the entire sampling period (Fig. 3). Site 3 completely lacked any filamentous or macro-colonial green algae (*Cladophora*, *Hydrodictyon*, and *Stigeoclonium*) and also lacked any *Gammarus*. Site 3 was inhabited by only *Echinogammarus* throughout the sampling period (Fig. 4).

A strong correlation existed between *Gammarus* relative abundance and the summed relative abundance of filamentous and macro-colonial green algae ($r_s = 0.748$, $n = 22$, $p < 0.001$). However, the predictive power of this relationship appears to be limited. During periods of high (> 80%) relative abundance of filamentous and macro-colonial green algae, *Gammarus* relative abundance ≈ 100%, whereas zero relative abundance of filamentous and macro-colonial green algae yielded zero relative

abundance of *Gammarus*. However, the relative abundances of filamentous and macro-colonial green algae between 5% and 20% correspond to a *Gammarus* relative abundance ranging approximately from 5% to 100% (Fig. 7).

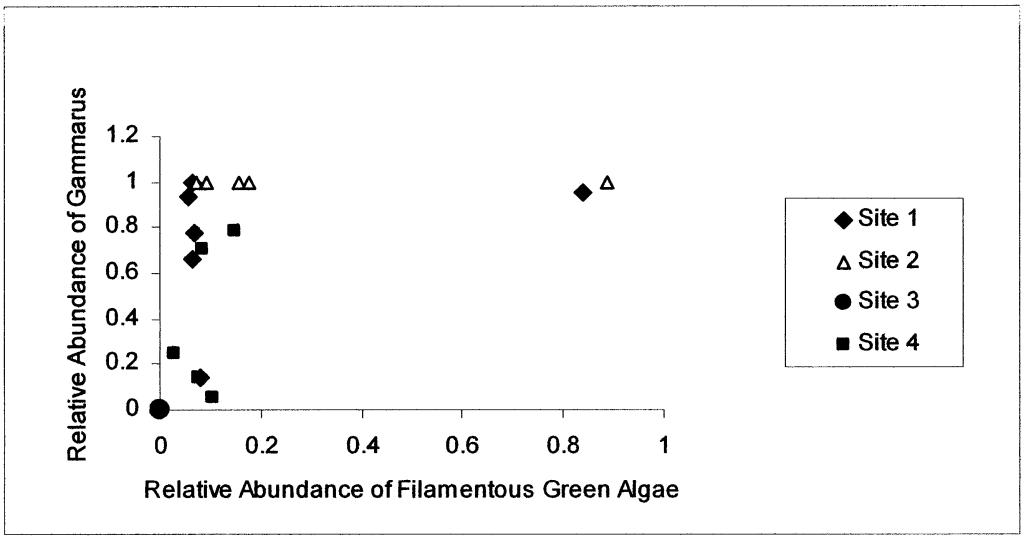

Fig. 7 Association of *Gammarus* relative abundance to the summed relative abundance of filamentous and macro-colonial green algae (*Cladophora*, *Stigeoclonium*, and *Hydrodictyon*) across all sampling dates and all sampling sites

DISCUSSION

During the summer sampling period, I observed three distinct patterns of relative abundance in the amphipod communities along the western shore (Fig. 1) of Lake Erie: (1) *Echinogammarus* only, (2) *Gammarus* only, and (3) mixed populations with *Echinogammarus* and *Gammarus* co-occurring. At Site 3, only *Echinogammarus* was present, and it had presumably completely replaced *Gammarus*. In contrast, at Site 2, *Gammarus* apparently resisted displacement by *Echinogammarus*, as *Gammarus* was the sole amphipod collected during the entire sampling period. At Sites 1 and 4, coexistence was observed between *Echinogammarus* and *Gammarus* throughout the sampling period.

Presumably, *Gammarus* was present at Site 3 prior to the invasion of *Dreissena* and increased thereafter, as has been observed in many areas throughout the Great Lakes (e.g., Dermott et al. 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Bially and MacIsaac 2000). My results suggest that *Echinogammarus* displaced *Gammarus* at Site 3 and support the speculation of previous studies (Witt et al. 1997, Dermott et al. 1998, Nalepa et al. 2001, Vanderploeg et al. 2002) that displacement of *Gammarus* by *Echinogammarus* would occur on hard substrata. Site 3 substrata consisted of simulated rocks (suspended cement blocks), which were encrusted with *Dreissena* colonies. Other studies have indicated a greater abundance of *Echinogammarus* than of *Gammarus* on *Dreissena*-encrusted substrata in the Great Lakes (Dermott et al. 1998, Van Overdijk et al. 2003, Gonzales and Burkart 2004). However, prior to the invasion of *Echinogammarus*, Stewart and Haynes (1994) observed greater abundances of *Gammarus* within *Dreissena* colonies than on un-colonized substrata.

Both *Echinogammarus* and *Gammarus* can use *Dreissena*-encrusted substrata, and both have an affinity for *Dreissena*, as well as other complex habitats (Gonzales and Downing 1999, Bially and MacIsaac 2000, Van Overdijk et al. 2003). Possible benefits for amphipods inhabiting *Dreissena*-encrusted substrata include protection from predators and physical stressors (Stewart et al. 1998b, Bially and MacIsaac 2000) and an additional food resource (Hargrave 1970, Wisenden and Bailey 1995, Vanderploeg et al. 2002, Gonzales and Burkart 2004).

Several hypotheses have been proposed as to why *Echinogammarus* might exclude *Gammarus* from *Dreissena*-encrusted substrata. In its native habitat, *Echinogammarus* is closely associated with *Dreissena* colonies (Vanderploeg et al. 2002). Thus, through co-evolution, *Echinogammarus* may be better adapted than *Gammarus* to inhabit *Dreissena* substrata (Palmer and Ricciardi 2005). *Echinogammarus* are more agile than *Gammarus* and more capable of moving across *Dreissena* shells (Dermott et al. 1998). *Echinogammarus*, which is dark reddish in color, may act as camouflage while inhabiting *Dreissena* colonies, thereby further mitigating the effects of predation (Gonzales and Burkart 2004). Thus, these characteristics may confer on *Echinogammarus* a competitive advantage over *Gammarus* in food foraging and securing shelter within *Dreissena* colonies.

Food resources afforded by *Dreissena* habitats have also been suggested as a possible explanation for *Echinogammarus* displacement of *Gammarus* within *Dreissena*-rich habitats. *Dreissena's* outer shells support micro-algal communities (Table 1 and Fig. 6) that may serve as a supplemental food source for amphipods (Hargrave 1970), along with detritus (Clemons 1950) that settles within the interstitial spaces. The energy-rich

feces and pseudofeces expelled by *Dreissena* are also considered to be a potential food resource for amphipods (Wisenden and Bailey 1995, Vanderploeg et al. 2002). However, Gonzales and Burkart (2004) demonstrated that although both *Gammarus* and *Echinogammarus* incorporated feces and pseudofeces in their diets, *Gammarus* had greater survivorship and faster growth rates than *Echinogammarus* when fed these food items. In addition, stable isotope analysis suggests that *Dreissena* feces and pseudofeces are not major components of *Echinogammarus* diets but are important in the diet of *Gammarus* (Limen et al. 2005). Thus, these two studies offer an opposing view of the hypothesis that *Dreissena* facilitates the expansion of *Echinogammarus* via the added food sources of feces and pseudofeces.

Carbon and nitrogen isotopic signatures indicate that *Echinogammarus* is more carnivorous than *Gammarus* and thus occupies a different feeding niche (Limen et al. 2005). *Echinogammarus* may consume other amphipods and small invertebrates, that is, meiofauna, which also inhabit *Dreissena* colonies and submerged vegetation (Limen et al. 2005). Other studies have demonstrated an increase in overall invertebrate abundance and species richness following a *Dreissena* invasion, thereby enhancing food availability for amphipods and other benthic organisms (Griffiths 1992, Dermott et al. 1993, Stewart and Haynes 1994). Thus, agility and camouflage, along with increased invertebrate food resources (i.e., meiofauna), may give *Echinogammarus* a competitive advantage over *Gammarus* in the complex habitat of *Dreissena* colonies. Habitat complexity may be the driving factor for the increased populations of *Echinogammarus* within the Great Lakes, providing refuge from predation and abiotic stresses (Wisenden and Bailey 1995, Gonzales and Downing 1999, Bially and MacIsaac 2000, Van Overdijk et al. 2003).

At Site 2, the substrata were composed of broken concrete, cobble, and small stones covered with dense mats of the macroscopic, filamentous green alga *Cladophora* and the colonial green alga *Hydrodictyon*. The data collected from Site 2 suggested that *Gammarus* resisted displacement by *Echinogammarus*, as *Gammarus* was the sole amphipod collected during the entire sampling season (Fig. 3). These results support previous studies (Stewart and Haynes 1994, Dermott et al. 1998, Van Overdijk et al. 2003, Gonzales and Burkart 2004), indicating that *Gammarus* has an affinity for filamentous green algae and other submerged vegetation in addition to hard substrata (broken concrete, rocks, cobble, *Dreissena* colonies, etc) and may continue to fair well within these habitats.

Gammarus has a strong association with *Cladophora* in the Great Lakes (Stewart and Haynes 1994, Van Overdijk et al. 2003). As is the case with *Dreissena* colonies, *Cladophora* and other submerged vegetation increase the complexity of benthic habitats, affording refuge and providing food that are utilized by amphipods (Clemens 1950, Hargrave 1970, Stevenson and Stoermer 1982, Stewart and Haynes 1994, Van Overdijk et al. 2003, Gonzales and Burkart 2004, Palmer and Ricciardi 2004). Increased densities of *Gammarus* were observed in Lake St. Clair following an increased abundance of submerged vegetation (Griffiths 1992).

Several possible explanations have been proposed as to why *Gammarus* may resist exclusion by *Echinogammarus* on filamentous green algae and other submerged vegetation. First, *Gammarus* have well-developed claws at the terminus of each their pereopods, which better enables them to cling to vegetation, often in a "C-shaped posture" (Clemens 1950). Gonzales and Burkart (2004) suggested that *Gammarus* may

use this "C-shaped posture" as a predator-avoidance mechanism that may mitigate fish predation by making handling by predatory fish difficult. Second, *Gammarus* is light-greenish grey in color compared to the dark reddish color of *Echinogammarus*. Therefore, *Gammarus* may be better camouflaged in aquatic vegetation than *Echinogammarus* (Gonzales and Burkart 2004). Third, *Gammarus* is less active than *Echinogammarus* (Van Overdijk et al. 2003); thus, it may be less noticeable to predators. These characteristics may allow *Gammarus* to continue to predominate in habitats consisting of dense, submerged vegetation (Dermott et al. 1998), whereas *Echinogammarus* may experience increased predation.

Differential fish predation may influence amphipod populations and explain the differences in relative abundance of *Gammarus* and *Echinogammarus* on filamentous green alga and submerged vegetation (Gonzales and Burkart 2004, Limen et al. 2005). In a predation experiment conducted within macrophyte beds, *Echinogammarus* were consumed by yellow perch (*Perca flavescens*) and round gobies (*Neogobious melanostomus*) in greater quantities than were *Gammarus* (Gonzales and Burkart 2004). The combined characteristics of *Echinogammarus's* motility on substrata (Dermott et al. 1998, Van Overdijk et al. 2003), active swimming within the water column (Nalepa et al. 2001), and dark reddish color appear to make *Echinogammarus* more visible to predators in submerged vegetation (Gonzales and Burkart 2004).

Intraguild predation represented an important characteristic in the establishment of exotic amphipods in streams of Ireland (Dick et al. 1993). Gonzales and Burkart (2004) indicate that *Gammarus* prey more on *Echinogammarus* than *Echinogammarus* do on *Gammarus*; therefore, a strong vulnerability to fish predation plus intraguild predation

may limit the abundance of *Echinogammarus*, thereby preventing it from becoming competitively dominant and thus promoting coexistence (Palmer and Ricciardi 2005) or possibly allowing *Gammarus* to exclude *Echinogammarus*, as observed at this particular site in Lake Erie.

An alternative explanation for the lack of *Echinogammarus* at Site 2 is that *Echinogammarus* has not yet reached this area. Within the Great Lakes, *Echinogammarus* was discovered in the Detroit River in 1995 (Witt et al. 1997). Its downstream migration through Lake Erie, Lake Ontario, and the upper St. Lawrence River is thought to have occurred by linear diffusion via strong, long shore currents moving eastward (Csanady and Scott 1974, Simons 1976, as cited in Dermott et al. 1998). However, Palmer and Ricciardi (2004) indicated that *Echinogammarus* densities were not always greater at upstream sampling sites compared to downstream sites and therefore concluded that the spread of *Echinogammarus* from Lake Ontario (the source point) through the St. Lawrence River to Quebec was not accomplished by linear diffusion. Jump dispersal and its subsequent radial population growth could be another possible mechanism for the migration of *Echinogammarus* though the Great Lakes (MacIsaac et al. 2001). This could explain the isolated population of *Gammarus* that was observed at Site 2. If jump dispersal is operating in the Western Basin of Lake Erie, then it may be that *Echinogammarus* hasn't yet invaded Site 2. Future studies involving longer sampling periods and incorporating more sampling sites dispersed both spatially along the shore and into the lake may better explain the processes that have thus far excluded *Echinogammarus* from this particular site in Lake Erie.

At Sites 1 and 4, the substrata consisted of rocks, cobble, and small stones. Substrata at Site 1 were covered with the green alga *Cladophora*, whereas substrata at Site 4 were covered with *Cladophora* and the green alga *Stigeoclonium*. *Gammarus* and *Echinogammarus* coexisted in these filamentous-green-algae-rich habitats during the sampling period, with the exception of the last sampling date at Site 1, where no *Echinogammarus* was collected. These results support previous studies, indicating coexistence of *Echinogammarus* and *Gammarus* (Van Overdijk et al. 2003, Gonzales and Burkart 2004, Palmer and Ricciardi 2004, 2005, Limen et al. 2005) and the speculation that *Gammarus* should continue to fair well in these habitats (Dermott et al. 1998). Further studies incorporating sampling over multiple years are needed in order to address the possibility of long-term coexistence of *Echinogammarus* and *Gammarus*.

Previous studies have indicated that both *Echinogammarus* and *Gammarus* prefer complex habitats and that *Echinogammarus* has a higher affinity for *Dreissena*, whereas *Gammarus* has an affinity for *Cladophora*, yet both *Gammarus* and *Echinogammarus* will inhabit both substrata (Stewart and Haynes 1994, Dermott et al. 1998, Van Overdijk et al. 2003, Gonzales and Burkart 2004). Within *Cladophora*, *Gammarus* is able to effectively occupy the spaces between filaments (Palmer and Ricciardi 2004). Thus, *Gammarus* appears to be better able than *Echinogammarus* to inhabit filamentous green algae and other submerged vegetation (Van Overdijk et al. 2003, Palmer and Ricciardi 2004) and is therefore able to compete with *Echinogammarus* within these habitats (Dermott et al. 1998).

Cladophora growth may inhibit competition by supplying sufficient food and habitat resources that *Gammarus* and *Echinogammarus* can segregate (Palmer and

Ricciardi 2005). Niche differentiation may promote coexistence between *Echinogammarus* and *Gammarus* (Palmer and Ricciardi 2004). The isotope signatures of *Gammarus* and *Echinogammarus* suggest that they may not be competing for the same food resources. *Echinogammarus* appears to be more carnivorous than *Gammarus* and demonstrates an ability to consume a variety of foods. Therefore, *Echinogammarus* and *Gammarus* may be occupying different feeding niches (Limen et al. 2005). Other studies have indicated the coexistence of amphipods through niche differentiation (Dick and Platvoet 1996, MacNeil et al. 1999, MacNeil et al. 2000, MacNeil et al. 2001, as cited in Palmer and Ricciardi 2004).

Another factor previously mentioned that may influence the coexistence of *Gammarus* and *Echinogammarus* is predation. *Echinogammarus* appears to be more vulnerable to predation in filamentous green algae and other submerged vegetation than does *Gammarus* (Gonzales and Burkart 2004), thereby preventing *Echinogammarus* from becoming competitively dominant, and promoting coexistence between *Gammarus* and *Echinogammarus* (Palmer and Ricciardi 2005).

Relative to Site 2, Sites 1 and 4 are extensively used for recreational shore fishing, which may suppress local fish-population densities. Lower populations of predatory fish may mitigate predation pressure on *Echinogammarus* and further promote coexistence between *Gammarus* and *Echinogammarus* within these areas. Future studies investigating local fish-population densities, habitat utilization, and selected pressures due to predation may contribute to a better understanding of both habitat preferences and coexistence between *Gammarus* and *Echinogammarus*.

The amphipod *Gammarus* was observed inhabiting only sites containing filamentous and macro-colonial algae. Previous studies have shown an affinity between *Gammarus* and submerged vegetation (Clemons 1950, Dermott et al. 1998, Van Overdijk et al. 2003, Gonzales and Burkart 2004). Relative abundance of *Gammarus* was correlated to the relative abundance of filamentous and macro-colonial algae. High relative abundance (> 80%) of filamentous and macro-colonial green algae yielded high relative abundances of *Gammarus* (ca. 100%), whereas zero abundance of filamentous and macro-colonial algae yielded zero relative abundance of *Gammarus*. Due to the variability (5%-100%) of *Gammarus* relative abundance as seen at lower concentrations (5%-20%) of filamentous and macro-colonial algae, and the lack of any data in the mid-range (20%-80%) of filamentous and macro-colonial green algae's relative abundance, the predictive powers of these results are limited. Further studies utilizing absolute abundances of filamentous and macro-colonial green algae and encompassing a wider range of algal abundance may enable a better understanding of the relationship between algal and amphipod community structure.

In summary, this study suggests that *Echinogammarus* has competitively replaced *Gammarus* on *Dreissena*-encrusted substrata at Site 3, as predicted by Dermott et al. (1998), whereas at Site 2, *Gammarus* has been able to resist exclusion and remain the dominant amphipod within filamentous- and macro-colonial-algae-rich habitats. *Echinogammarus* and *Gammarus* coexisted at the remaining two sites (Sites 1 and 4), which were also rich in filamentous algae. Differential predation may be a key factor in mitigating the relative abundance of *Echinogammarus* on filamentous and macro-colonial algal habitats, thereby possibly promoting either the coexistence of both amphipods or

the exclusion of *Echinogammarus* (Gonzales and Burkart 2004). Further multiple-year studies should include more sampling sites and include sampling from more than one depth. In addition, this study revealed that *Gammarus* was always associated with filamentous, or filamentous and macro-colonial, algae. A strong correlation existed between *Gammarus* and the relative abundance of filamentous and macro-colonial algae, although its predictive power is limited. Further studies examining the relationship between the absolute abundance of filamentous and macro-colonial algae and amphipod absolute abundances may lead to further insight about amphipod requirements and habitat preferences.

WORKS CITED

Bially A, MacIsaac HJ. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. Freshwater Biology 43:85-97.

Clemens HP. 1950. Life cycle and ecology of *Gammarus fasciatus* Say. Columbus, OH: The Ohio State University Press. 63 p.

Dick JTA, Montgomery WI, Elwood RW. 1993. Replacement of the indigenous amphipod *Gammarus duebeni celticus* by the introduced *G. pulex*: differential cannibalism and mutual predation. J Animal Ecol 62:79-88.

Dick JTA, Platvoet D. 1996. Intraguild predation and species exclusions in amphipods: the interaction of behavior, physiology and environment. Freshwater Biology 36:375-383.

Dillard GE. 1999. Common freshwater algae of the United States. Berlin-Stuttgart, Germany: Gebruder Borntraeger. 174 p.

Dermott R, Mitchell J, Murray I, Fear E. 1993. Biomass and production of zebra mussels (*Dreissena polymorpha)* in shallow waters of Northeastern Lake Erie. In: Nalepa TF, Schlosser DW, editors. Zebra mussels: biology, impacts and controls. Ann Arbor, MI: Lewis Pub. p 399-413.

Dermott R, Witt J, Um M, Gonzalez M. 1998. Distribution of the Pont-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus.* J Great Lakes Res 24:442-452.

Griffiths RW. 1992. Effects of zebra mussel (*Dreissena polymorpha*) on benthic fauna of Lake St. Clair. In: Nalepa TF, Schlosser DW, editors. Zebra mussels: biology, impacts and controls. Ann Arbor, MI: Lewis Pub. p 415-438.

Gonzales MJ, Downing A. 1999. Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish amphipod interactions. Can J Fish Aquat Sci 56:679-685.

Gonzales MJ, Burkart GA. 2004. Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species, *Gammarus fasciatus* and *Echinogammarus ischnus*. J Great Lakes Res 30(1):100-113.

Hargrave JL. 1970. The utilization of benthic micro-flora by *Hyalella azteca* (Amphipoda). Journal of Phycology 39:427-437.

Hebert PDN, Muncaster BW, Mackie GL. 1989. Ecological and genetic studies on *Dreissena polymorpha* Pallas: a new mollusk in the Great Lakes. Can J Fish Aquat Sci 46:1587-1591.

John DM. 2003. Filamentous and plantlike green algae. In: Wehr JD, Sheath RG, editors. Freshwater algae of North America. New York: Academic Press. p 311-352.

Limen H, Van Overdijk CDA, MacIsaac HJ. 2005. Food partitioning between the amphipods *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyalella azteca* as revealed by stable isotopes. J Great Lakes Res 31:97-104.

Lowe RL, Rosen BH, Kingston JC. 1982. A comparison of epiphytes on *Bangia atropurpurea* (Rhodophyta) and *Cladophora glomerata* (Chlorophyta) from northern Lake Michigan. J Great Lakes Res 8(1):164-168.

MacIsaac HJ, Grigorovich IA, Ricciardi A. 2001. Reassessment of species invasions concepts: the Great Lakes basin as a model. Biological Invasions 3:405-416.

MacNeil C, Elwood RW, Dick JTA. 1999. Differential micro-distributions and interspecific interactions in coexisting *Gammarus* and *Crangonyx* amphipods. Ecography 22:415-423.

MacNeil C, Montgomery WI, Dick JTA, Elwood RW. 2000. Factors influencing the distributions of native and introduced *Gammarus* spp. in Irish river systems. Arch Hydrobiol 1551:353-368.

MacNeil C, Dick JTA, Elwood RW, Montgomery WI. 2001. Coexistence among native and introduced freshwater amphipods (Crustacea): habitat utilization patterns in littoral habitats. Arch Hydrobiol 151:591-607.

Marks JC, Power ME. 2001. Nutrient induced changes in the species composition of epiphytes on *Cladophora glomerata* Kutz. Hydrobiologia 450:187-196.

Mills EL, Leach JH, Carlton JT, Secor CL. 1993. Exotic species in the Great Lakes: a history of biotic crisis and anthropogenic introductions. J Great Lake Res 19:1-54.

Mills EL, Dermott RM, Roseman EF, Dustin D, Mellina E, Conn DB, Spidle AP. 1993. Colonization, ecology, and population structure of the "quagga" mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. Can J Fish Aquat Sci 50:2305-2314.

Mills EL, Chrisman JR, Baldwin B, Owens RW, Gorman RO, Howell T, Roseman EF, Rath MK. 1999. Changes in the Dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. J Great Lakes Res 25(1):187-197.

Nalepa TF, Schloesser DW, Pothoven SA, Hondorp DW, Fanslow DL, Tuchman ML, Fleischer GW. 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. J Great Lakes R27(3):384-391.

Palmer ME, Ricciardi A. 2004. Physical factors affecting the relative abundance of native and invasive amphipods in the St. Lawrence River. Can J Zoology 82:1886-1893.

Palmer ME, Ricciardi A. 2005. Community interactions affecting the relative abundance of native and invasive amphipods in the St. Lawrence River. Can J Fish Aquat Sci 62:1111-1118.

Patrick R, Reimer R. 1996. The diatoms of the United States. Volume 1. Philadelphia, PA: Sutter House. 688 p.

Smith DG, editor. 2001. Pennak's freshwater invertebrates of the United States. 4th ed. New York: Wiley and Sons. 638 p.

Prescott GW. 1982. Algae of the Western Great Lakes area. Koenigstein, West Germany: Otto Koeltz Science Publishers. 977 p.

Ricciardi A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Can J Fish Aquat Sci 58:2513-2525.

Simons TJ. 1976. Continuous dynamical computations of water transport in Lake Erie for 1970. J Fish Res Board Can 33:371-384.

Stevenson RJ, Stoermer EF. 1982. Seasonal abundance patterns of diatoms on *Cladophora* in Lake Huron. J Great Lakes Res 8(1):169-183.

Stewart TW, Haynes JM. 1994. Benthic macroinvertebrate communities of Southwestern Lake Ontario following invasion of *Dreissena*. J Great Lakes Res 20:479-493.

Stewart TW, Miner JG, Lowe RL. 1998a. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. J Great Lakes Res 24:868-879.

Stewart TW, Miner JG, Lowe RL. 1998b. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. J N Am Benthol Soc 17(1):81-94.

Taft CE, Taft CW. 1990. The algae of Western Lake Erie. Columbus, OH: College of Biological Sciences, Ohio State University. 189 p.

ter Braak CJF. 1995. Ordination. In RHG Jongman, CJF ter Braak, OFR Van Tongeren, editors. Data analysis in community and landscape ecology. 2nd ed. Cambridge: Cambridge University Press. p 91-173.

ter Braak CJF, Smilauer P. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4.0). Ithaca, NY: Microcomputer Power. 500 p.

Vanderploeg HA, Nalepa TF, Jude DJ, Mills EL, Holeck KT, Liebig JR, Grigorovich IA, Ojaveer H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can J Fish Aquat Sci 59:1209-1228.

Van Overdijk CDA, Grigorovich IA, Mabee T, Ray WJ, Ciborowski JJH, MacIsaac HJ. 2003. Microhabitat selection by the invasive amphipod *Echinogammarus ischnus* and native *Gammarus fasciatus* in laboratory experiments and in Lake Erie. Freshwater Biology 48:567-578.

Wehr JD, Sheath RG. 2003. Freshwater algae of North America. New York: Academic Press. 918 p.

Wisenden PA, Bailey RC. 1995. Development of macroinvertebrate community structure associated with zebra mussel (*Dreissena polymorpha*) colonization of artificial substrates. Can J Zoology 73:1438-1443.

Witt JDS, Hebert PDN, Morton WB. 1997. *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. Can J Fish Aquat Sci 54:264-268.