

Density and Distribution of Amphipods in Oneida Lake, New York, after the Introduction of the Exotic Amphipod *Echinogammarus ischnus*

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Abstract - The exotic amphipod *Echinogammarus ischnus*, first reported in North America from western Lake Erie in 1995, was recorded in Oneida Lake, NY in 2001. Some North American studies have suggested that *E. ischnus* was replacing native amphipods, but other studies found no evidence for this. We sampled amphipods at six depths (<0.2, 0.6, 1.2, 1.8, 3.0, and >3.8 m) along six transects in Oneida Lake to quantify variation in densities of amphipod species as a function of depth, substrate (cobble with *Dreissena* and with or without macroalgae, sand with or without *Dreissena*, and macroalgae or submersed vascular plants) and density of *Dreissena*, and compared the present amphipod density to the historical record. Four species of amphipods, *Gammarus fasciatus*, *Hyaella azteca*, *E. ischnus*, and *Crangonyx* sp., were collected from Oneida Lake. *Gammarus fasciatus* was 9 to 90 times more abundant (mean = 0.09 individuals/cm²) than other amphipod species and was collected on all substrates and at all depths, as was *H. azteca*. Statistical comparisons were made with non-parametric tests between mean ranks of density of amphipods and *Dreissena* and the other variables. Mean ranks of density of *G. fasciatus* were correlated with depth (Spearman rank = 0.28, $P < 0.0001$), but mean ranks of density of *H. azteca* were not, and neither species was correlated with mean ranks of density of *Dreissena*. Mean ranks of density of *G. fasciatus* were greater on sand with or without macroalgae or submersed vascular plants (SVP) or *Dreissena* than on cobble with macroalgae and *Dreissena* ($H = 28.2$, $P < 0.0001$). Mean ranks of density of *H. azteca* were greater on sand with SVP, with or without *Dreissena*, than on sand with *Dreissena* and without SVP ($H = 21.8$, $P = 0.0013$). *Echinogammarus ischnus* was collected only in water less than 1.8 m depth and always with *Dreissena*. Mean ranks of density of *E. ischnus* were correlated with depth (Spearman rank = -0.29, $P < 0.0001$) and with *Dreissena* mean ranks of density (Spearman rank = 0.14, $P = 0.01$). Mean ranks of density of *E. ischnus* was greater on cobble with *Dreissena* than on sand with *Dreissena* regardless of the presence or absence of macroalgae or SVP ($H = 35.4$, $P < 0.0001$). Although *E. ischnus* is established in the near-shore zone of Oneida Lake, we found no evidence that it will replace the native amphipods *G. fasciatus* and *H. azteca*.

Introduction

The exotic amphipod *Echinogammarus ischnus* Stebbing, native to the Ponto-Caspian region, was introduced into the North American Great Lakes through

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ballast-water releases of commercial ships (Holeck et al. 2004) in the 1990s, and colonized the lower Great Lakes and the upper St. Lawrence River within three years (Dermott et al. 1998, Nalepa et al. 2001, Witt et al. 1997).

Establishment of exotic species can have profound effects on the pre-existing biological communities (Bailey et al. 2006, Mills et al. 1993, Pimentel 2005). For example, predatory behavior of the exotic amphipod *Dikerogammarus villosus* Sovinskij in Europe was implicated in the rapid decline of macroinvertebrate abundance (Krisp and Maier 2005), as well as the replacement of the native amphipod *Gammarus duebeni* Lilljeborg and an exotic North American amphipod *Gammarus tigrinus* Sexton (Dick and Platvoet 2000). Interspecific competition and predation have been hypothesized as causes for the observed displacement of *Gammarus fasciatus* Say (native to North American Great Lakes) by *E. ischnus* from hard substrates in the Great Lakes (Dermott et al. 1998, Van Overdijk et al. 2003). Several studies demonstrated that intensity of predator-prey interactions between native and exotic amphipods were dependant on specific conductivity (Dick and Platvoet 1996; Kestrup and Ricciardi 2009, 2010, 2011).

Echinogammarus ischnus has been associated most often with hard substrate (cobble, concrete), *Dreissena* (Kang et al. 2007, Kohn and Waterstraat 1990), and shallow water (0.2–3.6 m; Kohn and Waterstraat 1990, Van Overdijk et al. 2003), but it has been collected at depths from 5 to 7 m in Lake Ontario (Haynes et al. 2005), and from 16 m to 94 m in Lake Michigan (Nalepa et al. 2001). Kang et al. (2007) found *E. ischnus* to be more abundant in high-energy shorelines than in the slower-moving water of Great Lakes wetlands. In the upper St. Lawrence River, Palmer and Ricciardi (2004) found positive correlations between *E. ischnus*, current velocity, and abundance of gravel-sized substrate.

Gammarus fasciatus, more of a generalist in habitat preferences, has previously been associated with algae and rooted vegetation in the slow-moving water of lakes and large rivers from shoreline to 12 m depth (Beckett and Miller 1982, Bousfield 1958, Clemens 1950). In Lake Erie, *G. fasciatus* showed no preference for *Dreissena* over *Cladophora* but did prefer *Cladophora* over bare rock (Van Overdijk et al. 2003); *G. fasciatus* abundance increased in the Great Lakes after the introduction of *Dreissena*, which it utilized as habitat (Ricciardi et al. 1997). Abundance of *G. fasciatus* relative to *E. ischnus* in the St. Lawrence River has varied temporally and spatially: *E. ischnus* was not present at some sampling sites where it had been found previously (Palmer and Ricciardi 2004), and increased abundance of *E. ischnus* in one year was followed by a decline in abundance in the second year of an experimental study (Palmer and Ricciardi 2005). The authors noted that these results were in contrast to those found in the Great Lakes, where *E. ischnus* dominance progressed over time at several sites. *Gammarus fasciatus* is a major food resource for *Perca flavescens* (Mitchill) (Yellow Perch) (Keast 1977, Pothoven et al. 2000), which, in turn, is a major forage species for *Sander vitreus* (Mitchill) (Walleye) in Oneida Lake (Forney 1974, VanDeValk et al. 2005). If *G. fasciatus* is replaced by *E. ischnus*,

changes in abundance of near-shore amphipods might alter foraging success by young-of-the-year Yellow Perch. It is less likely that adult Yellow Perch would be affected since a greater proportion of young-of-the-year Yellow Perch occur at near-shore areas.

The native amphipod *Hyaella azteca* de Saussure, considered by Bousfield (1958) to be the most widely distributed North American freshwater amphipod, has been associated with fine sand substrate and various forms of aquatic vegetation (Baker 1918, Beatty and Hooper 1958, Edwards and Cowell 1992). *Hyaella azteca* has been recorded at 13 m water depth (Dionne et al. 2011) but more often from water <5 m in depth (Hargrave 1970, Wood 1952).

Four native amphipod species were reported from Oneida Lake in 1916 (Baker 1918): *Hyaella knickerbockeri* (Bate) (= *Hyaella azteca*), *Gammarus fasciatus*, *Eucrangonyx gracilis* (= *Crangonyx gracilis* Smith), and *G. limnaeus* S.I. Smith. The most abundant species was *H. azteca*, followed distantly by *G. fasciatus*, and both species were associated with a variety of substrates ranging from mud to cobble at depths of 0.5 to 4.5 m water depth. *Crangonyx gracilis* and *G. limnaeus* were relatively rare and were recorded from depths <1.2 m and 3 m, respectively.

Our study site, Oneida Lake, forms part of the Erie Barge Canal (EBC) that links the Hudson River, and the Finger Lakes in central NY, with lakes Ontario and Erie (Fig. 1). The EBC has facilitated the introduction of more than 30 exotic species into Oneida Lake since the early 1900s (K. Holeck, Cornell University, Bridgeport, NY, pers. comm.). Two of the exotic species in Oneida Lake, *Dreissena polymorpha* Pallas (Zebra Mussel) and *D. bugensis* Andrusov (Quagga Mussel), introduced in 1991 and 2001, respectively, were considered as a suitable

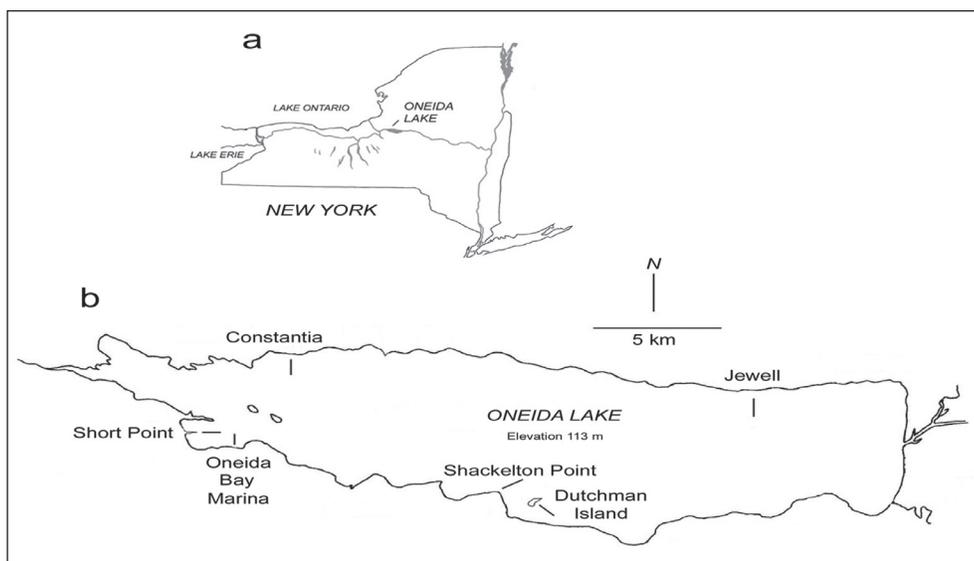


Figure 1. Location of Oneida Lake (a) and its position relative to the Erie Barge Canal system linking the Hudson River to lakes Ontario and Erie; and (b) transects (shown as lines) sampled for amphipods and *Dreissena*.

habitat for *E. ischnus* colonization due to the established association of *Dreissena* and this exotic amphipod (Kohn and Waterstraat 1990). *Echinogammarus ischnus* was first recorded in Oneida Lake in 2001 (at <1 m depth; C.M. Mayer, University of Toledo, Toledo, OH, unpubl. data).

The objectives of this study were 1) to determine the relative density of native and exotic amphipods in relation to depth, substrate, and *Dreissena* in Oneida Lake and 2) to compare the present amphipod density to that in the historical record.

Methods

Study lake characterization

Oneida Lake (43°10'N, 76°00'W) is a large, shallow, mesotrophic lake (surface area = 207 km²; mean depth = 6.8 m; Fig. 1), and is located northeast of Syracuse, NY. The shallow water substrate is predominately cobble or sand, becoming primarily sand and silt in deeper water, and there are extensive cobble shoals offshore. The two species of *Dreissena* have formed aggregated colonies on cobble substrates, and filamentous benthic macroalgae cover many cobble substrates and the submersed vascular plants (SVP) in deeper water. The New York State Canal Corporation lowers the lake water level by 1 m in winter to accommodate spring snowmelt.

Amphipod sampling and identification

Six permanent transects were established (Fig. 1); we expected that five of these represented suitable habitat for *E. ischnus* (presence of cobble and *Dreissena*) and that one transect (Oneida Bay Marina) would not (fine sand, no *Dreissena* in water <1.8 m depth). Oneida Bay Marina was included because the same area had been sampled in the past (Baker 1918, Clady 1975, Mayer et al. 2002), which would enable comparisons to the present study. Paired quantitative samples (each sample was either a single cobble-sized rock or a sand grab, 12 samples per transect) were taken at each of six depths starting at the shoreline (<0.2 m, 0.6 m, 1.2 m, 1.8 m, 3.0 m, and >3.8 m) along each transect (Table 1). Samples were taken within a 15-m diameter circle at the appropriate depth. All transects were set perpendicular to shore, with the length of each transect determined by the distance required to reach >3.8 m depth. Lengths of transects were: Short Point, 1250 m; Oneida Bay Marina, 800 m; Jewell, 600 m; and 400 m each for Constantia, Dutchman Island, and Shackelton Point. The end point of each transect was referenced to latitude and longitude using a handheld global positioning device. Conductivity, water temperature, and dissolved oxygen were measured at the water surface and bottom at the deepest point of each transect; the latter two parameters were used to calculate percent oxygen saturation. Conductivity was considered to be intermediate between 121–215 µS/cm and high at >276 µS/cm (Kestrup and Ricciardi 2010). Conductivity values taken in 2005 and 2006 were compared to data from a long-term data set (1975 to 2006) measured at five open-water

Table 1. Substrate characteristics at six sampling depths along six transects in Oneida Lake. *Echinogammarus ischnus* was collected on the substrates shown in bold. SVP = submersed vascular plants.

Depth (m)	Transects					
	Short Point	Oneida Bay Marina	Dutchman Island	Shackelton Point	Constantia	Jewell
< 0.2	Cobble <i>Dreissena</i> No macroalgae	Fine sand No <i>Dreissena</i> SVP	Cobble <i>Dreissena</i> Macroalgae	Cobble <i>Dreissena</i> Macroalgae	Cobble <i>Dreissena</i> Macroalgae	Cobble <i>Dreissena</i> No macroalgae
0.6	Cobble <i>Dreissena</i> No macroalgae	Fine sand No <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> Macroalgae	Cobble <i>Dreissena</i> Macroalgae	Cobble <i>Dreissena</i> Macroalgae	Cobble <i>Dreissena</i> No macroalgae
1.2	Cobble <i>Dreissena</i> No macroalgae	Fine sand No <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> SVP	Coarse sand <i>Dreissena</i> Macroalgae	Fine sand <i>Dreissena</i> SVP	Coarse sand <i>Dreissena</i> No vegetation
1.8	Cobble <i>Dreissena</i> No macroalgae	Fine sand <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> SVP	Coarse sand <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> SVP	Coarse sand <i>Dreissena</i> No vegetation
3	Fine sand <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> SVP	Fine sand <i>Dreissena</i> No vegetation
> 3.8	Fine sand <i>Dreissena</i> No vegetation	Fine sand No <i>Dreissena</i> No vegetation	Fine sand No <i>Dreissena</i> No vegetation	Fine sand No <i>Dreissena</i> No vegetation	Fine sand <i>Dreissena</i> No vegetation	Fine sand <i>Dreissena</i> No vegetation

stations (Cornell Biological Field Station). Calcium values were obtained from several sources: from 1960 to 1990 (US Geological Survey, <http://water-data.usgs.gov/nwis/qwdata>), for 2001 (Limburg and Siegel 2006), and recent determinations (2011) by the first author. Transects at Short Point, Oneida Bay Marina, and Dutchman Island were sampled in August 2005. Shackelton Point, Constantia, and Jewell were sampled in October 2005, and all transects were sampled in May, June, and July 2006. Single rocks were retrieved in cobble-dominated areas by hand or with an Ekman dredge and placed quickly into a bucket after being transported to the water surface. Rocks were then scraped to remove amphipods and *Dreissena*. Sand samples were sampled by dredge. Scraped material from rocks and entire sand samples were washed through a 500- μm screen, and the collected material was preserved in 70% ethanol. Colonizable surface area of collected rocks was estimated by measuring length, width, and height (mm) to the point of burial, and sand sample area was quantified as the flat benthic area of the dredge (225 cm²/sample). *Dreissena* density in 2005 was estimated from colonizable rock surface area, and, for sand samples, from the area sampled by the dredge. Abundance of SVP, macroalgae, and *Dreissena* were not quantified in 2006; however, their presence or absence from a plot was recorded.

Gammarus fasciatus and *Echinogammarus ischnus* were identified using morphological characteristics (Holsinger 1976, Witt et al. 1997) of uropods and antennae. *Hyaletta azteca* was identified by gnathopod morphology and the presence of dorsal teeth (Fig. 2): dorsal teeth are not present in *G. fasciatus* or *E. ischnus*. The characteristics of the base of pereopod 7 and the basal segments of the second antennae in the male were used to identify *Crangonyx* sp. (Holsinger 1976, Zhang and Holsinger 2003). The presence of red-pigmented antennae (Dermott et al. 1998) was not used as an identifying character for *E. ischnus* as

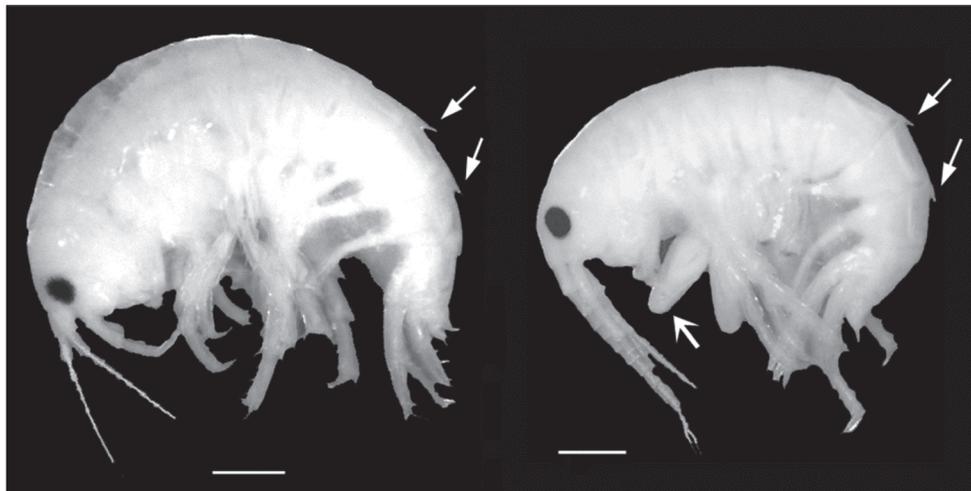


Figure 2. *Hyaletta azteca* female (left) and male (right) showing dorsal teeth (paired arrows) and the large gnathopods on the male (concave arrow) used as identifying characteristics. Scale bar = 0.5 mm.

many Oneida Lake *G. fasciatus* also have red pigment on their antennae, which remains visible for several months after collection.

Statistical analyses

Mean amphipod species densities were compared in relation to transect, water depth, and substrate using the non-parametric Kruskal-Wallis (KW; SAS 2001) test on non-transformed data. The distribution of the test statistic, H, approximates that of the chi-square distribution and compares the ranks of the measured variable. The KW test does not require assumptions of normality of data distribution. KW tests were used to compare the means of the ranks of density of each of three amphipod species in relation to transect and depth ($\alpha = 0.008$ after Bonferroni correction for multiple comparisons), and to compare means of ranks of density of each of three amphipod species to seven substrates (Table 1): cobble with or without macroalgae (cobble always had *Dreissena*), sand with macroalgae and *Dreissena*, sand with SVP (with or without *Dreissena*), and sand without vegetation (with or without *Dreissena*). The cumulative distributions of mean density by depth for the three more abundant amphipod species were compared using the Kolmogorov-Smirnov test. Calculated values for oxygen saturation were compared to mean ranks of amphipod density at six depths for July (time of lowest oxygen saturation) using KW to determine if there was any effect of low oxygen saturation on density; a significantly lower mean rank at >3.8 m depth compared to other depths would indicate an effect. Density of *Dreissena* was compared across transects and depths using KW. Mean ranks (based on density) of the three amphipod species were compared to the mean ranks of conductivity, depth, and density of *Dreissena* using Spearman rank correlation. An additional amphipod species, *Crangonyx*, was excluded from statistical analysis because only one individual was recorded.

Results

We collected four species of amphipods in Oneida Lake. *Gammarus fasciatus* was the most abundant amphipod species with a mean density of 0.09 individuals/cm² (SE = 0.01) and accounted for 83.1% of all amphipods collected. *Hyalella azteca* was second in abundance with a mean density of 0.01 individuals/cm² (SE = 0.004) and accounted for 15.1% of all amphipods collected, while *E. ischnus* was collected at low density (0.001 individuals/cm², SE = 0.0007; 1.8% of all amphipods collected). One *Crangonyx* sp. was collected at Short Point. *Dreissena* was present at all sampling locations except for depths <1.8 m at Oneida Bay Marina and >3.8 m depth at Dutchman Island, Oneida Bay Marina, and Shackelton Point (Table 1) and had a mean density of 0.85 individuals/cm² (SE = 0.28).

Percent dissolved oxygen saturation was lowest in July (27%) at depths > 3.8 m but was $>50\%$ at all depths in other sampling months. The low saturation did not result in lower mean ranks of density; *G. fasciatus* mean ranks were significantly

greater ($H = 24.4$, $P < 0.0002$) at depths between 1.8 and >3.8 m than at shallower depths, and there was no apparent effect on *H. azteca* abundance as there was no significant difference ($H = 13.9$, $P = 0.02$) in mean ranks by depth. Conductivity measured in this study ranged from intermediate to high (220–400 $\mu\text{S}/\text{cm}$, mean = 327 ± 32), and was 40% lower at Constantia (220 $\mu\text{S}/\text{cm}$) and Jewell (230 $\mu\text{S}/\text{cm}$) than at the other transects. We found no significant correlation between the mean ranks of the three amphipod species and conductivity (Spearman rank = 0.38, $P = 0.6$). Our conductivity values were similar to those in the long-term data set measured at the five open-water stations.

Amphipod density as a function of transect and depth

There was considerable variation in amphipod species density by transect. *Gammarus fasciatus* was collected at all transects, but its density was nearly twice as great at Short Point than at Jewell, which had the second greatest density, and more than three times as great as at Constantia, where density was least. Mean ranks of density of *G. fasciatus* were significantly greater at Short Point than at Constantia ($H = 17.9$, $P = 0.003$) but not statistically different from other transects. Density of *H. azteca* was three times greater at Oneida Bay Marina than at Dutchman Island, 60 times greater than at Shackelton Point, and mean ranks of density were significantly greater at Dutchman Island, Oneida Bay Marina, and Short Point than at Shackelton Point, Constantia, or Jewell ($H = 48.5$, $P < 0.0001$). *Echinogammarus ischnus* was collected at four of the six transects, but two transects, Jewell and Constantia, accounted for nearly 80% of all *E. ischnus*, and mean ranks of density at Jewell and Constantia were significantly greater than at Shackelton Point and Short Point ($H = 20.2$, $P = 0.001$). *Dreissena* collected at Short Point, Jewell, and Constantia accounted for nearly 80% of all *Dreissena*, and mean ranks were significantly greater at Short Point than at other transects. Mean ranks of density at Jewell and Constantia were significantly greater than at Dutchman Island, Oneida Bay Marina, and Shackelton Point ($H = 108.8$, $P < 0.0001$).

Gammarus fasciatus was collected at all depths, as was *H. azteca*, while *E. ischnus* was collected only at depths 1.8 m or less (Fig. 3), primarily at <0.2 m and 0.6 m (73.1% and 24.6% of all *E. ischnus*). Each amphipod species showed a different cumulative distribution in density by depth. *Gammarus fasciatus* density was more evenly distributed over depth (Fig. 3) than was *H. azteca*, from which it was significantly different (KS = 0.26, D = 0.52, $P < 0.0001$). The distribution of *E. ischnus* was more limited and was significantly different from that of the other species (*G. fasciatus*: KS = 0.41, D = 0.83, $P < 0.0001$; *H. azteca*: KS = 0.19, D = 0.39, $P < 0.0001$). Mean ranks of *G. fasciatus* density were significantly less at <0.2 m depth ($H = 31.0$, $P < 0.0001$) than at other depths, while there was no significant difference in mean ranks of *H. azteca* density by depth ($H = 10.7$, $P = 0.06$). *Echinogammarus ischnus* mean ranks of density were greater at <0.2 and 0.6 m than at 1.8 m and 3 m depth ($H = 30.9$, $P < 0.0001$). *Dreissena* was collected at all depths (Fig. 4) but not at all transect–depth combinations (Table 1). Mean ranks of *Dreissena* density were not significantly different by depth ($H = 13.3$, $P = 0.02$,

critical $\alpha = 0.008$). There was a significant correlation between *Dreissena* mean ranks of density and *E. ischnus* mean ranks of density (Spearman rank = 0.14, $P = 0.01$), but there was no significant correlation ($P > 0.4$) between *Dreissena* mean ranks and the mean ranks of *G. fasciatus* or *H. azteca* density.

Amphipod density as a function of substrate

More than half (58.9%) of all *G. fasciatus* collected occurred on sand substrates, and the mean ranks of density for *G. fasciatus* were significantly greater

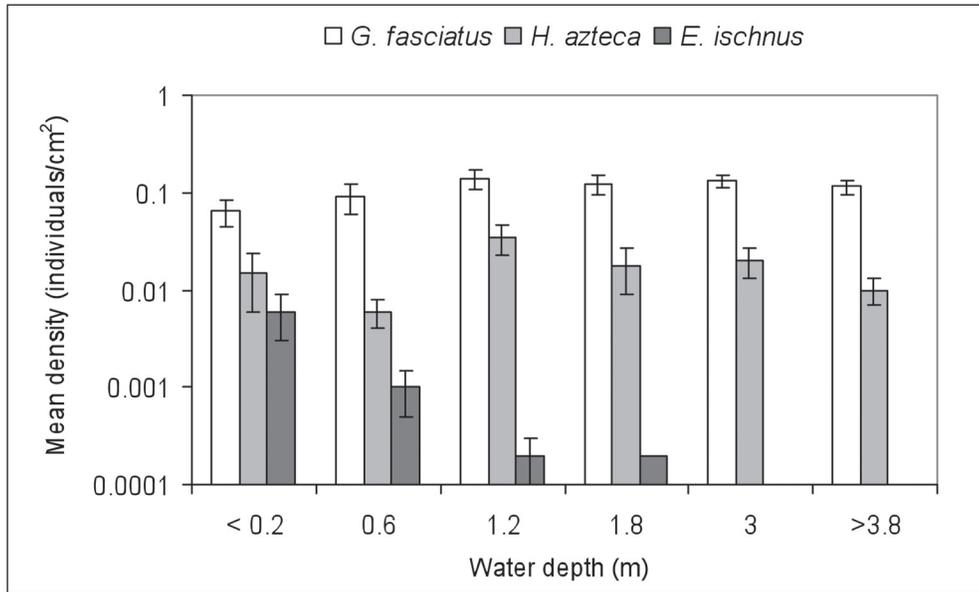


Figure 3. Mean density (individuals/cm², bars = 1 SE) by depth of three amphipod species collected (all transects combined) in Oneida Lake in 2005 and 2006.

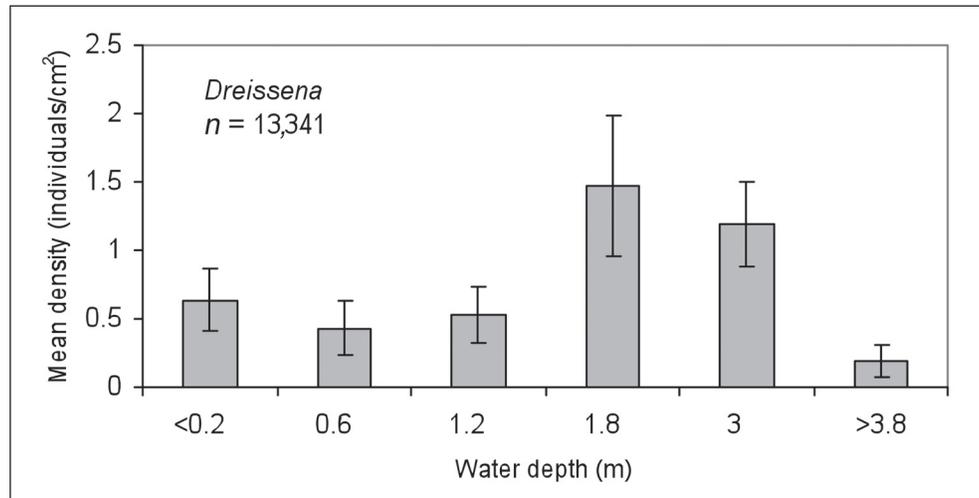


Figure 4. Mean density (individuals/cm², bars = 1 SE) by depth of *Dreissena* collected in 2005 (all transects combined).

($H = 28.2$, $P < 0.0001$) on sand substrates (with or without SVP or *Dreissena*) than on cobble with macroalgae and *Dreissena* (Tables 2, 3).

Nearly 87% of *H. azteca* were collected from sand substrates, with 40.9% coming from sand substrate with SVP in the absence of *Dreissena*. Mean ranks of density of *H. azteca* were significantly greater ($H = 21.8$, $P = 0.001$) on sand substrate with SVP (with or without *Dreissena*) than on sand substrate without vegetation but with *Dreissena*. Mean ranks of *H. azteca* were significantly correlated with *G. fasciatus* mean ranks (Spearman rank = 0.33, $P < 0.0001$).

Echinogammarus ischnus was generally less abundant than *G. fasciatus* or *H. azteca* and occurred primarily on shallow cobble substrate (97.7% of all *E. ischnus*) with or without macroalgae, but always with *Dreissena*. Mean ranks of density were greater ($H = 35.4$, $P < 0.0001$) on cobble substrate with macroalgae, and cobble without macroalgae, than on sand substrate with SVP and *Dreissena*, and sand substrate with *Dreissena* but without vegetation.

Table 2. Amphipod and *Dreissena* mean density (individuals/cm² with 1 SE in parentheses) collected on sand (fine and coarse sand combined) substrate with or without vegetation or *Dreissena*. Percent refers to the proportion of the total collected of each species. SVP = submersed vascular plants.

Taxa	Sand / <i>Dreissena</i> / macroalgae		Sand / <i>Dreissena</i> / no vegetation		Sand / no <i>Dreissena</i> / no vegetation		Sand / <i>Dreissena</i> / SVP		Sand / no <i>Dreissena</i> / SVP	
	Density (1 SE)	%	Density (1 SE)	%	Density (1 SE)	%	Density (1 SE)	%	Density (1 SE)	%
<i>Gammarus fasciatus</i>	0.153 (0.086)	7.1	0.102 (0.025)	14.9	0.070 (0.023)	5.3	0.098 (0.020)	26.1	0.076 (0.017)	5.5
<i>Hyalella azteca</i>	0.004 (0.002)	4.5	0.007 (0.004)	5.6	0.014 (0.007)	5.7	0.020 (0.007)	29.8	0.10 (0.009)	40.9
<i>Echinogammarus ischnus</i>	0	0.0	0.0005 (0.00005)	0.6	0	0.0	0.0005 (0.00009)	1.7		
<i>Dreissena</i>	0.02 (0.01)	0.6	0.23 (0.04)	13.6	0	0.0	0.99 (0.13)	33.8		
Number of samples			16		48		24		88	

Table 3. Amphipod and *Dreissena* mean density (individuals/cm² with 1 SE in parentheses) collected on cobble substrate with or without macroalgae. All cobble samples were colonized by *Dreissena*. Percent refers to the proportion of the total collected of each species.

Taxa	Cobble / <i>Dreissena</i> / macroalgae		Cobble / <i>Dreissena</i> / no macroalgae	
	Mean density (1 SE)	%	Mean density (1 SE)	%
<i>Gammarus fasciatus</i>	0.025 (0.005)	6.5	0.143 (0.034)	34.5
<i>Hyalella azteca</i>	0.005 (0.001)	4.2	0.007 (0.003)	9.2
<i>Echinogammarus ischnus</i>	0.005 (0.002)	46.2	0.004 (0.002)	51.5
<i>Dreissena</i>	0.25 (0.04)	5.0	1.79 (0.07)	47.0
Number of samples		40		48

Dreissena occurred in 83% of all possible samples (Table 1), and density on cobble substrate without macroalgae was nearly double the density occurring on sand with SVP, the two substrates with greater density (Tables 2, 3). Mean ranks of density were greater on cobble without macroalgae than on sand with SVP, cobble with macroalgae, sand with macroalgae, or sand without vegetation ($H = 100.6$, $P < 0.0001$).

Discussion

Gammarus fasciatus was the most abundant amphipod species in Oneida Lake, with a mean density nine times greater than *H. azteca*, and 90 times greater than the exotic *E. ischnus*. Significant differences in mean ranks of density among transects could be due to effects of relative wave energy, substrate, depth, and conductivity. *Gammarus fasciatus* had greater density at Short Point, Dutchman Island, and Oneida Bay Marina, where wave energy would be relatively low; these transects have less fetch from the prevailing westerly winds than the other transects. Kang et al. (2007) did not find *G. fasciatus* to be abundant in high-energy habitats in the Great Lakes. *Gammarus fasciatus* density in Oneida Lake was also less in the most shallow areas (<0.2 m) of each transect, perhaps as a result of amphipods avoiding the higher-energy shoreline. We did not find a significant correlation between conductivity and mean ranks of density for *G. fasciatus* in Oneida Lake, perhaps because abundance would only be affected by low conductivity and not by the intermediate or high conductivity levels we measured. Kestrup and Ricciardi (2010) reported that *G. fasciatus* was more abundant at intermediate and high conductivity than low conductivity in the upper St. Lawrence River at 0.5–1 m depth. *Gammarus fasciatus* was collected at similar depths in Oneida Lake to those in western Lake Erie (up to 3.6 m; Van Overdijk et al. 2003). The reported preference by *G. fasciatus* for macrophytes rather than *Dreissena* (Gonzalez and Burkart 2004) was not evident in Oneida Lake, where more *G. fasciatus* was collected on substrates colonized by *Dreissena* than on substrates with only SVP (macrophytes), although the difference was not significant.

Hyaella azteca was more abundant over sand substrate than cobble substrate at all transects, and was 5 times more abundant at Oneida Bay Marina than at other transects, similar to the results of Baker (1918). The association of *H. azteca* with low-energy transects was not as apparent as was found for *G. fasciatus*, and, although mean density was generally greater at low-energy transects (with higher conductivity) than at high-energy transects (with intermediate conductivity), we did not find a significant correlation with conductivity. We collected *H. azteca* at all depths to >3.8 m, as did Baker (1918), in contrast to Limen et al. (2005), who collected *H. azteca* only in water less than 1 m deep in western Lake Erie.

In Oneida Lake, *E. ischnus* was most abundant in shallow water (0.6 m or less) at two transects, Constantia and Jewell, which had higher wave energy,

cobble substrate colonized by *Dreissena*, and an intermediate level of conductivity. Our results were similar to the results of Dermott et al (1998; <1 m depth), Kang et al. (2007), and Palmer and Ricciardi (2004), who reported greater *E. ischnus* abundance in habitats of greater wave energy or current velocity, and Gonzalez and Burkart (2004), who reported that *E. ischnus* was more abundant in *Dreissena* colonies than in macrophytes. However, our findings were contrary to that of Kestrup and Ricciardi (2010) from the upper St. Lawrence River, where *E. ischnus* was rare at intermediate levels of conductivity. Habitats occupied by *H. azteca* were not considered by Kang et al. (2007) to be suitable for *E. ischnus* because the species shared fewer habitat requirements, and our results would support this to the extent that *H. azteca* was more abundant on sand than cobble substrate, and that *E. ischnus* was associated more with shallow water, whereas *H. azteca* showed no significant difference in abundance by depth.

The lowering of the water level in winter in Oneida Lake would reduce *Dreissena* density at depths of less than 1 m (*Dreissena* density was greater at 1.8 and 3 m), and would prevent *E. ischnus* from utilizing the preferred cobble substrate that predominates at <0.6 m during normal lake-elevation periods. This artificial limitation of cobble-and-*Dreissena* habitat available to *E. ischnus* in Oneida Lake could reduce the relative survival of *E. ischnus* in comparison to *G. fasciatus* and *H. azteca*, which can utilize the deeper areas of the lake as well as shallow water.

Two environmental factors, calcium and dissolved oxygen saturation, were not limiting to amphipods in Oneida Lake. Calcium values ranged from 18–74 mg/l (mean = 38 ± 0.6) from 1967 to 2011, which are greater than the level implicated in reducing post-molting survival in *Gammarus pseudolimnaeus* Bousfield (<0.2 mg/l; Zehmer et al. 2002). Adverse effects of low oxygen saturation were determined to be 14% for *H. azteca* and 3.6% for *Gammarus lacustris* G.O. Sars (Nebeker et al. 1992); these percentages are much lower than those observed in Oneida Lake. Amphipods also have the option of moving to more favorable areas of the lake.

Mean density of *G. fasciatus* was much lower in Oneida Lake than in Lake Ontario and the Niagara and St. Lawrence rivers (2.1/cm²; Dermott et al. 1998) or Lake Erie (0.4/cm²; Van Overdijk et al. 2003), and less on SVP in Oneida Lake than in Lake Erie (0.5/cm²; Gonzalez and Burkart 2004). Density of *G. fasciatus* was similar between Oneida Lake and Lake Erie *Dreissena* beds. Mean density of *H. azteca* in Oneida Lake was greater than in Lake Erie (0.002/cm²; van Overdijk et al. 2003) but less than that from the Niagara River to the St. Lawrence River (1.8/cm²; Dermott et al. 1998). The mean density of *E. ischnus* in Oneida Lake was much less than the range reported (0.01–1.09/cm²) in Dermott et al. (1998), Gonzalez and Burkart (2004), and van Overdijk et al. (2003).

Dermott et al. (1998) suggested that *E. ischnus* had displaced *G. fasciatus* on shallow rocky substrates colonized by *Dreissena* within 1 year, based on an

inverse relationship in density of the two species. Van Overdijk et al. (2003) also reported an inverse relationship in field surveys where the measured density of *E. ischnus* was $>0.7/\text{cm}^2$, and concluded that this could be a density-dependent threshold. In Oneida Lake, density of *E. ischnus* was always at least one order of magnitude less than the density-dependent threshold, and there was no evidence that *E. ischnus* had replaced *G. fasciatus*, despite having been present for at least five years at the end of our study. Kang et al (2007) did not find evidence that *E. ischnus* was replacing *G. fasciatus* in the Great Lakes nor did Palmer and Ricciardi (2004) in the St. Lawrence River, rather that habitat heterogeneity was promoting coexistence by allowing the amphipod species to utilize different physicochemical gradients.

Fish predation on amphipods has been suggested as a controlling factor of the amphipod assemblage. *Gammarus fasciatus* might be less vulnerable to predation as it is less active on a complex benthic surface than is *E. ischnus* (Palmer and Ricciardi 2005), but activity of *G. fasciatus* increases as habitat complexity decreases (Mayer et al. 2001); thus, *G. fasciatus* might be more susceptible on bare sand substrates. Density of *G. fasciatus* was lower on bare sand substrate in Oneida Lake but not significantly less than on a sand substrate with SVP. The presence of SVP would afford some refuge from predators for *G. fasciatus*, but perhaps not for *E. ischnus* because their red coloration would make them more visible to Yellow Perch (Gonzalez and Burkart 2004). Although *E. ischnus* was more active on *Dreissena* than *G. fasciatus*, a laboratory study showed that Yellow Perch consumed more *G. fasciatus* than *E. ischnus* on a *Dreissena* substrate, and more *E. ischnus* than *G. fasciatus* on macrophytes (Gonzalez and Burkart 2004).

Historical amphipod abundance

Hyalella azteca was the most abundant amphipod in the Lower South Bay area of Oneida Lake in 1916 (Baker 1918), comprising 96% of the amphipods collected; *G. fasciatus* was second in abundance at 3.5%. Lower South Bay (LSB) was represented by the Short Point and Oneida Bay Marina transects in the present study. *Gammarus fasciatus* accounted for 77.4% of amphipods collected and *H. azteca* accounted for 13.3%, a reversal from that seen in Baker (1918). Mean density of *H. azteca* at LSB has declined, while mean density of *G. fasciatus* has increased (Table 4). The shift to greater abundance of *G. fasciatus* (as well as total amphipod abundance) was apparent in LSB in 1967 (Clady 1975) and was attributed to increased organic matter inputs to the lake from extensive

Table 4. Mean density (individuals/cm²) of *Hyalella azteca* and *Gammarus fasciatus* and percent change at two sites in Oneida Lake. Data for 1916 is from Baker (1918).

Species	Oneida Bay Marina			Short Point		
	1916	2005–2006	% change	1916	2005–2006	% change
<i>Hyalella azteca</i>	0.12	0.06	-50	0.08	0.01	-87.5
<i>Gammarus fasciatus</i>	0.002	0.07	+3500	0.02	0.21	+1050

agriculture and home construction. Mayer et al. (2002) replicated the methods of Baker (1918) and reported amphipod abundance similar to that in Clady (1975). Our use of a 0.5-mm screen may have reduced the number of smaller juveniles in our samples (Cooper 1965), and the resulting amphipod density, but our results show the same relative abundance of *G. fasciatus* as was reported by Clady (1975). The reason for the amphipod density increase was suggested by Mayer et al. (2002) to be due to a precipitous decline in total phosphorus (TP) from 1961 to 1976: the decline in TP resulted in increased water clarity and depth of light penetration that increased benthic algae and amphipod abundance. The introduction of *Dreissena* into Oneida Lake has increased habitat complexity but has not altered amphipod density as much as light penetration has (Mayer et al. 2002), in contrast to the increase in *G. fasciatus* following the introduction of *Dreissena* in the North American Great Lakes and the St. Lawrence River (Palmer and Ricciardi 2005), and the increase in *D. villosus* in Europe (Gergs and Rothhaupt 2008). Habitat complexity might have been increased to a greater extent in the latter two areas compared to Oneida Lake.

Baker (1918) reported four species of amphipods in Oneida Lake: *Gammarus fasciatus*, *G. limnaeus*, *Eucrangonyx gracilis* (= *Crangonyx gracilis*), and *Hyalella knickerbockeri* (= *Hyalella azteca*). The identification of the amphipods in Baker is confounded by the possible representation of an undescribed species (related to *E. shoemakeri* = *Crangonyx shoemakeri* Hubricht and Mackin) (Shoemaker Crangonyctid) in the description of *E. gracilis*, and the identification of *G. fasciatus*, as described by Weckel (1907), having been based, in part, on specimens of *G. limnaeus* (Hubricht and Mackin 1940). *Gammarus fasciatus* has been confused with several amphipod species in earlier studies (Holsinger 1976), and has created uncertainty as to whether its native distribution would include Oneida Lake. Furthermore, Smith (1933) reported that *G. fasciatus* was present in Cayuga Lake (NY) as well as in several locations in western New York, and noted that stocking of amphipods (including *G. fasciatus* and *G. limnaeus*) was a common practice in New York in the early 1900s. Chace et al. (1959) suggested that *G. fasciatus* may represent an introduced species in the North American Great Lakes but did not elaborate on the evidence. The native distribution of *G. fasciatus* cannot be determined from the historical records due to this uncertainty of identification, but we are assuming that *G. fasciatus* was native to Oneida Lake until contrary evidence is forthcoming.

Oneida Lake is highly productive with a diverse habitat that favors the native amphipods *G. fasciatus* and *H. azteca*, which can utilize all areas of the lake. The distribution of *E. ischnus* was limited to shallow high-energy sites with intermediate conductivity that were colonized by *Dreissena*. This combination of habitat characteristics might limit the success of *E. ischnus* since its abundance is greatest at high conductivity, which was found only at lower-energy sites in Oneida Lake. We did not find any evidence that *E. ischnus* will replace *G. fasciatus* or *H. azteca*.

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Literature Cited

- Bailey, R.J.E., J.T.A. Dick, R.W. Elwood, and C. MacNeil. 2006. Predatory interactions between the invasive amphipod *Gammarus tigrinus* and the native opossum shrimp *Mysis relicta*. *Journal of the North American Benthological Society* 25:393–405.
- Baker, F.C. 1918. The productivity of invertebrate fish food on the bottom of Oneida Lake, with special reference to mollusks. *New York State College of Forestry Technical Bulletin* 9:1–264.
- Beatty, L.D., and F.F. Hooper. 1958. Benthic associations of Sugarloaf Lake. *Michigan Academy of Science, Arts, and Letters* 43:89–106.
- Beckett, D.C., and M.C. Miller. 1982. Macroinvertebrate colonization of multiplate samplers in the Ohio River: The effect of dams. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1622–1627.
- Bousfield, E.L. 1958. Freshwater amphipod crustaceans of glaciated North America. *Canadian Field-Naturalist* 72:55–113.
- Chace, F.A., Jr., J.G. Mackin, L. Hubricht, A.H. Banner, and H.H. Hobbs, Jr. 1959. Malacostraca. Pp. 869–901, *In* W.T. Edmonson (Ed.). *Freshwater Biology*, 2nd Edition. John Wiley and Sons, New York, NY.
- Clady, M. 1975. Comparison of the bottom fauna in 1916 and 1967 in a bay of Oneida Lake, New York. *New York Fish and Game Journal* 22:114–121.
- Clemens, H.P. 1950. Life cycle and ecology of *Gammarus fasciatus* Say. Stone Institute of Hydrobiology Contribution No. 12, Ohio State University, Put-in-Bay, OH.
- Cooper, W.E. 1965. Dynamics and production of a natural population of a fresh-water amphipod, *Hyaella azteca*. *Ecological Monographs* 35:377–394.
- Dermott, R., J. Witt, Y.M. Um, and M. Gonzalez. 1998. Distribution of the Ponto-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus*. *Journal of Great Lakes Research* 24:442–452.
- Dick, J.T.A., and D. Platvoet. 1996. Intraguild predation and species exclusions in amphipods: The interaction of behavior, physiology, and environment. *Freshwater Biology* 36:375–383.
- Dick, J.T.A., and D. Platvoet. 2000. Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society London B* 267:977–983.
- Dionne, K., R. Vergilino, F. Dufresne, F. Charles, and C. Nozais. 2011. No evidence for temporal variation in a cryptic species community of freshwater amphipods of the *Hyaella azteca* species complex. *Diversity* 3:390–404.
- Edwards, T.D., and B.C. Cowell. 1992. Population dynamics and secondary production of *Hyaella azteca* (Amphipoda) in *Typha* stands of a subtropical Florida lake. *Journal North American Benthological Society* 11:69–79.

- Forney, J.L. 1974. Interactions between Yellow Perch abundance, Walleye production, and survival of alternate prey in Oneida Lake, New York. *Transactions of the American Fisheries Society* 103:15–24.
- Gergs, R., and K-O. Rothhaupt. 2008. Effects of Zebra Mussels on a native amphipod and the invasive *Dikerogammarus villosus*: The influence of biodeposition and structural complexity. *Journal of the North American Benthological Society* 27:541–548.
- Gonzalez, M., and G.A. Burkart. 2004. Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species *Gammarus fasciatus* and *Echinogammarus ischnus*. *Journal of Great Lakes Research* 30:100–113.
- Hargrave, B.T. 1970. Distribution, growth, and seasonal abundance of *Hyalella azteca* (Amphipoda) in relation to sediment microflora. *Journal of the Fisheries Research Board of Canada* 27:685–699.
- Haynes, J.M., N.A. Tisch, C.M. Mayer, and R.S. Rhyne. 2005. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena* and *Echinogammarus*: 1983 to 2000. *Journal of the North American Benthological Society* 24:148–167.
- Holeck, K.T., E.L. Mills, H.J. MacIsaac, M.R. Dochoda, R.I. Colautti, and A. Ricciardi. 2004. Bridging troubled waters: Biological invasions, transoceanic shipping, and the Laurentian Great Lakes. *BioScience* 54:919–929.
- Holsinger, J.R. 1976. The freshwater amphipod crustaceans (Gammaridae) of North America. US Environmental Protection Agency, Water Pollution Control Research Series 18050 ELDO4/72. Washington, DC.
- Hubricht, L., and J.G. Mackin. 1940. Descriptions of nine new species of freshwater amphipod crustaceans with notes and new localities for other species. *American Midland Naturalist* 23:187–218.
- Kang, M., J.J.H. Ciborowski, and L.B. Johnson. 2007. The influence of anthropogenic disturbance and environmental suitability on the distribution of the nonindigenous amphipod, *Echinogammarus ischnus*, at Laurentian Great Lakes coastal margins. *Journal of Great Lakes Research* 33 (Special Issue 3):198–210.
- Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the Yellow Perch (*Perca flavescens*). *Environmental Biology of Fish* 2:53–70.
- Kestrup, A.M., and A. Ricciardi. 2009. Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. *Biological Invasions* 11:2095–2105.
- Kestrup, A.M., and A. Ricciardi. 2010. Influence of conductivity on life-history traits of exotic and native amphipods in the St. Lawrence River. *Fundamental and Applied Limnology* 176:249–262.
- Kestrup, A.M., J.T.A. Dick, and A. Ricciardi. 2011. Interactions between invasive and native crustaceans: Differential functional responses of intraguild predators towards juvenile hetero-specifics. *Biological Invasions* 13:731–737.
- Kohn, J., and A. Waterstraat. 1990. The amphipod fauna of Lake Kummerow (Mecklenburg, German Democratic Republic) with reference to *Echinogammarus ischnus* Stebbing, 1899. *Crustaceana* 58:74–82.
- Krisp, H., and G. Maier, 2005. Consumption of macroinvertebrates by invasive and native gammarids: A comparison. *Journal of Limnology* 64:55–59.
- Limburg, K.E., and D.I. Siegel. 2006. The hydrogeochemistry of connected waterways: The potential of linking geology to fish migrations. *Northeastern Geology and Environmental Sciences* 28:254–265.

- Limen, H., C.D.A. van Overdijk, and H.J. MacIsaac. 2005. Food partitioning between the amphipod *Echinogammarus ischnus*, *Gammarus fasciatus*, and *Hyaella azteca* as revealed by stable isotopes. *Journal of Great Lakes Research* 31:97–104.
- Mayer, C.M., L.G. Rudstam, E.L. Mills, S.G. Cardiff, and C.A. Bloom. 2001. Zebra Mussels (*Dreissena polymorpha*), habitat alteration, and Yellow Perch (*Perca flavescens*) foraging: System-wide effects and behavioural mechanisms. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2459–2467.
- Mayer, C.M., R.A. Keats, L.G. Rudstam, and E.L. Mills. 2002. Scale-dependent effects of Zebra Mussels on benthic invertebrates in a large eutrophic lake. *Journal of the North American Benthological Association* 21:616–633.
- Mills, E.L., J.H. Leach, J.T. Carlton, and C.L. Secor. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19:1–54.
- Nalepa, T.F., D.W. Schloesser, S.A. Pothoven, D.W. Hondrop, D.L. Fanslow, M.L. Tuchman, and G.W. Fleischer. 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. *Journal of Great Lakes Research* 27:384–391.
- Nebeker, A.V., S.E. Dominguez, G.A. Chapman, S.T. Onjukka, and D.G. Stevens. 1992. Effects of low dissolved oxygen on survival, growth, and reproduction of *Daphnia*, *Hyaella*, and *Gammarus*. *Environmental Toxicology and Chemistry* 11:373–379.
- Palmer, M.E., and A. Ricciardi. 2004. Physical factors affecting the relative abundance of native and invasive amphipods in the St. Lawrence River. *Canadian Journal of Zoology* 82:1886–1893.
- Palmer, M.E., and A. Ricciardi. 2005. Community interactions affecting the relative abundances of native and invasive amphipods in the St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1111–1118.
- Pimentel, D. 2005. Aquatic nuisance species in the New York State Canal and Hudson River systems and the Great Lakes Basin: An economic and environmental assessment. *Environmental Management* 35:692–702.
- Pothoven, S.A., T.F. Nalepa, and S.B. Brandt, 2000. Age-0 and age-1 Yellow Perch diet in southeastern Lake Michigan. *Journal of Great Lakes Research* 26:235–239.
- Ricciardi, A., F.G. Whoriskey, and J.B. Rasmussen. 1997. The role of the Zebra Mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2596–2608.
- SAS. 2001. SAS/STAT User's guide, Version 8.2. SAS Institute Inc., Cary, NC.
- Smith, O.R. 1933. The Caledonia shrimp *Dikerogammarus*. *Transactions of the American Fisheries Society* 63:120–128.
- van Overdijk, C.D.A., I.A. Grigorovich, T. Mabee, W.J. Ray, J.J.H. Ciborowski, and H.I. MacIsaac. 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.
- VanDeValk, A.J., J.L. Forney, J.R. Jackson, L.G. Rudstam, T.E. Brooking, and S.D. Krueger. 2005. Angler catch rates and catchability of Walleyes in Oneida Lake, New York. *North American Journal of Fisheries Management* 25:1441–1447.
- Weckel, A.L. 1907. The freshwater amphipoda of North America. *Proceedings of the US National Museum* 32:25–58.

- Witt, J.D.S., P.D.N. Hebert, and W.B. Morton. 1997. *Echinogammarus ischnus*: Another crustacean invader in the Laurentian Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences* 54:264–268.
- Wood, K.G. 1952. The bottom fauna of Louisa and Redrock Lakes, Algonquin Park, Ontario. *Transactions of the American Fisheries Society* 82:203–212.
- Zehmer, J.K., S.A. Mahon, and G.M. Capelli. 2002. Calcium as a limiting factor in the distribution of the amphipod *Gammarus pseudolimnaeus*. *American Midland Naturalist* 148:350–362.
- Zhang, J., and J.R. Holsinger. 2003. Systematics of the freshwater amphipod genus *Crangonyx* (Crangonyctidae) in North America. *Virginia Museum of Natural History Memoir* 6, Martinsville, VA.