CHAPTER 39

Interactions between Exotic Ecosystem Engineers (*Dreissena* spp.) and Native Burrowing Mayflies (*Hexagenia* spp.) in Soft Sediments of Western Lake Erie

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CONTENTS

ABSTRACT

Exotic ecosystem engineers (i.e., *Dreissena polymorpha* and *D. rostriformis bugensis*) have changed soft-bottom habitats of lakes in many ways. The most noticeable change is the presence of hard clusters of mussels found between expanses of otherwise soft sediments. We hypothesized that this shift in available habitat type is likely to affect the distribution of infaunal invertebrates, such as burrowing mayflies (*Hexagenia* spp.). We examined effects of dreissenid clusters on *Hexagenia* presence through analyses of field-measured distributions of mussels and *Hexagenia* throughout western Lake Erie and in laboratory experiments (viewing chamber observation and habitat-selection experiments). In western Lake Erie, distribution analyses indicated that *Dreissena* did not inhibit *Hexagenia* presence and *Hexagenia* were more likely to be present where *Dreissena* were also present. However, there was no spatial cross-correlation between densities of the two species. At sites with no *Dreissena, Hexagenia* could achieve very high densities that were unattained at sites with *Dreissena*. In habitat-selection experiments with three habitat types: (1) live *Dreissena* clusters; (2) dead *Dreissena* clusters; and (3) bare sediments, *Hexagenia* strongly selected to colonize below clusters of live dreissenids. In observation experiments, *Hexagenia* also selected to colonize below live *Dreissena* that covered sediments, but this selection was not stronger in the presence of a predator (yellow perch, *Perca flavescens*). Our findings showed that at a small spatial scale in laboratory experiments, *Hexagenia* prefer *Dreissena*-covered sediment, but at a large spatial scale in western Lake Erie, *Hexagenia* do not select for or avoid *Dreissena*. Our results suggested that at a basin-wide scale, *Dreissena* presence does not inhibit *Hexagenia* colonization, but *Dreissena* are not strong determinants of *Hexagenia* distribution and abundance in western Lake Erie.

INTRODUCTION

Zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. rostriformis bugensis*) have changed the Great Lakes ecosystem in many ways as a result of their effects as ecosystem engineers (Karatayev et al. 2002, Zhu et al. 2006). Ecosystem engineers are organisms that alter physical, chemical, and biotic components of the ecosystem, leading to wide-scale changes that are both direct and indirect (Jones et al. 1994, 1997). Zebra mussels, first discovered in the Great Lakes in 1986 (Carlton 2008), colonize primarily hard substrates. Benthic invertebrates associated with these hard substrates increased as a result of two changes: zebra mussels imported food to the bottom through filter-feeding material from pelagic waters and also increased structural complexity (e.g., Botts et al. 1996, Stewart et al. 1998, González and Downing 1999). The latter change can lead to decreased fish predation on invertebrates within mussel colonies (González and Downing 1999, Mayer et al. 2001, Beekey et al. 2004a).

Quagga mussels were first recorded in the Great Lakes in 1989 (Mills et al. 1993) and, while initially found in deeper, cooler waters, have now replaced some zebra mussel colonies (Mills et al. 1999) and have become the dominant dreissenid species in most areas of the Great Lakes (Stoeckmann 2003). Quagga mussels are capable of inhabiting soft substrates where their colonies fundamentally shift habitat structure because they cover sediments and create a hard, structurally complex substrate. The addition of this structure will likely influence the infaunal (sediment-dwelling) benthic invertebrate community (Dermott and Kerec 1997, Bially and MacIsaac 2000, Freeman et al. 2011). The effects of quagga mussels on native benthic invertebrates are likely to differ from those of zebra mussels because quagga mussels are more likely to be found on soft sediment and will therefore interact more strongly with different guilds of native organisms. In this study, we focused on the effects of dreissenid clusters on *Hexagenia* spp. (*H. limbata* and *H. rigida*) in soft sediments, an infaunal mayfly species important to fish and ecosystem function.

Historically, *Hexagenia* were abundant in many warm, shallow bays and basins of the Great Lakes including western Lake Erie, but populations declined to near extirpation in the 1950s (e.g., Nebeker 1972, Winter et al. 1996, Gerlofsma and Ciborowski 1998). In the early-1990s, abundances began to increase in western Lake Erie and recolonization has now been well-documented (Krieger et al. 1996, Schloesser et al. 2000, Schloesser and Nalepa 2001). The resurgence of *Hexagenia* was temporally coincident with the expansion of dreissenid populations in this portion of the lake (Krieger et al. 1996). *Hexagenia* have been shown to prefer soft sediment colonized by *Dreissena* in small-scale laboratory experiments (DeVanna et al. 2011), similar to the way that epifaunal invertebrates respond to *Dreissena* colonies on hard substrate. However, *Hexagenia* have been shown to select for live *Dreissena* clusters over artificial ones, suggesting that increased substrate structure, and resulting protection from predation, is not the only reason *Hexagenia* select this habitat (DeVanna et al. 2011). Burrowing animals are already protected from predation and, therefore, may respond differently to the threat of predation than invertebrates living on the sediment surface. Although much is known about the effects of dreissenid clusters on epifaunal invertebrates, burrowing infaunal invertebrates like *Hexagenia* may respond very differently to dreissenid clusters due to their presence in the sediment.

Factors influencing spatial distributions of a species occur at multiple biotic and abiotic scales that may be important at one level, but are not always predictive at a different level (Turner et al. 1989, Wiens 1989, Graf et al. 2005). Different levels of scale can be viewed as a hierarchy, from large to small scales, with each level having its own natural cycles and processes structuring it (Senft et al. 1987, Urban et al. 1987). Levels in the hierarchy are not independent of one another, but rather higher-order scales can act to control processes at smaller scales, and smaller scales can drive processes at larger scales (Urban et al. 1987, Peterson 2000). Understanding processes regulating populations at both the local (small) and regional (large) scales has shown to be important due to the connections between hierarchical levels for predicting trout populations in Michigan Rivers (Zorn and Nuhfer 2007), vegetation patterns in North American boreal forests (Peterson 2000), and ecological land classification (Klijn and Udo de Haes 1994). Thus, spatial associations between *Dreissena* and *Hexagenia* may differ depending on what scale observations are made. We hypothesize that *Dreissena* will affect *Hexagenia* at a small spatial scale in a variety of ways including (1) modifying habitat by the addition of shells to soft sediment, (2) providing structural refuge from predation, (3) adding food resources by means of feces and pseudofeces, and (4) increasing flow of well-oxygenated pelagic water to areas close to clusters via filter feeding. Whereas at a larger scale, physical processes, such as sediment type, water currents, and oxygen availability, may be more important in structuring both *Dreissena* and *Hexagenia* distributions than species interactions. Quantifying the spatial relationship between these two taxa at multiple scales may help in understanding what mechanisms are structuring their distributions.

The goal of our study was to examine the spatial association between invasive *Dreissena* and native *Hexagenia* at differing hierarchical levels of scale, from large to small, in soft sediment habitats of western Lake Erie. Firstly, the relationship between *Hexagenia* and *Dreissena* was examined on a large scale by analyzing density relationships of the two taxa at 30 sites sampled over 10 years in the western basin of Lake Erie. Spatial analyses included spatial autocorrelation and cross-correlation across the basin. Secondly, two separate habitat preference experiments were conducted in the laboratory: (1) *observation experiments*, which examined the effect of a predator on the habitat preference of *Hexagenia* when given a choice of bare and *Dreissena*-covered sediments, and (2) *habitat-selection experiments*, which tested whether *Hexagenia* select for *Dreissena*-colonized habitat, artificial *Dreissena* clusters, or bare sediment.

METHODS

Analysis of Spatial Association

We assessed the large-scale spatial association of *Dreissena* and *Hexagenia* at over 30 sites across the western basin of Lake Erie, 1999–2009 (Figure 39.1). Thirty-one sites were sampled in 2000–2002 and 2004–2007, 24 in 1999, 60 in 2003, 19 in 2008, and 14 sites in 2009 for a total of 334 measurements for each taxon. Both taxa were sampled simultaneously with a standard Ponar grab (0.048 m^2 opening; three replicate samples per site). Collection and enumeration methods are in Schloesser et al. (1991).

Our spatial association analyses were designed to determine if there was a relationship between the co-occurrences and densities of *Hexagenia* and *Dreissena*. First, to test the null hypothesis that the presence of *Hexagenia* was independent of the presence of *Dreissena*, we conducted a chi-square test of independence. We also examined the probability of occurrence as determined from the proportion of sites with just *Dreissena*, with just *Hexagenia*, and with both taxa using Bayes' Theorem (McCarthy 2007). Second, we examined the correlation (r) between *Dreissena* and *Hexagenia* densities at each site for all available data, as well as the mean, standard deviation, and coefficient of variation of *Hexagenia* densities when *Dreissena* were present versus absent. We examined the standard deviation of *Hexagenia* densities to understand the dispersion of *Hexagenia* densities from the mean, whereas the coefficient of variation (standard deviation/mean) allowed us to examine the variability of the data relativized to the mean. Third, to examine spatial patterns of each taxon independently, we conducted spatial autocorrelations, as well as cross-correlations between taxa densities for all available data using Moran's correlation coefficient (I). Moran's I is an extension of Pearson's product moment correlation; however, because we assume points close to one another will be more similar, weights are given to each pair of points, with large values given to points close to one another and points further away having smaller weights (Reich et al. 1994, Kalkhan and Stohlgren 2000). When examining the spatial autocorrelation of a species and the cross-correlation between species, values of I range from −1 to +1 with values close to +1 indicate clustering, values close to −1 indicate dispersion, and values near zero suggest randomness

Figure 39.1 Location of 30 sites sampled to examine the distributions and densities of *Hexagenia* and *Dreissena* in the western basin of Lake Erie, 1999–2009.

(Reich et al. 1994, Kalkhan and Stohlgren 2000). The spatial autocorrelation of each taxa and the cross-correlation between taxa (Moran's I) was plotted for the range of distances between points, split into 10 equal distance classes (R, version 2.13.0), with correlations at a distance of zero representing the same site across years.

Laboratory Experiments

To examine small-scale associations between *Hexagenia* and *Dreissena*, both observation experiments and habitat-selection experiments (from DeVanna et al. 2011) were conducted. Sediments (sampled up to 6 cm depth) for the experiments were obtained with a grab sampler at a nearshore site (41.6885 W, 83.4250 N) in western Lake Erie. Sediments were washed through a 1.0 mm mesh sieve to remove both taxa. Sediment composition was silt with a soft texture. *Dreissena* and *Hexagenia* were collected from soft substrates at many sites in western Lake Erie to obtain enough individuals for experiments. Age 1 *Hexagenia* (>10 mm, but without black wing pads) were collected so individuals would be large enough for observation yet be at low risk for emergence during experiments. Both *H. limbata* and *H. rigida* were collected at their natural occurring proportions. Quagga mussels dominated *Dreissena* clusters collected; however, zebra mussels were present in small numbers.

Observation Experiments

Hexagenia behavior in observation experiments was monitored in small (25.4 cm × 1.90 cm × 25.4 cm) chambers that only allowed *Hexagenia* to choose between two habitat types, bare sediment and sediment that was covered by live *Dreissena* clusters (Figure 39.2). Also, *Hexagenia* in both habitats were either exposed (N = 5) or not exposed (n = 5) to a predator (yellow perch, *Perca flavescens*, a common generalist predator). Hence, we tested whether *Hexagenia* selected for habitat type or were distributed randomly and how this selection was affected by the presence of a predator. Prior to experimentation, *Hexagenia* were kept in the laboratory in the same soft sediment as used in the experiment and were able to feed *ad libitum* on organic matter from fresh Lake Erie sediments. Viewing chambers were constructed of acrylic sheets and filled with collected sediments. To establish habitat types (e.g., bare sediment and live *Dreissena*-covered sediment) in chambers, a thin metal sheet divided the chamber into two equal sections that was removed before addition of experimental organisms (e.g., predators and *Hexagenia*). Live *Dreissena* clusters in the chambers were equivalent to a density of 3400 *Dreissena*/m^2 that has been observed in western Lake Erie (Patterson et al. 2005). Organisms were added 24 h after experimental setup; thus, sediments were in place and settled. All treatments were aerated throughout the course of the experiment.

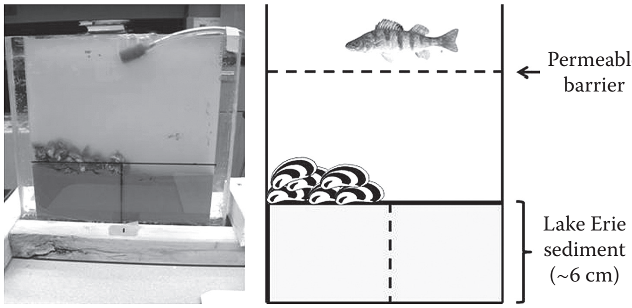

Figure 39.2 Observation chamber constructed of acrylic sheets and filled with sediments from Lake Erie; note two habitat types (bare sediment and live *Dreissena* clusters). In some chambers, fish were added to determine role of the potential predators on *Hexagenia* habitat preferences.

In treatments with fish present, we added a single, age 1 yellow perch 1 h prior to addition of *Hexagenia* nymphs. All chambers, regardless of fish treatment, had a plastic, permeable barrier hung 10 cm from the top of the chamber to allow the fish an area to swim but kept fish 15.4 cm from the sediment and prevented consumption of *Hexagenia*. The barrier did have holes to allow movement of *Hexagenia* through the entire water column. Yellow perch were not allowed to function as predators due to the size of the chambers. After fish acclimated for about an hour, six *Hexagenia* (equivalent density of 1400/m^2; Krieger 1999) were released in the center of the chamber and watched to determine initial habitat selection by nymphs. Initial habitat selection was determined to be the first habitat in which a mayfly began to actively burrow. Observation trials were started one at a time in each of five chambers, and for each chamber, observations lasted 15 min to give *Hexagenia* enough time to choose a habitat and burrow.

Habitat-Selection Experiments

We tested to determine if *Hexagenia* selected for habitats with or without *Dreissena* clusters on soft sediments. We used experimental tanks (circular plastic tubs; 41 cm diameter and 43 cm height) filled with collected sediment and dechlorinated tap water aerated throughout the experiment and separated into three equal "pie-slice"–shaped sections (0.046/m^2) with metal dividers. Three treatment types were then created: (1) bare sediment, (2) live *Dreissena* clusters, and (3) dead *Dreissena* clusters. Live and dead *Dreissena* treatments contained approximately 250 individuals representing a density of 5434/m^2, which has recently been observed in western Lake Erie (Patterson et al. 2005). Dead *Dreissena* clusters were created from empty shells attached together with nontoxic glue. Clusters were glued to 1 g lead weights so they were stable on sediments. Weights were also added to the other two treatments for sake of consistency. Metal dividers were removed after habitat types were established.

Experiments were conducted using five densities of *Hexagenia* that were within the range of densities found in western Lake Erie (0–2000/m^2; Krieger 1999). The number of added individuals and achieved densities per experimental tank were 5 individuals (~100/m^2), 9 (~200/m^2), 18 (~400/m^2), 36 (~800/m^2), and 54 (~1200/m^2). Each *Hexagenia* density was replicated three times (total N = 15). *Hexagenia* were added to the center of tank at the surface of the water and allowed to select between habitat types. One replicate of each density was run at the same time, and tanks were placed in a straight line in random order. After 48 h, metal dividers were pushed into sediments between habitat types, water was removed, sediments from each habitat were removed and sieved through 250 µm mesh, and *Hexagenia* were counted.

To analyze results of both experiments, the percentage of *Hexagenia* in each habitat type was arcsine square root transformed to help achieve a normal distribution (Zar 1999). Data were analyzed using a split-plot analysis of variance (ANOVA) model (SAS 9.1, $\alpha = 0.05$), because each experimental unit was split into different habitat types and treatments were applied to different scales (Potvin 2001). In the observation experiment, predators were applied to the whole chamber (main plot factor) but habitat type was applied to only half of the chamber (subplot factor). For the habitat-selection experiment, *Hexagenia* density was applied to the whole mesocosm (main plot factor), whereas each habitat type was applied to only one-third of the experimental unit (subplot factor). When appropriate, split-plot ANOVAs were followed by a Tukey multiple comparison test.

RESULTS

Analysis of Spatial Association

At the basin-wide scale, the presence of *Hexagenia* was related to *Dreissena* presence (chi-square, $\chi^2 = 7.51$, $p = 0.006$; Table 39.1, Figure 39.3). Of the 334 observations (sites and years), 65% had both *Hexagenia* and *Dreissena* present, 23% had only *Hexagenia*, 6% had only *Dreissena*, and 6% had neither taxa present. The percentage of sites with neither taxa present was very low, and this could be due to the sites being chosen specifically to monitor *Hexagenia* populations. Overall, using Bayes' Theorem (McCarthy 2007), the probability of finding only *Hexagenia* at any site was 0.88, *Hexagenia* at a site with *Dreissena* was 0.91, and the probability of *Hexagenia* at a site without *Dreissena* was 0.80. Although the presence of *Hexagenia* was most likely at sites where *Dreissena* were present, densities were slightly lower than densities at sites where *Dreissena* was absent. *Hexagenia* at sites without *Dreissena* (n = 97) achieved very high densities (>1500/m^2); the mean density of nymphs was 384/m^2 with a high variability (SD = 483.8). However, at sites where *Dreissena* were present (n = 237), the mean density of *Hexagenia* was 270/m^2, and variability was lower (SD = 341.2) than without *Dreissena* (Figure 39.3), and very high densities of *Hexagenia* (>1000/m^2) were unattained. However, once variability was normalized to the mean of the data, no difference existed in the dispersion for sites with and without *Dreissena* (coefficient of variation = 1.26 for both groups). Even though the mean density of *Hexagenia* was lower when *Dreissena* was present, it is within the range rated "excellent" in the Lake Erie Index of Biotic Integrity (Ohio Lake Erie Commission 2004). There was no significant linear correlation between densities of *Hexagenia* and *Dreissena* in western Lake Erie ($p = 0.9381$, $r = -0.0043$, Figure 39.3). There was no spatial autocorrelation for either *Hexagenia* or *Dreissena* (Figure 39.4a and b) and no spatial cross-correlation between the two taxa (Figure 39.4c), which means that there was no relationship between the two taxa at distances across the western basin. For *Dreissena* alone, across all distances, the greatest correlation (Moran's I) was 0.06, which is relatively low and suggests no relationship to distance (Figure 41.4a). *Hexagenia* showed a slight correlation at a distance of zero (same site across all years, I = 0.30), but from site to site, no spatial autocorrelation was found (Figure 39.4b).

Table 39.1 Chi-Square Contingency Table Showing Number of Sites (n = 334) in Western Lake Erie Collected between 1999 and 2009 with Both *Hexagenia* and *Dreissena* Present and/or Absent

		Hexagenia		
		Present	**Absent**	**Total**
Dreissena	Present	216	21	237
	Absent	78	19	97
	Total	294	40	334

Laboratory Experiments

Hexagenia selected live *Dreissena* clusters over bare sediment in both types of laboratory experiments (Figures 39.5 and 39.6). In observation experiments, *Hexagenia* selected *Dreissena* clusters over bare sediment (split-plot ANOVA: $F_{1,18} = 11.44$, $p = 0.0017$, Figure 39.5). However, there was no significant effect for the presence of a predator (split-plot ANOVA: $F_{1,18} = 0.84$, $p = 0.4408$), which indicates *Hexagenia* did not select clusters more often when a predator was present. In habitat-selection experiments, the percentage of *Hexagenia* differed among all habitats (split-plot ANOVA: $F_{2,20} = 95.17$, $p < 0.0001$, Tukey: $p < 0.05$, Figure 39.6). The highest percentage of *Hexagenia* was found in the presence of live *Dreissena* clusters, followed by dead *Dreissena* clusters, and lastly by bare sediment. There was a significant interaction between percentages of *Hexagenia* in each habitat based on *Hexagenia* density (split-plot ANOVA: *habitat*density*: $F_{8,20} = 4.86$, $p < 0.0001$), which indicated the percentage of *Hexagenia* that select each habitat type changed with *Hexagenia* density.

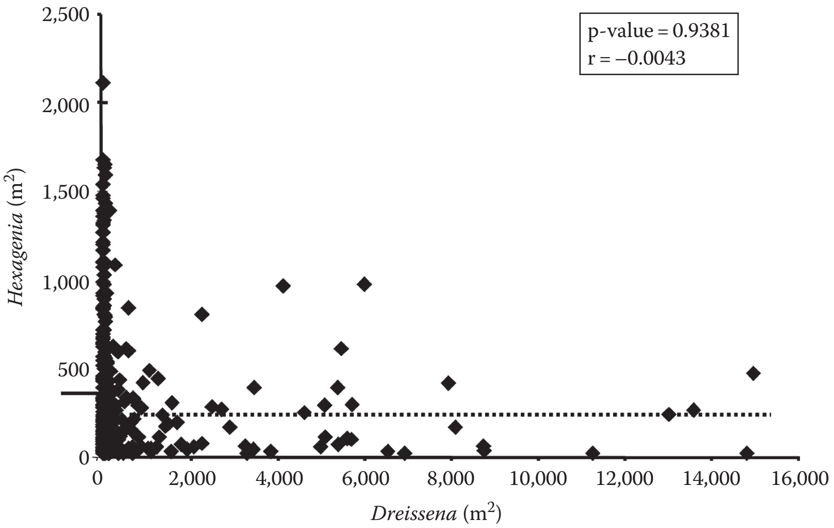

Figure 39.3 Scatter plot of *Hexagenia* and *Dreissena* densities at 30 sites in western Lake Erie 1999–2009. Each point (n = 334) represents the density of *Hexagenia* and *Dreissena* at a site each year. Solid line to the left of the y-axis equals the mean density of *Hexagenia* when *Dreissena* are absent (384/m²) and dotted line equals the mean density when *Dreissena* are present (270/m²).

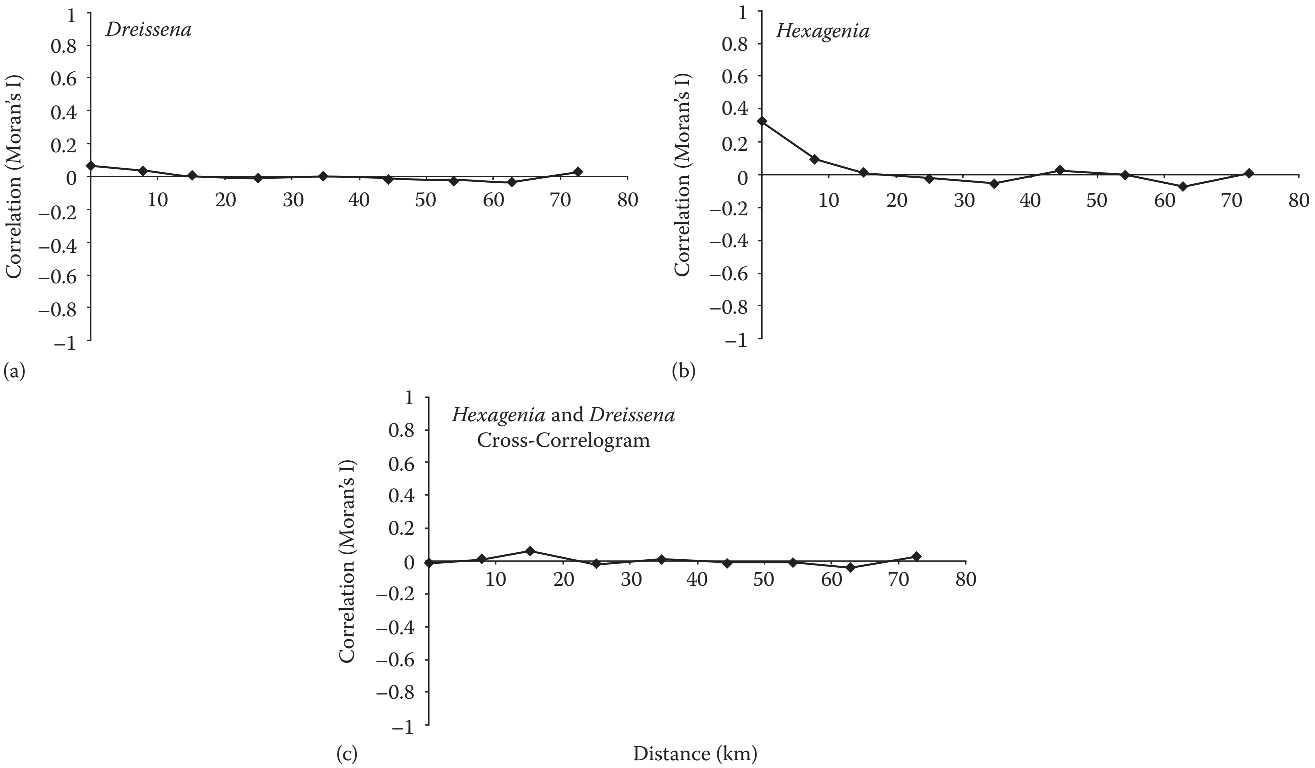

Figure 39.4 Spatial autocorrelation (Moran's I) of (a) *Dreissena*, (b) *Hexagenia*, and (c) cross-correlation between *Hexagenia* and *Dreissena* for 10 distance classes of all sampled sites in western Lake Erie 1999–2009. Correlations at a distance of zero represent the same sampled site across years. Moran's I values range from −1 to +1 where values close to +1 indicated clustering, −1 dispersion, and values near zero indicated randomness.

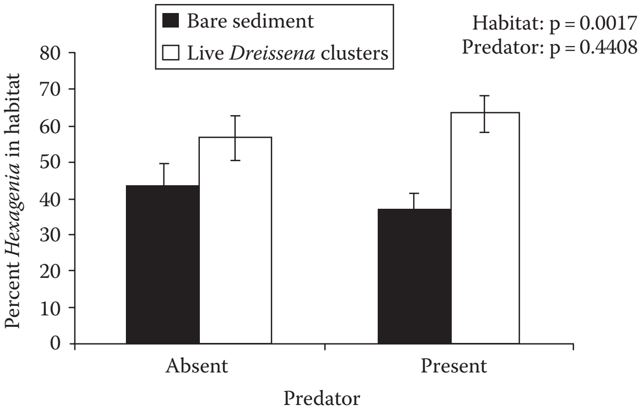

Figure 39.5 Mean percent of total number of *Hexagenia* found in two habitat types (bare sediment and live mussel clusters) in the presence and absence of a fish predator (yellow perch). Bars represent ±1 standard error. Statistics were conducted on arcsine square root transformed values.

DISCUSSION

Analysis of Spatial Association

Our results agree with those of other studies that show *Dreissena* can have great impacts on benthic invertebrates on a small-scale level (e.g., Mayer et al. 2001, Beekey et al. 2004b, Ward and Ricciardi 2007). However, at a large lake scale, many other processes can affect distributions of benthic invertebrates besides presence or absence of *Dreissena*. For our study organism, *Hexagenia*, the distribution and abundance of each life stage may be affected by different factors. For example, eggs of *Hexagenia* are deposited at the surface of the water (Hunt 1951) and so their distribution in the water column is likely to be influenced by large-scale physical processes, such as wind and currents. Once eggs settle out of the water, substrate types and oxygen levels (Gerlofsma and Ciborowski 1999) undoubtedly affect survival. Our laboratory-based, small-scale experiments only examined *Hexagenia* after they hatched, and thus, they were able to move and exhibit habitat selection, which is probably the period of time when small-scale, ecosystem engineer effects of *Dreissena* are important. On the other hand, our large-scale spatial analyses of basin-wide distributions of *Hexagenia* and *Dreissena* incorporated outcomes of many biological and physical processes that can affect different life stages of *Hexagenia*.

Hexagenia and *Dreissena* were found to co-occur at the majority of sites sampled in the western basin of Lake Erie, which suggested *Dreissena* do not inhibit *Hexagenia*. Not only did *Hexagenia* co-occur with *Dreissena*, they were more likely to occur with *Dreissena* than occur without *Dreissena*. Our finding suggests that *Hexagenia*, even at a large scale, are positively associated with the presence of *Dreissena*, which may be due to *Hexagenia* selection for sediment covered with live *Dreissena* clusters as shown in the small-scale experiments. However, associations between *Dreissena* clusters and *Hexagenia* under natural lake conditions are more complex and difficult to interpret than in simple laboratory experiments because we do not know how far individual *Hexagenia* will actively move to select for a habitat type. Physical processes, such as currents, may move planktonic *Dreissena* veligers and *Hexagenia* eggs to similar locations. It is likely that a combination of behavioral selection on a small-scale and physical processes on a large-scale determine the spatial relationship between these two benthic taxa.

Although *Hexagenia* presence was positively associated with *Dreissena*, densities of the two taxa were not correlated. At sites where *Dreissena* were absent, the mean density of *Hexagenia* was high, but a high proportion of these sites had no *Hexagenia*, while a few sites had very high densities (>1500/m^2). Alternatively, at sites where *Dreissena* were present, the mean density of *Hexagenia* was slightly lower. *Hexagenia* densities have previously been shown to be higher at field sites without than with *Dreissena* (Freeman et al. 2011). Therefore, while the presence of *Dreissena* may have a positive influence on *Hexagenia*, dreissenid-induced habitat alterations may serve to limit abundances. *Hexagenia* may not have

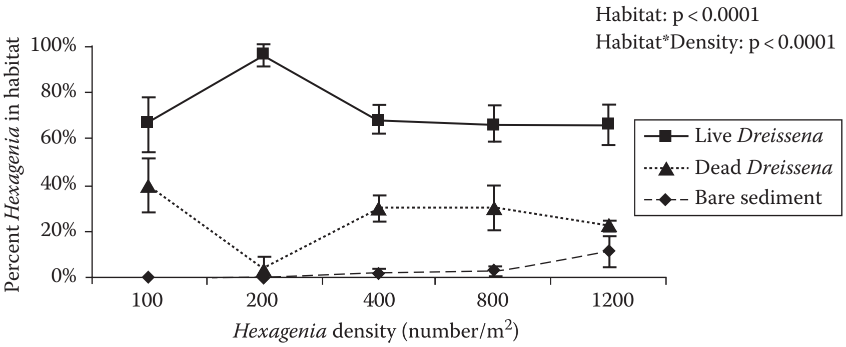

Figure 39.6 Mean percent of total number of *Hexagenia* found in three habitat types (bare sediment and live and dead mussel clusters) at five densities of *Hexagenia* nymphs in laboratory habitat–choice experiments. Bars represent ±1 standard error.

been able to reach high densities (maximum <1000/m^2) when *Dreissena* were present due to low oxygen beneath *Dreissena* (Burks et al. 2002, Beekey et al. 2004b). Also, unlike epifaunal invertebrates that show a positive, linear response to increased densities of *Dreissena* (Mayer et al. 2002), *Hexagenia* in our study did not show such a positive response. These different responses are likely related to differences in habitat preferences of the organisms. As dreissenid density increases, habitat complexity and available surface area for epifaunal invertebrates also increases (e.g., Botts et al. 1996, Stewart et al. 1998, González and Downing 1999); however, for sediment-dwelling invertebrates like *Hexagenia*, favored habitat surface area would not change as dreissenid density increased. *Hexagenia* was more likely to be found in areas with *Dreissena* and, although *Hexagenia* did not occur at densities >1000 nymphs/m^2 when in the presence of *Dreissena*, *Dreissena* presence may decrease *Hexagenia* to population density levels considered to be more "healthy" and sustainable (Ohio Lake Erie Commission 2004).

Densities of *Hexagenia* and *Dreissena* appear to have a high degree of spatial and temporal variability. At the spatial scale of the western basin of Lake Erie, both *Hexagenia* and *Dreissena* densities were distributed independently of distances sampled (Figure 39.4); however, they were both found at the majority of sites. This finding may be a result of the sites sampled. Sites were all well spaced apart, which may inhibit our ability to see spatial autocorrelation at small distances. Also, the distance-independent spatial distributions may be due to both species having a planktonic early life-history stage, that is, *Dreissena* veligers and *Hexagenia* eggs. *Hexagenia* eggs are deposited at a location that is highly variable and dependent on wind speed and direction. Both eggs and veligers act as passive particles carried by water currents until they settle out of the water column (Hannan 1984, Jackson 1986). Although both taxa have planktonic stages, water currents in lakes are highly variable (Beletsky et al. 1999) and, if the two species are not in the water column at the same time or have different settling rates, they may be distributed very differently. *Hexagenia* eggs can sink quickly (1.9 cm/s; Hunt 1951) unlike *Dreissena* veligers, which stay in the water column for 2–4 weeks or longer (Sprung 1989). Once settled from the water column and grown to a developed stage, how far either *Dreissena* or *Hexagenia* can move to select for suitable habitat is not known. We would hypothesize movement over a short distance due to limited mobility of the organisms and susceptibility to predation. For *Hexagenia* across years, there is a weak positive correlation of density at a spatial distance of zero (Figure 39.4b), which indicates a correlation at the same site through time. This suggests that *Hexagenia* densities at a number of sites are consistent from year to year; that is, some sites always have *Hexagenia*, possibly due to favorable sediment conditions, and some sites never have *Hexagenia* due to conditions that are uninhabitable. We present here spatial autocorrelation and cross-correlations across all years. Therefore, temporal variations in data were masked. However, correlograms were run for individual years and yielded similar results. At larger spatial scales, there appear to be many factors influencing the distributions and densities of both *Hexagenia* and *Dreissena*.

Laboratory Experiments

At the small spatial scale examined in laboratory experiments, *Hexagenia* consistently preferred sediments covered by live *Dreissena* clusters compared to bare sediments and sediments covered by dead *Dreissena* clusters in both sets of experiments. Bare soft sediment, thought to be the preferred habitat of *Hexagenia* (e.g., Wang et al. 2001, Bachteram et al. 2005, Chaffin and Kane 2010), was the least selected habitat type in our experiments. However, long-term mesocosm experiments indicate *Hexagenia* survival declined with *Dreissena* (Osterling et al. 2007, Freeman et al. 2011), but *Hexagenia* condition was not affected (Freeman et al. 2011). *Hexagenia* may experience lower survival in the presence of dreissenid mussels because food resources can become limiting in long-term tank experiments. *Hexagenia* reside under and in clusters and may become densely aggregated, leading to high food competition per unit area. Our field data showed that *Hexagenia* were more likely to occur but were slightly less abundant in mussel-dominated habitat. This observation is consistent with both our short-term choice experiments and observational studies. While *Hexagenia* show a behavioral preference for the structured mussel clusters, this habitat may not be beneficial over long time spans (Freeman et al. 2011).

Addition of physical structure in the form of dreissenid clusters was not the only mechanism that affected *Hexagenia* selection because *Hexagenia* preferred live *Dreissena* to dead *Dreissena* clusters. Both live and dead *Dreissena* change the physical structure of available habitat; however, live *Dreissena* also change chemical and biological structure around clusters. For example, live *Dreissena* filter feed, respire, and excrete feces and pseudofeces. Most epifaunal invertebrates in interstitial spaces of mussel clusters located on hard substrates have been shown to occur in equal densities in live and dead *Dreissena* habitats (Botts et al. 1996, González and Downing 1999). Similar to *Hexagenia* in our experiments though, some benthic fauna (tubificid worms and some chironomids and snails) prefer clusters of live mussels over dead clusters (Ricciardi et al. 1997, Stewart et al. 1998). Therefore, the preference of *Hexagenia* for live dreissenid clusters may simply be a response to additional food provided by mussels (Roditi et al. 1997). Another explanation for *Hexagenia* preference for live *Dreissena* clusters may be related to mussel filtration activity. Individual dreissenids filter a relatively high volume of water (between 0.1 and 1 L/h), and the resultant increased flow of oxygenated water near the sediments may benefit *Hexagenia* (Kryger and Riisgard 1988). Although water below *Dreissena* clusters may have lower dissolved oxygen and be diminished in quality (Burks et al. 2002, Beekey et al. 2004b), some of the oxygenated water may be available to *Hexagenia* burrows immediately adjacent to clusters. Therefore, microhabitat alterations in the presence of *Dreissena* clusters may increase selection of this habitat by *Hexagenia*, which is analogous to *Dreissena* effects on other benthic invertebrates.

Sediment covered by live *Dreissena* was the preferred habitat over bare sediment for *Hexagenia* when a predator (yellow perch) was present. However, contrary to expectations, preference for *Dreissena*-covered sediment was not stronger than preference for the same habitat with fish absent (Figure 39.5). We hypothesized that *Hexagenia* would show stronger selection for *Dreissena*-covered sediment when the predator was present, since another genus of mayfly has been shown to change its behavior in the presence of fish, suggesting an ability to detect predators (Kolar and Rahel 1993). The lack of increased selection for *Dreissena* with a predator is consistent with results from the habitat-selection experiment that suggests *Hexagenia* choose live *Dreissena* clusters for reasons other than protection from predation. Although *Hexagenia* did not select for *Dreissena*-covered habitat primarily as protection from predation, *Hexagenia* have been shown to be consumed by fish at lower levels of efficiency when beneath clusters under highly turbid conditions, as compared with levels found at conditions of low turbidity, high light, and no clusters (DeVanna et al. 2011).

CONCLUSIONS AND FUTURE DIRECTIONS

Range expansion of dreissenid mussels onto soft sediments and the observed small-scale habitat selection by burrowing mayflies under and near *Dreissena* clusters may have potential cascading effects to higher trophic levels and overall ecosystem function. Burrowing mayflies of the genus *Hexagenia* are used as a mesotrophic indicator associated with pollution-abatement programs in the Laurentian Great Lakes and other water bodies throughout the world (e.g., Great Lakes [Reynoldson et al. 1989], Mississippi River [Fremling and Johnson 1990], The Netherlands [bij de Vaate et al. 1992]). As a result, it is extremely important that habitat alterations associated with *Dreissena* do not affect the behavior and tolerance of *Hexagenia* to changing oxygen concentrations. The spatial association between *Hexagenia* and *Dreissena* can have dramatic consequences for higher trophic levels. Many scientists were optimistic about the return of *Hexagenia* to western Lake Erie, as *Hexagenia* are an additional food source to many economically important fish species, such as yellow perch (Hayward and Margraf 1987, Schaeffer et al. 2000). It has been shown that consumption of *Hexagenia* by yellow perch decreases in turbid systems when *Hexagenia* are burrowed beneath *Dreissena* clusters (DeVanna et al. 2011). Therefore, given the highly turbid conditions in the western basin where both organisms co-occur, *Hexagenia* may not be available to fish as a food source. As a result, the potential benefit of *Hexagenia* recolonization may be tempered by spatial associations with *Dreissena* clusters.

This study examined the spatial pattern of *Hexagenia* and *Dreissena* at two spatial and temporal scales, and both showed evidence for *Hexagenia* and *Dreissena* co-occurring in western Lake Erie. Future work should examine the processes governing these observed small- and large-scale patterns. On a small scale, it is important to understand what is driving *Hexagenia* to select sediment covered by live *Dreissena* clusters, that is, whether selection is a result of an added food resource, protection from predation, or a combination of both. On a large scale, processes constraining *Hexagenia* densities, such as sediment type, location of adults laying eggs, egg predation by other invertebrates (Plant et al. 2003), and short-term periods of hypoxia (Bridgeman et al. 2006), should be examined using a modeling approach. Connections between these two levels of scale can begin to be explored once the processes constraining and driving spatial relationships between *Hexagenia* and *Dreissena* at each scale are established. Understanding the large- and small-scale processes that interact to determine *Hexagenia* population size and distribution in western Lake Erie will help us better understand *Hexagenia* as an indicator organism and important prey resource for fish, as well as lead to a better understanding of how an invasive ecosystem engineer can have cascading effects throughout the foodweb.

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