8-2015

Changes in the Benthic Macroinvertebrate Community of Southwestern Lake Ontario Following Invasion by Dreissena Mussels, the Amphipod Echinogammarus ischnus, and the Round Goby Neogobius melanostomus: A Long-term (1983-2014) Perspective

Katherine L. Bailey
The College at Brockport, kbail3@u.brockport.edu

Repository Citation

Bailey, Katherine L., "Changes in the Benthic Macroinvertebrate Community of Southwestern Lake Ontario Following Invasion by Dreissena Mussels, the Amphipod Echinogammarus ischnus, and the Round Goby Neogobius melanostomus: A Long-term (1983-2014) Perspective" (2015). *Environmental Science and Ecology Theses*. 99.
https://digitalcommons.brockport.edu/env_theses/99

Changes in the Benthic Macroinvertebrate Community of Southwestern Lake Ontario Following Invasion by *Dreissena* Mussels, the Amphipod *Echinogammarus ischnus,* and the Round Goby *Neogobius melanostomus*:

A Long-term (1983-2014) Perspective

By

Katherine L. Bailey

A thesis submitted to the Department of Environmental Science and Biology of the State University of New York College at Brockport in partial fulfillment of the requirements for the degree of Master of Science

August, 2015

Abstract

Successive invasions of the Laurentian Great Lakes by zebra (*Dreissena polymorpha*) and quagga (*D. bugensis*) mussels, the amphipod *Echinogammarus ischnus,* and the round goby (*Neogobius melanostomus*), all of Ponto-Caspian origin, have altered benthic macroinvertebrate communities, but the impacts of these invasions may differ short- and long-term and in magnitude. Changes in diversity and abundance of benthic macroinvertebrate communities at long-term cobble and artificial reef study sites in southwestern Lake Ontario were quantified using dome suction sampling in July and September 2014, following invasion of the round goby after the year 2000. Using Non-metric Multi-dimensional Scaling (nMDS), Analysis of Similarities (ANOSIM) and Similarity Percentages (SIMPER), abundance estimates for native benthic macroinvertebrate taxa were compared with past sampling years (1983, pre-invasion of dreissenids; 1991-1992, early post-invasion of dreissenids; and 1999-2000, ~10 years post-invasion of dreissenids and early post-invasion of *E. ischnus*). Oligochaetes were the dominant taxon in 2014 (1193.9 ± 18.3 [SEM] m^{-2} at the cobble and 982.3 ± 32.2 m^{-2} at the reef sites, July and September abundances combined), followed by *E. ischnus* (101.2 ± 2.1 m^{-2} at the cobble and 599.9 ± 5.5 m^{-2} at the reef sites), and Chironomidae (63.4 ± 26.5 m^{-2} at the cobble and 215.9 ± 19.3 m^{-2} at the reef sites). By 2014, chironomid richness had increased >100% since 1991-1992. For the first time during the 31 year sampling period, gastropods and sphaeriid clams were absent, which contributed to low Simpson's Diversity in 2014. Between 2000 and 2014, *D. bugensis* almost completely replaced *D. polymorpha*, and *E. ischnus* replaced *Gammarus fasciatus* as the dominant amphipod. Results in 2014 were in strong contrast with those reported from 1983, 1991-1992, and 1999-2000, when gastropods and sphaeriid clams, as well as the native amphipod *G. fasciatus*, were dominant members of the benthic macroinvertebrate community. These results suggest that the 2014 benthic macroinvertebrate communities underwent greater change after invasion of the round goby than the communities did after the dreissenid and *E. ischnus* invasions (~1990 and ~1994, respectively). The loss of gastropods and native clams, coupled with increases in oligochates and chironomids at the study sites, likely will have important effects on benthic and pelagic food webs in Lake Ontario.

Dedication

I dedicate my thesis to my late grandfather, my Papa, who inspired me to pursue the path of science, always to keep learning, and to appreciate each and every discovery, no matter how small.

Acknowledgments

The completion of this thesis would not be possible without the help of many who volunteered their time in the field and in the lab. I thank my major advisor, Dr. James M. Haynes, for giving me the opportunity to contribute to his long-term data set, for his patience and guidance in the field, and for his critical reviews of this thesis. The two other members of my committee are also deserving of many thanks. Dr. Douglas Wilcox provided me with an opportunity to be a graduate assistant on his wetlands monitoring project, which allowed me to appreciate the value of aquatic invertebrates in different wetland habitats. Dr. Ely Kosnicki willingly introduced me to the family Chironomidae and allocated several hours to instructing me on the proper method of slide-mounting and identifying chironomid larvae. I thank him for his patience and for his willingness to confirm and correct all of my chironomid identifications. I also thank Gary Neuderfer for introducing me to macroinvertebrate identification prior to my field collections and for his support during my first year as a graduate student. Several people outside of my committee have helped me throughout the preparation of this thesis. Mr. Rod Hedley provided me with invaluable references, documents, and GPS coordinates of the Olcott reef. He also provided our field crew with a dock for the RV Madtom. Many thanks to Anthony Marsocci, who assisted as boat captain and helped to repair the dome suction sampler. I thank Kelly Owens, who dove to assist with sample collections. I also thank David Sanderson-Kilchenstein for his help in preparing and repairing the dome suction sampler prior to field use. Finally, I thank my future husband, Kingdon Barrett, for his willingness to participate in the three days of sampling, for his patience, and for his support throughout my graduate career at Brockport.

Table of Contents

List of Tables

List of Figures

List of Appendices

Introduction

After successive introductions of non-native aquatic species in the Great Lakes, researchers have long expressed concerns about the effects of such introductions on benthic macroinvertebrate community structure and ecosystem functions (Mills et al. 1993). When alterations in benthic macroinvertebrate community composition occur after introductions of non-native species, potential exists for modifications in both pelagic and benthic systems, as well as changes in nutrient cycling (Mills et al. 2003, Nalepa et al. 2009). The establishment of zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis* Pallas, respectively; hereafter referred to as dreissenids) in the late 1980s, the amphipod *Echinogammarus ischnus* Stebbing in the mid- 1990s, and the round goby, *Neogobius melanostomus* Pallas, in the early 2000s has likely impacted benthic macroinvertebrate communities in the nearshore of Lake Ontario. My thesis aims to understand and assess changes in nearshore benthic communities since 1983 at long-term artificial reef and natural cobble study sites in southwestern Lake Ontario.

Dreissenids

Zebra mussels invaded the Great Lakes in 1988, followed by the invasion of their close cousin, the quagga mussel, in 1991 (Mills et al. 2003). Due to their high reproductive rates and ability of zebra and quagga mussels to colonize both hard and soft substrates, respectively, dreissenids increase the surface area and complexity of these substrates (Wilson et al. 2006, Ozersky et al. 2011). Increased surface area has been beneficial not only for habitat and grazing space but also for refuge from predators for epifaunal taxa (Stewart et al. 1998a, b). In addition, the high filtering capacity of dreissenids increases the amount of nitrogen- and phosphorus-rich food available to benthic communities in the form of feces and pseudofeces (Ozersky et al. 2011). The combined increase in habitat complexity and food has largely resulted in positive, short-term changes in benthic macroinvertebrate communities at one nearshore site in southwestern Lake Ontario (Stewart 1993, Haynes et al. 1999, Haynes et al. 2005).

In a large-scale analysis of the effects of *Dreissena* on native benthic macroinvertebrate communities, leeches, isopods, gastropods, flatworms, and mayflies increased in abundance in the presence of dreissenids (Ward and Ricciardi 2007). In addition, epifaunal taxa, and scrapers in particular, responded positively to dreissenid colonization, while infaunal (burrowing) taxa showed negative changes in density (Ward and Ricciardi 2007). Stewart et al. (1998b) found that *Echinogammarus* biomass was 22 times greater on experimental bricks that had high densities of dreissenids than on low density bricks. As ecosystem engineers that modify nutrient dynamics of lake ecosystems with their high filtering capacity and large population densities, dreissenids also redirect nutrients from the water column to benthic habitats and induce significant community-level effects (Hecky et al. 2004, Ward and Ricciardi 2007), which has caused concerns regarding Great Lakes food webs and fisheries welfare (Stewart et al. 1998a, b).

Despite short-term positive effects on benthic macroinvertebrate communities, dreissenids are implicated in the biofouling and demise of native unionid mussels and sphaeriid clams (Lauer and McComish 2001, Ozersky et al. 2011). Lauer and McComish (2001) found that fingernail clams (Sphaeriidae) >2 mm in Lake Michigan almost always had some evidence of zebra mussel impact, particularly byssal thread attachment, and that fingernail clams 3 mm and larger were practically extirpated from the study sites just three years after zebra mussel invasion. In Lake Simcoe, sphaeriid densities declined by an annual mean of 20% from 1992 to 1997, and this decline was attributed to interference competition due to zebra mussel byssal thread entanglement (Lauer and McComish 2001). At my study sites, unionids (pers. comm., J. M. Haynes, The College at Brockport, SUNY) and sphaeriids (Haynes et al. 2005) also declined in abundance after the establishment of dreissenids.

Echinogammarus ischnus

In its native habitat, *E. ischnus* is part of the lithophilic community of large rivers, where dreissenids are a major component (Dermott et al. 1998). *Echinogammarus ischnus* entered Lake Erie in 1994 and is commonly associated with dreissenid colonies in the Laurentian Great Lakes (González and Burkart 2004). This invasive amphipod superficially resembles the native amphipod *Gammarus fasciatus*;

however, where *G. fasciatus* has long inner rami attached to the third uropods, *E. ischnus* has minute inner rami, which is the distinguishing feature of the genus (Dermott et al. 1998). *Echinogammarus ischnus* likely invaded Lake Ontario via the Welland Canal, as it was reported first at several sites at the outlets of the Niagara River and Welland Canal in 1996 (Dermott et al. 1998).

In its introduced habitat of the Great Lakes, especially at the outlet of the Niagara River, *E. ischnus* became the dominant amphipod within one year (Dermott et al. 1998). Several researchers have suggested that *E. ischnus* will replace *G. fasciatus* as the dominant amphipod in the nearshore zone elsewhere (cf. van Overdijk et al. 2003). Since dreissenids occurred with *E. ischnus* in their native Ponto-Caspian habitats, the establishment and expansion of *E. ischnus* may be facilitated by dreissenids in the Great Lakes (van Overdijk et al. 2003).

Round goby

As the fastest advancing and one of the most widely distributed aquatic invasive species in the Laurentian Great Lakes, the round goby is implicated in declines of benthic invertebrate abundance and changes in native predator feeding behavior (Kuhns and Berg 1999, Barton et al. 2005, Lederer et al. 2006). The round goby was first reported in the St. Clair River in 1990 (Lederer et al. 2006) and likely arrived at my study sites in 2003 (Walsh et al. 2007). This generalist predator possesses molariform pharyngeal teeth that allow it to consume an increasing proportion of dreissenids as it matures (Ray and Corkum 1997, French and Jude 2001, Brush et al. 2012, Kipp and Ricciardi 2012). Dermott et al. (2012) suggested that the round goby is likely responsible for the reduction of epibenthic species in the Bay of Quinte because it also exploits non-shelled taxa such as chironomids and amphipods (Brush et al. 2012). Carman et al. (2006) reported that in the absence of zebra mussels, round gobies fed heavily on heptageniid mayflies and chironomids, which also constitute the primary diet of darters and sculpins which have largely disappeared from the near shore of Lake Ontario (cf. French and Jude 2001, Janssen and Jude 2001). Likewise, the round goby is implicated in the decline of benthic macroinvertebrate species richness in nearshore areas of Lake Erie (Krakowiak and Pennuto 2008).

Goby predation on mollusks (mainly dreissenids) and soft-bodied invertebrates may cause a shift from large-bodied taxa to small-bodied taxa. Kipp et al. (2012) found that the median size of gastropods correlated negatively with round goby density across sites in the upper St. Lawrence River. However, late-invasion stages were characterized by the large-bodied gastropod families Pleuroceridae and Hydrobiidae (Kipp et al. 2012). Similarly, Kipp and Ricciardi (2012) demonstrated that invertebrate body-size decreased across sites with increasing goby density; in most cases where goby density exceeded 2.5 fish m^{-2}, chironomids became the most dominant taxon by biomass.

Differences in round goby effects on non-dreissenid macroinvertebrates across sites, seasons, and times of day are likely the result of direct and indirect effects of round goby predation on dreissenid populations (Lederer et al. 2006). Direct predation on dreissenid colonies could displace certain epifaunal invertebrates that rely on dreissenid shells for habitat (Lederer et al. 2006). Dreissenids may also indirectly reduce predation risk of small-bodied benthic invertebrates because of the added substrate complexity and refuge in mussel colonies (Lederer et al. 2006).

Previous investigations of round goby impacts have occurred without the benefit of a long-term data set. Here, I had the opportunity to compare benthic macroinvertebrate communities at the same sites in Lake Ontario that have responded to the dreissenid invasion for ~30 years that are now responding to the *E. ischnus* and round goby invasions. Depending on the extent of the round goby abundance at my study sites, I made two predictions as to how it may influence the benthic macroinvertebrate communities. First, I hypothesized that I would detect a shift in body-size dominance from larger- to smaller-bodied taxa (Kipp and Ricciardi 2012, Kipp et al. 2012). Second, I hypothesized that overall invertebrate densities would be lower than found previously at the long-term cobble and reef sites (Krakowiak and Pennuto 2008, Brush et al. 2012, Dermott et al. 2012).

Coevolution of dreissenids, E. ischnus, and the round goby

Several researchers (cf. Ricciardi 2001, Kestrup and Ricciardi 2009, DeVanna et al. 2011) have suggested that dreissenid colonization may have facilitated round goby and *E. ischnus* invasion success in the Laurentian Great Lakes because these species coevolved in similar habitats of the Ponto-Caspian region (Lederer et al. 2006, Wilson et al. 2006). Proposed co-evolutionary mechanisms include 1) the role of dreissenids as ecosystem engineers that change the availability of nutrients and alter substrate complexity (DeVanna et al. 2011); 2) the presence of dreissenids, which provided an immediate food source for the round goby (Barton et al. 2005, DeVanna et al. 2011); and 3) round goby predation, which facilitates the replacement of *G. fasciatus* by *E. ischnus* (Kestrup and Ricciardi 2009).

Two hypotheses suggest that the direct and indirect effects of dreissenids allowed for subsequent invasions of Ponto-Caspian species in the Laurentian Great Lakes. One of these, invasional meltdown, emphasizes facilitative rather than antagonistic interactions among introduced species (Simberloff 2006). This theory predicts that community integrity is threatened by cumulative numbers of attempted invasions, and that once established, some invaders alter habitat conditions in favor of other invaders (Ricciardi 2001). Altered habitat conditions then create a positive feedback system that accelerates the accumulation of invasive species. Positive feedback mechanisms include direct and indirect facilitation: the former involves effects that directly benefit other invaders, while the latter emphasizes effects that reduce an invader’s risk of predation or enhance the invader’s prey (Ricciardi 2001).

The second hypothesis is that dreissenids alter the availability of nutrients to other species by causing changes in the physical state of biotic and abiotic resources (DeVanna et al. 2011) (i.e., they are ecosystem engineers). These changes benefit some benthic invertebrates, such as grazing gastropods and amphipods, while other taxa are negatively affected (e.g., filter-feeding sphaeriid clams). By increasing the amount of resources in the benthic nearshore of Lake Ontario in the form of feces and pseudofeces, as well as increasing surface area of the substrate, dreissenids may have facilitated the subsequent invasions of other Ponto-Caspian species that were present at my study site, the round goby, and *E. ischnus* (Kestrup and Ricciardi 2009).

Methods

Study area

The study area included an artificial reef habitat (N 43° 20’ 10.5”, W 78° 45’ 25”) and adjacent natural cobble site (N 43° 19’ 84”, W 78° 45’ 49”) in southwestern Lake Ontario, located 0.8 km offshore and 1.6 km west from Olcott, NY, at depths ranging from 5 to 7 m (Stewart 1993; Figures 1 & 2). The cobble habitat consisted of a mixture of cobble, sand and silt, which provides suitable habitat for infaunal (burrowing) and epifaunal (non-burrowing) taxa (Stewart 1993), and is representative of the benthic environment found along the southwestern nearshore region of Lake Ontario. Approximately 60 m long and 11 m wide, the artificial reef, which was constructed in 1982 to attract spawning lake trout (*Salvelinus namaycush*), consisted of siltstone, cinder blocks, and shale and provides favorable habitat for epifaunal organisms (Stewart 1993).

Experimental design

I collected benthic macroinvertebrate samples from the study sites in July and September 2014. To compare relative abundances of benthic invertebrates from the same study sites in past sampling years, I only compared my results with those reported from July and September of 1983, 1991-1992, and 1999-2000. Since four years, two habitats (cobble and reef), and two months were compared, a total of 16 sets of benthic macroinvertebrate samples were compared by multivariate analyses.

Sampling

My sampling methods in July and September 2014 were identical to those used in the past (Stewart 1993, Haynes et al. 1999, Haynes et al. 2005). SCUBA divers laid out one 30-m transect at each of the cobble and reef sites, and from each transect, five replicate benthic samples were collected using a dome suction sampler (Gale and Thompson 1975). The dome suction sampler is an apparatus consisting of stainless steel enclosing an area of 0.164 m^2, a bilge pump connected to a 12-V motorcycle battery, and a plexiglass cover with two armholes. A hose (with a nozzle containing steel rods spaced 1.27 cm x 1.27 cm apart to reduce clogging of the pump) was attached to the pump. Collecting bags with mesh size 0.5 µm x 0.5 µm were connected to the pump by another hose. Samples were collected by vacuuming the substrate enclosed within the circumference of the dome suction sampler for 3 min.

Sample processing

Samples were transported to the surface, where they were rinsed into 5-gallon buckets and passed through a 600 µm sieve to retain benthic invertebrates. Benthic invertebrates and associated algae and sediments retained on the sieve were then rinsed into plastic jars with carbonated water to relax the organisms before fixing them in 10% buffered formalin. After 24 hours, the formalin was decanted and replaced with a solution of 70% ethanol and rose Bengal. The rose Bengal imparted a pink color to soft-bodied organisms, allowing for ease of sorting.

In the laboratory, macroinvertebrates were separated from algae and other debris by carefully examining samples under a dissecting microscope. Macroinvertebrates were counted and incorporated into abundance estimates only if the shell aperture was intact or the head was attached to the body. Organisms were identified to the lowest practical taxonomic resolution to allow for comparisons of relative abundances with those reported in previous sampling years. To allow for comparisons across years, sites, and months, the taxa Isopoda and Hydracarina were combined into the group “other.” Since there many oligochaetes in the samples, only whole individuals were counted in abundance estimates. Whole, undamaged dreissenid mussels were counted, blotted dry and weighed to calculate the average mass/individual. Remaining damaged mussels and fragments of shells and tissue were blotted dry, and weighed. Abundance estimates were determined based on the average mass/individual and the total mass of dreissenids for each replicate sample (Stewart 1993).

Chironomid taxa were identified using the key in Epler (2001). Prior to identification, chironomids were sorted by subfamily and tribe and then slide-mounted using CMCP mounting media to clear body tissues and improve visualization of the head capsule. To facilitate comparisons of midge taxa enumerated by Stewart (1993), all midges I identified as *Orthocladius* and *Cricotopus* were combined into the split genus *Cricotopus-Orthocladius.* It was a conservative decision to combine these taxa since identification and differentiation of these genera has been historically difficult (pers. comm., Dr. Ely Kosnicki, The College at Brockport, State University of New York).

Data analyses

Sample mean abundances (# organisms/m²), standard errors for abundance estimates, and 95% confidence limits were calculated for each artificial reef and cobble site taxon from each sampling date.

Simpson's Diversity is a mathematical expression that takes into account species richness and relative abundance (evenness). I calculated Simpson's Diversity for each sampling date in 2014, 1999, 1991, and 1983 using the equation:

$$SD = \frac{\sum n(n-1)}{N(N-1)},$$

where n is the total number of organisms of a particular taxon and N is the total number of organisms in all taxa.

Significant differences of Simpson's Diversity between pairs of the four sampling years were determined by calculating the variance and then performing a t-test.

The variance was calculated using the equation:

$$s^2 = 4[\Sigma p_i^3 \; - \frac{(\Sigma p_i^2)^2}{N}],$$

where p_i is the proportion of the number of organisms in the i^{th} species to the total number of organisms in the sample (N).

The test statistic was calculated with the following equation:

$$t = \frac{D_1 - D_2}{\sqrt{S_1^2 - S_2^2}},$$

where D is the Simpson's Diversity of a community and s^2 is the variance.

Determining significant differences among Simpson's Diversity required Bonferroni corrections to account for the risk of inflating Type I error. Since six year-pairs were compared statistically, the adjusted alpha value was 0.0083.

Multivariate methods, including Analysis of Similarities (ANOSIM), Similarity Percentages-Species Contributions (SIMPER), cluster analysis, and non-metric multidimensional scaling (nMDS), were used to evaluate changes in benthic macroinvertebrate community composition among sampling years (Plymouth Routines in Multivariate Ecological Research version 6, PRIMER 6). Prior to all analyses, abundances for all sampling dates in July and September from 1983 to 2014 were screened for normality, missing data, and outliers using statistical software (Minitab 17). In addition, all abundance data were log (n+1) transformed and transcribed to a resemblance matrix, which displays the similarities (in this case, Bray-Curtis similarity), ranging from 0 to 100 between every pair of samples in a triangular matrix.

Analysis of Similarities (ANOSIM) and Similarity Percentages (SIMPER) are resampling techniques that use permutation methods applied on Bray-Curtis similarity matrices to identify differences among groups of samples that are specified by one or more factors. The ANOSIM test statistic, R, is centered around zero if there are no differences between samples, and large values of R that approach 1 indicate large separation of groups. ANOSIM was performed on the macroinvertebrate communities excluding *Dreissena* and *E. ischnus* to ensure that I was evaluating changes in the indigenous community and treating the invasive species as external stressors, or covariates, to the communities. Two-Way ANOSIMs were performed by crossing year groups with months and habitats, respectively, to test for differences in the benthic macroinvertebrate communities between months (July, September) and habitats (cobble, reef) to determine if those factors influenced differences among years.

Similarity Percentages (SIMPER) incorporates the role of individual species contributing to the separation between two groups of samples, or the closeness of samples within a group. This routine decomposes average Bray-Curtis dissimilarities between all pairs of samples, one from each group, into percentage contributions from each species, with the species listed in order of decreasing contributions. A two-way crossed layout (Year x Habitat, Year x Month) was used to investigate which species were important in dissimilarities and similarities between year groups, months, and habitats.

Non-metric multi-dimensional scaling (nMDS) represents samples as points in low-dimensional space so that the relative distances of all points are in the same rank order as the relative Bray-Curtis dissimilarities of the samples. The distances between samples are derived from a resemblance matrix calculated from the original data matrix. Points that are close together on the ordination represent benthic macroinvertebrate communities that are similar in species composition and relative abundance, and points that are far apart correspond to samples that are different from each other. Non-metric multi-dimensional scaling is an iterative algorithm, and for this dataset, 50 restarts were chosen to converge on the most optimal solution, which results in the lowest stress value. Stress measures the departure of points from the best-fitting regression; I used the criterion that stress levels under 0.2 were acceptable representations of the samples on the 2-d ordination plots.

Weather data (air temperature, precipitation, and solar radiation) from the Buffalo, NY weather station were collected for the 30 days before each sampling date in July and September 2014. Using one-way ANOVA, these data were compared with weather data collected in past sampling years.

Results

Abundance of non-dreissenid benthic macroinvertebrate taxa in 2014

In 2014 oligochaetes were the most abundant benthic macroinvertebrate taxon at the cobble (1193.9 ± 18.3 [SEM] m^{-2}) and reef (982.3 ± 32.2 m^{-2}) sites, contributing 80.4 ± 7.3% and 48.9 ± 8.1% of total community abundance in July and September combined, respectively (Table 1, Figure 3). *Echinogammarus ischnus* was the second most abundant taxon at the cobble (101.2 ± 2.1m^{-2}) and reef (599.9 ± 5.5 m^{-2}) sites, contributing 6.8 ± 2.2% and 29.8 ± 3.7% to those communities, respectively (Table 1, Figure 3). Chironomidae was the third most abundant taxon at the cobble (63.4 ± 26.5 m^{-2}) and reef (215.9 ± 19.3 m^{-2}) sites, contributing 4.3 ± 3.3% and 10.7 ± 5.1% to those communities, respectively (Table 1, Figure 3). For the first time, gastropods and clams (Sphaeriidae) were absent in both habitats in 2014 (Tables 2a, b). Sample abundances for all taxa collected in July and September of 2014 are in Appendix 1.

Echinogammarus ischnus was the dominant amphipod in nine of ten replicates from the 2014 cobble and reef samples (Appendix 1b). Among amphipods in July and September combined, the proportion of *E. ischnus* at the cobble site increased from 11.6 ± 5.5% in 1999-2000 to 78.3 ± 10.0% in 2014. At the reef, the proportion of *E. ischnus* increased from 32.4 ± 48.2% in 1999-2000 to 91.2 ± 3.0% in 2014. Since

1983, 2014 was the first year in which *G. fasciatus* was not the dominant amphipod at the cobble and reef sites (Figure 4).

The highest-ever recorded abundances of soft-bodied oligochaetes and chironomids, along with the new dominance among amphipods of *E. ischnus*, contrasted strongly with previous sampling years, while the absence of native mollusks contributed to the low Simpson's Diversity in 2014.

Long-term trends in Simpson's Diversity Index

Simpson's Diversity of benthic macroinvertebrate taxa, excluding *Dreissena*, was lowest in 2014 (0.377; cobble and reef abundances combined; Table 3a). Diversity was highest in 1991-1992 (0.686; Table 3a). Differences in Simpson's Diversity of non-*Dreissena* taxa were significantly different among all pairs of years (Table 3a). Snail diversity also changed significantly from 1983 to 2014; diversity of snails was highest in 1991-1992 (0.695; Table 3b) and lowest in 2014 (0.000; Table 3b). Snail diversity was significantly different among all pairs of years (Table 3b) except between 1983 and 1999-2000 (T-test, $df = 9$, $p > 0.5$).

In 2014, the diversities of non-dreissenid macroinvertebrates and snails reached the lowest levels reported in this dataset. Long-term changes in diversity and the role of individual taxa in driving changes in the benthic macroinvertebrate communities in each sampling year were further investigated by multivariate analyses of community composition.

Pairwise comparisons of each previous sampling year with 2014

The benthic macroinvertebrate communities sampled in 1983 and 2014 spanned the entire period of pre-invasion to post-invasion by *Dreissena*, *E. ischnus*, and *N. melanostomus*. Excluding these invasive taxa, the communities sampled in 1983 and 2014 were 34.68% similar (Bray-Curtis), those sampled in 1991-1992 and 2014 were 40.5% similar, and those sampled in 1999-2000 and 2014 were 24.5% similar (Table 4). Sampling years before 2014 were more similar to each other than any were to 2014 (Table 4). The low similarities between the three communities sampled from 1983 to 1999-2000 and 2014 were consistent with the absence of historically abundant *Musculium* spp. and all gastropod taxa, as well as the greater importance of Oligochaeta and Chironomidae, in 2014 (Figure 5).

Similarity percentages (SIMPER) further examined the role of individual benthic taxa in contributing to the similarities and dissimilarities of the benthic communities among the four sampling periods. Four taxa contributed more than 10% each to the dissimilarity between 1983 and 2014 (Table 5): *Elimia livescens* (14.5%), Other (isopods, mites; 13.5%), Oligochaeta (13.2%), and *Physella sp*. (11.4%). Three taxa contributed more than 10% each to the dissimilarity between 1991-1992 and 2014 (Table 5): *A. limosa* (13.0%), *E. livescens* (12.3%), and *S. catascopium* (10.7%). Four taxa contributed more than 10% each to the dissimilarity between 1999-2000 and 2014 (Table 5): Oligochaeta (13.9%), Chironomidae (13.7%), *S. catascopium* (13.6%), and Other (isopods, mites; 11.0%).

Not only was the benthic macroinvertebrate community in 2014 (cobble and reef habitats combined) considerably different from previous sampling years, but average similarity of the cobble and reef communities was highest in 2014 (79.3%) when Oligochaeta and Other dominated samples from both habitats, followed by 1991-1992 (76.5%) when *G. fasciatus* and *A. limosa* (and gastropods generally) dominated samples from both habitats (Table 6). Community similarity was lower in 1999-2000 (61.1%) and 1983 (66.9%).

The pairwise comparisons emphasized the role of oligochaetes and chironomids in 2014, in contrast to the greater importance of gastropods and the native amphipod *G. fasciatus* during the three previous sampling years. Considered together, the benthic macroinvertebrate communities of the three previous sampling periods were more similar to each other than any were to the benthic community in 2014.

Analysis of community similarities (ANOSIM)

Preliminary analyses determined that year was the most important factor when crossed with month (Two-Way ANOSIM, R = 0.958, p = 0.001) and habitat (Two-Way ANOSIM, R = 0.854, p = 0.001). One-Way ANOSIM analyses for month (R = -0.006, p = 0.414) and habitat (R = -0.061, p = 0.711) were not significant, but there were significant differences among all years (One-Way ANOSIM, R = 0.845, p = 0.001). Therefore, only combined data for years were used in subsequent nMDS analyses. Previous comparisons of community similarity among the benthic communities sampled in each year showed that 2014 had experienced more changes than observed in any previous sampling year (Table 7).

The results from ANOSIM analyses suggest that the benthic macroinvertebrate communities did not change much between months or habitats; rather, these communities experienced greatest change from one sampling year to the next, which coincided with the invasion of each of the three Ponto-Caspian species.

Changes in the chironomid community: 1991-1992 to 2014

Considered alone, the chironomid assemblages at the cobble and reef communities also underwent considerable changes in community similarity and dominant taxa from 1991-1992 to 2014 (Table 8). Chironomid taxa richness increased >100% from 1991-1992 to 2014; in 1991, eight distinct Chironomidae were identified, and in 2014, 19 taxa were enumerated, excluding unidentified taxa (Figure 6). The dominant genera at the cobble site in 2014 were *Chironomus* (53.5 ± 10.1m^{-2}) and *Dicrotendipes* (19.4 ± 5.3 m^{-2}; Figure 7). The 2014 reef community was dominated by *Dicrotendipes* (84.8 ± 9.8 m^{-2}) and *Psectrocladius* (124.8 ± 13 m^{-2}; Figure 8). In contrast, the 1991-1992 cobble and reef communities were both dominated by *Cricotopus-Orthocladius* and *Psectrocladius* (Figure 6). Average Bray-

Curtis similarity for chironomids between the cobble and reef habitats increased from 21.55% in 1991-1992 to 52.12% in 2014.

Just as the benthic macroinvertebrate community changed significantly from 1983 to 2014 (Tables 5 & 6), so did the chironomid community from 1991-1992 to 2014 (Figure 6). The increase in genera richness, as well as increased importance of chironomids in 2014 corresponded with the disappearance of snails and native clams at the study sites.

Non-metric multi-dimensional scaling (nMDS)

Two-dimensional ordinations of the benthic macroinvertebrate communities provided a visual interpretation of the changes reflected in the ANOSIM analyses. The yearly community groupings coincided with successive species invasions: 1983, pre-invasion; 1991-1992, early post-invasion of *D. polymorpha*; 1999-2000, late post-invasion of *D. polymorpha* and early invasion of *D. bugensis* and *E. ischnus*; and 2014, late post-invasion of *D. bugensis* and *E. ischnus* and strong establishment of the round goby at the study sites. The 2-d ordination had a stress value of 0, which indicated that the arrangement of the 4 communities (years with habitats and months combined) was the best representation of the true Bray-Curtis similarities among those communities (Figure 9). The 1983, 1991-1992, and 1999-2000 year groups clustered more closely together than the 2014 year group did with any of the other years, indicating that the post-round goby invasion benthic macroinvertebrate community of 2014 had undergone greater change than earlier post-invasion

Dreissena spp. and *E. ischnus* communities. Taxa whose presence weighted significantly with year groups (Table 5) were important vectors on the nMDS ordination. For instance, Oligochaeta, Chironomidae, and *E. ischnus* were vectors that pointed toward 2014, while *Musculium,* all seven gastropod taxa, and *G. fasciatus* weighted strongly toward the communities of 1983 and 1991-1992.

The 2-d nMDS ordination of the benthic communities showed a distinct trajectory of change with each sampling year. The year 2014 was far away from the three points that represented previous sampling years, which reinforces how years, rather than month or habitat, was important in detecting significant changes in the benthic communities.

Chironomid communities were also visualized using 2-d ordination (2 years x 2 habitats, for a total of 4 points). Similar to the benthic communities across four years, the chironomid communities of 1991-1992 and 2014 showed distinct groupings (Figure 10). In addition, the chironomid ordination included specific genera as vectors that were important for each year: *Psectrocladius, Chironomus, Tanytarus, Dicrotendipes,* and *Cricotopus-Orthocladius* weighted strongly toward 2014, while *Paratendipes* pointed toward 1991-1992.

Visualizing the chironomid communities as its own distinct assemblage provided more resolution into how the composition of the study area changed from 1991-1992 to 2014. In addition, the 2-d ordination provided a visual interpretation of how community similarity between the reef and cobble habitats increased from 1991-1992 to 2014.

Weather data one month before each sampling event

Daily air temperatures (mean, maximum, minimum) and total daily precipitation were obtained from Buffalo, NY weather station data (kbuf: www.weather.noaa.gov) for each of the 30 d before the eight sampling month-years reported here (Table 9). Only high daily air temperature was significantly different among years (Kruskal-Wallis Test, df = 3, p = 0.046). The high daily air temperature was significantly different between 2014 and 1991-1992 (Pairwise comparison, df = 3, p = 0.020) and 1999-2000 and 1991-1992 (Pairwise comparison, df = 3, p = 0.024). Although the daily low air temperature was higher in 2014 than in any of the three previous sampling years, this parameter was not significantly different among years (Kruskal-Wallis Test, df = 3, p = 0.618).

Weather data in nMDS showed no distinct groupings by year, as each of the points associated with the weather variables for each year on the 2-d ordination overlapped considerably with the other year-groups (Figure 11). These results indicate that weather was not a significant factor involved in changes observed in the benthic macroinvertebrate communities from 1983 to 2014.

Discussion

The effects of non-native species introductions on native community structure and ecosystem functions may be few or many, short-term or long-term, as evidenced by successive introductions of non-native aquatic species in the Great Lakes (Mills et al. 1993). My results show that benthic macroinvertebrate communities at the natural cobble and artificial reef sites changed together in a major way only after invasion by a third non-indigenous Ponto-Caspian species, the round goby. Several trends in the benthic macroinvertebrate community became apparent from 1983 to 2014: 1) a decline in overall diversity and simultaneous increase in cobble and reef community similarity; 2) a shift from large-bodied mollusks to small, soft-bodied oligochaetes and chironomids; 3) an increase in chironomid richness, and 4) replacement of *G. fasciatus* by *E. ischnus*, and *D. polymorpha* by *D. bugensis.*

Factors contributing to changed community similarity and decreased diversity in 2014

The 2014 benthic community was quite different from the three previous sampling periods (Figure 9), and community similarity between the cobble and reef habitats was highest (79.34%) in 2014 (Table 6). I attribute the large difference between 2014 and the three previous sampling years to the complete loss of gastropods and increased importance of oligochaetes and chironomids in 2014. In addition, native sphaeriid clams, which were already declining in 1999-2000 (Haynes et al. 2005), were absent from my samples in 2014, likely due to continuing presence of dreissenid mussels that directly compete with native clams for food particles suspended in the water column (Lauer and McComish 2001, Vanderploeg et al. 2002).

Interestingly, the 2014 community was most similar to the 1991-1992 community (Table 4), which could be due to higher abundances of oligochaetes in 1991-1992 and 2014 than in 1983 and 1999-2000 (Figure 4). Increased community similarity between the cobble and reef habitats in 2014 may be the result of round gobies as effective predators on the formerly diverse assemblage of gastropods (Kipp and Ricciardi 2012, Kipp et al. 2012). In addition, increased community similarity between cobble and reef habitats would be expected with time; the reef was constructed in 1982, and over time, colonization by indigenous organisms residing in adjacent cobble habitat would contribute to higher Bray-Curtis similarity.

The higher community similarity between the cobble and reef habitats in 2014 coincided with high round goby abundance and the lowest Simpson’s Diversity recorded during the 1983-2014 study period (Table 3a). In contrast, 1991-1992 had the highest Simpson’s diversity during the study period, which coincided with the highest gastropod diversity (Table 3b), as well as overall higher abundance of non-dreissenid taxa at the cobble and reef sites (Tables 2a & b). My results agree with those reported for Lake Erie tributaries where Shannon’s diversity of benthic invertebrate communities was negatively correlated with round goby density

(Krakowiak and Pennuto 2008, Kipp and Ricciardi 2012). Kipp et al. (2012) found not only a decline in the median size of gastropods and taxa richness in the upper St. Lawrence River where round gobies were present, but the persistence of smaller individuals of Hydrobiidae and large Pleuroceridae. Thus, smaller and larger gastropods may have been present at my sites in 2014, but I did not detect them in ten replicate samples.

Shifts in body-size dominance of the benthic non-dreissenid taxa

In 1999-2000, Haynes et al. (2005) reported very low abundances of oligochaetes and chironomids, but high abundances of gastropods. In 2014, I found the reverse: high abundances of oligochaetes and chironomids and no gastropods, as well as the highest chironomid richness recorded in this dataset (Bader 1985, Stewart and Haynes 1994, Haynes et al. 2005). My findings agree with Kipp and Ricciardi (2012), who found that round goby density was positively correlated with chironomid biomass and negatively correlated with gastropod body size and abundance. Similarly, Lederer et al. (2006) reported that round gobies had no detectable impact on midge larvae biomass.

Round gobies are probably exerting top-down control on benthic macroinvertebrates, which has likely resulted in a trophic cascade. Kuhns and Berg (1999) hypothesized that round goby predation on gastropods has released *Cladophora* and other macroalgae from grazing pressure, allowing for these algae to proliferate and increase microhabitat and grazing area for oligochaetes and chironomids. This hypothesis is supported by the thick macroalgal mats observed at my study site in 2014, especially on the artificial reef.

In Lake Erie, Burlakova et al. (2014) found that oligochaetes and chironomid densities increased by at least 50% during the first decade of the dreissenid invasion. I found similar trends for our long-term dataset, since oligochaetes increased by >50% at the cobble and reef sites from 1983 to 1991-1992 (Figure 4). However, my findings in 2014 contrasted with those of Burlakova et al. (2014), who found a reduction in the abundance of both oligochaetes and chironomids during 2009 to 2012. Varying oligochaete abundance between western Lake Erie and my study sites may be due to different sampling gear, as well as differences in substrate type, macroalgae, and dreissenid and round goby densities.

In a recent lake-wide Ponar-grab survey of benthic macroinvertebrates in Lake Ontario, Birkett et al. (2015) found that oligochaetes were the second-most abundant taxonomic group and accounted for 24% of all benthic macroinvertebrate densities recorded in 2008-2009, and that oligochaetes were the most abundant group in the western basin at 11 m depth. Oligochaetes are ubiquitous members of the Great Lakes benthic community and are more tolerant than most other benthic cohabitants to habitat degradation and environmental stressors (Birkett et al. 2015), which may partially explain why this taxonomic group experienced such large increases in abundance at my sites in 2014. I also think that the dense macroalgae mats provided refuge for midges and oligochaetes from round goby predation, since filamentous algae would not only hide these taxa from visual predators, but could potentially interfere with round goby feeding habits (Barton et al. 2005).

Changes in the chironomid community

In a strictly qualitative sense, the chironomid community of 2014 was more similar to the pre-invasion community of 1983 (Bader 1985) than to the 1991-1992 early post-invasion community (Stewart 1993). The communities of 1983 and 2014 had 12 of 24 genera in common, as opposed to the 2014 and 1991-1992 communities only having 6 of 19 genera in common (Appendix 2). (Chironomids were identified only to family in 1999-2000.) Stewart et al. (1998a) found that *Dreissena* caused a shift from a homogeneous community dominated by *Dicrotendipes* to a more diverse assemblage dominated by *Microtendipes pedellus*. Interestingly, both *Dicrotendipes* and *Microtendipes* were present in 1983, were not reported in July and September of 1991-1992, but reappeared in 2014. The trend in the chironomid community appears to be a decrease in richness following short-term invasion and then a return to pre-invasion richness levels in 2014. I hypothesize that the short-term, ecosystem engineering effects of *Dreissena* in 1991-1992 favored expansion of gastropods and *G. fasciatus*, which may have utilized foraging area and the nutrient-rich feces and pseudofeces more efficiently than the chironomid larvae. Following invasion of round goby, removal of scrapers (gastropods) and filter-feeding clams could have allowed for expansion of collector-gatherer midges such as *Dicrotendipes* and *Microtendipes,* and collector-filterers including *Tanytarsus*.

Trends in species replacements at the cobble and reef habitats

Rapid expansion of *E. ischnus,* declining populations of *G. fasciatus,* and the replacement of *D. polymorpha* by *D. bugensis* have been well-documented in several of the Great Lakes (cf. Nalepa et al. 2001, Wilson et al. 2006, Kestrup and Ricciardi 2009).

First reported at the cobble and reef habitats in 1999-2000 (Haynes et al. 2005), *E. ischnus* abundance exceeded that of *G. fasciatus* for the first time in 2014. Although *E. ischnus* became the dominant amphipod in 2014, its overall abundance at the cobble and reef sites did not increase dramatically since 1999-2000 (Tables 2a & b). Abundance of *E. ischnus* at the cobble habitat actually decreased, but increased slightly at the reef from 1999-2000 to 2014 (Figure 4). Unstable fine sediment such as silt and sand is unsuitable for *E. ischnus,* which may explain why abundance decreased only at the cobble site (Palmer and Ricciardi 2005). *Gammarus fasciatus* experienced a dramatic increase of >50% at both habitats following short-term invasion of *D. polymorpha* but began to decline >50% at the reef in 1999-2000 (Figure 4). In 2014, *G. fasciatus* populations at both cobble and reef were lower than pre-invasion levels (Figure 4; Table 2a, b). Although *E. ischnus* occurred in greater numbers than *G. fasciatus* in 2014, total abundance of this invasive amphipod was

<50% of that recorded for *G. fasciatus* during the three previous sampling periods (Tables 2a, b), suggesting that *E. ischnus* does not use detrital resources as efficiently as *G. fasciatus*; perhaps this has left more detrital resources available for oligochaetes and chironomids, which experienced unprecedented increases in abundance.

Echinogammarus ischnus is smaller than native gammarid amphipods and produces broods equal or greater in size (Grabowski et al. 2007). It also is a rocky substrate specialist that uses its uropods and antennae for stabilization while moving along hard substrates (Palmer and Ricciardi 2005) like the Olcott reef. Perhaps, dreissenid mussels facilitated the expansion of *E. ischnus* and decline of *G. fasciatus.* Because *E. ischnus* coevolved with dreissenids in the Ponto-Caspian region, in mussel colonies, it may be able to utilize resources more effectively than amphipods native to the Great Lakes (Nalepa et al. 2001, González and Burkart 2004). Food resources likely differ between dreissenid colonies and macroalgal mats, and since biodeposition of organic matter would be greater in dreissenid colonies, dreissenids may have facilitated invasion of *E. ischnus* by providing increased food resources (González and Burkart 2004). With potentially greater affinity for mussel colonies than *G. fasciatus, E. ischnus* also may be able to avoid round goby predation more than *G. fasciatus* (González and Burkart 2004). However, my findings at the cobble and reef habitats do not support the invasional meltdown hypothesis (Kestrup and Ricciardi 2009) but rather the general facilitation hypothesis (DeVanna et al. 2011), since indigenous chironomids experienced greater increase in abundance than *E. ischnus.*

In many nearshore areas of the Great Lakes, including my study sites, the native *G. fasciatus* has become rare (Dermott et al. 1998). Possible factors contributing to the persistence of *G. fasciatus* in some nearshore areas in the presence of the invasive *E. ischnus* include local genetic and phenotypic plasticity, such as euryhalinity and generalist foraging behavior, which increase success in invaded habitats (Derry et al. 2013). In addition, uninvaded microhabitats such as vegetation and the dense macroalgae mats I observed at the reef in 2014 may provide refuge for the native amphipod (Palmer and Ricciardi 2005, Derry et al. 2013). Besides potentially using different habitats, these two amphipods may not be competing directly for the same food resources; Limén et al. (2005) found through stable isotope analysis that *E. ischnus* did not utilize dreissenid feces and pseudofeces as a food source and that *G. fasciatus* did. Laboratory predation experiments found that round goby chose both *E. ischnus* and *G. fasciatus* for food (González and Burkart 2004), so round gobies may be utilizing both species as a food sources at my study sites.

Dreissena bugensis was the dominant dreissenid at my sites beginning in 1999-2000, which paralleled similar trends reported for sites in Lake Erie, Lake Ontario, and Lake Michigan (Nalepa et al. 2001, Patterson et al. 2002, Wilson et al. 2006, Burlakova et al. 2014). Zebra mussels may have facilitated the expansion of quagga mussels by reducing food availability to levels at which the quagga mussel was a better competitor (Ricciardi 2001). Other factors that may have contributed to the success of the quagga mussel include its higher filtration rates in warmer water, faster growth rate in the presence of predators, and its longer siphons and byssal threads that allow them to thrive on soft sediments (Birkett et al. 2015). Wilson et al. (2006) found that zebra mussels are nearly gone from the nearshore of Lake Ontario (as found at my study sites in 2014), and quagga mussel densities are similar to zebra mussel densities documented during the first decade of the dreissenid invasion.

Although *D. bugensis* was the dominant dreissenid at my sites in 2014, abundances and biomass of the mussel at the cobble and reef habitats were <50% of those reported in all three past sampling periods (Stewart and Haynes 1994, Haynes et al. 1999, Haynes et al. 2005). Dreissenid abundance and biomass (Appendices 3 & 4) were underestimated in 1999-2000 and 2014 because the dome suction sampler did not remove all dreissenids from the substrate or move them to the collection bag, whereas in 1991-1992 dreissenids were scraped from rocks transported to the boat. However, Pennuto et al. (2012) also reported a reduction in total numbers of dreissenids, which were collected by divers scraping the surfaces of rocks, from the nearshore of Lake Ontario, and both Barton et al. (2005) and Naddafi and Rudstam (2014) reported that round gobies reduce dreissenid biomass.

Changes in the fish community

Although fish abundances were not quantified in 2014, I observed high densities of round gobies, especially at the reef, and no other fish, except for a few pelagic alewife (*Alosa pseudoharengus*). A previous study on the pre-dreissenid reef and cobble sites reported 16 fish species caught in gill nets, including lake trout, white bass, and yellow perch (Merritt 1985). In 1999-2000, prior to round goby invasion, the historical assemblage of native fishes reported from 1983 had not changed (Haynes et al. 2005). Lauer et al. (2004) suggested that aggressive behavioral interactions of round gobies toward mottled sculpins (*Cottus bairdii*) and johnny darters (*Etheostoma nigrum*) in Lake Michigan contributed to declines in their populations from 1984 to 2002. Johnny darters and slimy sculpins (*C. cogatus*) were common before round gobies invaded my study sites (Haynes 1994) and across the nearshore benthos of Lake Ontario (Mills et al. 2005). My observation of high abundances of round gobies and no native fish (although seasonal changes in the fish community cannot be discounted) in 2014 speaks to the impact of this invader in potentially displacing native sculpins and other benthic-feeding fish, as well as driving major changes in the benthic macroinvertebrate community (Kornis et al. 2012).

Summary and conclusion

The benthic macroinvertebrate communities at my study sites underwent several changes in community structure and diversity following invasion of round gobies in ~2003. Perhaps the most dramatic change was the absence of gastropods in 2014 and the accompanying shift to the dominance of soft-bodied oligochaetes and chironomids. While overall diversity of the benthic macroinvertebrate community of 2014 was the lowest it had ever been in this long-term dataset, the simultaneous increase in chironomid abundance and richness in 2014 demonstrated that the effects of aquatic invasive species may be detrimental or beneficial for different benthic organisms.

Clearly, the benthic macroinvertebrate community of southwestern Lake Ontario has undergone many changes following successive invasions of three Ponto-Caspian species. The loss of gastropods and sphaeriid clams, presumably due to the establishment of a large round goby population, has resulted in a dramatic decline in benthic invertebrate biodiversity and a serious reduction of an important functional component of the macroinvertebrate community: grazing gastropods. While the effects of dreissenids on the benthic macroinvertebrate community were largely positive in the short-term (Haynes et al. 2005), the establishment of the round goby, and perhaps *E. ischnus*, appear to have caused major shifts in the benthic community (including no benthic fish except gobies observed at the cobble and reef sites in July and September 2014). As the Great Lakes continue to undergo ecological change with current and potential future Ponto-Caspian invaders (Vanderploeg et al. 2002), we need to understand better how changes in the benthic macroinvertebrate communities have ramifications for higher trophic levels and food-web dynamics in the benthic and pelagic communities of the Great Lakes.

Suggestions for future studies

Future studies evaluating changes in benthic macroinvertebrate communities in Lake Ontario, and the Great Lakes as a whole, should further investigate the predatory effects of round gobies on benthic community structure. In particular, the use of plot sampling, in addition to dome suction sampling, would provide a more reliable estimate of dreissenid abundance and biomass at the long-term cobble and reef sites. Future research could use enclosures to assess benthic macroinvertebrate community composition in areas with and without round gobies. Also, *G. fasciatus* and *E. ischnus* should be monitored to determine if the invasive amphipod continues to replace its native cousin.

Literature Cited

Bader, A. P. 1985. Dynamics of benthic macroinvertebrates inhabiting an artificial reef and surrounding areas in southwestern Lake Ontario. MS Thesis, State University of New York, College of Environmental Science and Forestry, Syracuse, New York.

Barton, D.R., Johnson, R.A., Campbell, L., Petruniak, J., Patterson, M., 2005. Effects of round gobies (*Neogobiusmelanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002-2004. J. Great Lakes Res. 31(Suppl. 2):252-261.

Birkett, K, S. J. Lozano, and L. G. Rudstam. 2015. Long-term trends in Lake Ontario's benthic macroinvertebrate community from 1994-2008. Aquatic Ecosystem Health & Management 18:76-88.

Brush, J., A. Fisk, N. Hussey, and T. Johnson. 2012. Spatial and seasonal variability in the diet of round goby (*Neogobiusmelanostomus*): stable isotopes indicate that stomach contents overestimate the importance of dreissenids. Can. J. Fish. Aquat. Sci. 69: 573-586.

Burlakova, L., A. Y. Karatayev, C. Pennuto, and C. Mayer. 2014. Changes in Lake Erie benthos over the last 50 years: Historical perspectives, current status, and main drivers. Journal of Great Lakes Research 40:560-573.

Carman, S., J. Janssen, D. Jude, and M. Berg. 2006. Diel interactions between prey behaviour and feeding in an invasive fish, the round goby, in a North American river. Freshwater Biology 51:742-755.

Dermott, R., D. Martchenko, and M. Johnson. 2012. Changes in the benthic community of the Bay of Quinte, Lake Ontario, over a 40 year period. Aquatic Ecosystem Health and Management 15:410-420.

Dermott, R., J. Witt, Y. M. Um, and M. González. 1998. Distribution of the Ponto-Caspian amphipod *Echinogammarusischnus*in the Great Lakes and replacement of native *Gammarusfasciatus.* Journal of Great Lakes Research 24:442-452.

Derry, A. M., A. M. Kestrup, and A. P. Hendry. 2013. Possible influences of plasticity and genetic/maternal effects on species coexistence: native *Gammarusfasciatus*facing exotic amphipods. Functional Ecology 27:1212-1223.

DeVanna, K. M., B. L. Bodamer, C. G. Wellington, E. Hammer, C. M. Mayer, and J. M. Bossenbroek. 2011. An alternative hypothesis to invasional meltdown in the Laurention Great Lakes: general facilitation by *Dreissena*. Journal of Great Lakes Research 37:632-641.

Epler, J. H. 2001. Identification manual for the larval Chironomidae (Diptera) of North and South Carolina. A guide to the taxonomy of the midges of the southeastern United States, including Florida. Special Publication SJ2001-SP13. North Carolina Department of Environment and Natural Resources, Raleigh, NC, USA, and St. Johns River Water Management District, Palatka, FL, USA.

French, J. and D. Jude. 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. J. Great Lakes Res. 27(3): 300-311.

Gale, W. F., and J. D. Thompson. 1975. A suction sampler for quantitatively sampling benthos on rocky substrates in rivers. Transactions of the American Fisheries Society 104:398–405.

González, M., and G. A. Burkart. 2004. Effects of food type, habitat, and fish predation on the relative abundance of two amphipod species, *Gammarusfasciatus*and *Echinogammarusischnus*. Journal of Great Lakes Research 30:100-113.

Grabowski, M., K. Bacela, and A. Konopacka. 2007. How to be an invasive gammarid (Amphipoda: Gammaroidea)-comparison of life history traits. Hydrobiologia 590:75-84.

Haynes, J. M. 1994. Community ecology of the Niagara County artificial reef and nearby natural areas of Lake Ontario. Fall 1994 Data and Progress Report, Niagara County Fishery Advisory Board, Niagara County, NY, USA.

Haynes, J. M., T. W. Stewart, and G. A. Cook. 1999. Benthic macroinvertebrate communities in southwestern Lake Ontario following Invasion of *Dreissena*: Continuing change. Journal of Great Lakes Research 25(4): 828-838.

Haynes, J., N. Tisch, C. Mayer, and R. Rhyne. 2005. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena*and *Echinogammarus*: 1983-2000. Journal of the North American Benthological Society 24(1): 148-167.

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 61(7): 1285-1293.

Kestrup, A., and A. Ricciardi. 2009. Are interactions among Ponto-Caspian invaders driving amphipod species replacement in the St. Lawrence River? Journal of Great Lakes Research 35:392-398.

Kipp, R., I. Hébert, M. Lacharité, and A. Ricciardi. 2012. Impacts of predation by the Eurasian round goby (*Neogobiusmelanostomus*) on molluscs in the upper St. Lawrence River. Journal of Great Lakes Research 38:78-89.

Kipp, R., and A. Ricciardi. 2012. Impacts of the Eurasian round goby (*Neogobiusmelanostomus*) on benthic communities in the upper St. Lawrence River. Can. J. Fish. Aquat. Sci. 69: 469-486.

Kornis, M.S., N. Mercado-Silva, and M.J. Vander Zanden. 2012. Twenty years of invasion: a review of round goby *Neogobiusmelanostomus*biology, spread and ecological implications. Journal of Fish Biology 80: 235-285.

Krakowiak, P., and C. Pennuto. 2008. Fish and macroinvertebrate communities in tributary streams of eastern Lake Erie with and without round gobies (*Neogobiusmelanostomus,* Pallas 1814). Journal of Great Lakes Research 34:675-689.

Kuhns, L., and M. Berg. 1999. Benthic invertebrate community responses to round goby (*Neogobiusmelanostomus*) and zebra mussel (*Dreissenapolymorpha*) invasion in southern Lake Michigan. J. Great Lakes Res. 25(4): 910-917.

Lauer, T.E., Allen, P.J., McComish, T.S., 2004. Changes in mottled sculpin and Johnny darter trawl catches after the appearance of round gobies in the Indiana waters of Lake Michigan. Trans. Am. Fish. Soc. 133:185-189.

Lauer, T. E., and T. S. McComish. 2001. Impact of zebra mussels (*Dreissenapolymorpha*) on fingernail clams (Sphaeriidae) in extreme southern Lake Michigan. J. Great Lakes Res. 27:230-238.

Lederer, A., Massart, J., Janssen, J., 2006. Impact of round gobies (*Neogobius melanostomus*) on dreissenids (*Dreissenapolymorpha*and *Dreissenabugensis*) and the associated macroinvertebrate community across an invasion front. J. Great Lakes Res. 32: 1-10.

Limén, H, C. D. A van Overdijk, and H. J. MacIsaac. 2005. Food portioning between the amphipods *Echinogammarusischnus, Gammarusfasciatus,* and *Hyalella Azteca* as revealed by stable isotopes. Journal of Great Lakes Research 31:97-104.

Merritt, G.D. 1985. Habitat use by fishes at an artificial reef and surrounding areas in southwestern Lake Ontario. MS Thesis. College of Environmental Science and Forestry, State University of New York, Syracuse, New York.

Mills, E. L., J. M. Casselman, R. Dermott, J. D. Fitzsimons, G. Gal, K. T. Holeck, J. A. Hoyle, O. E. Johannsson, B. F. Lantry, J. C. Makarewicz, E. S. Millard, I. F. Munawar, M. Munawar, R. O'Gorman, R. W. Owens, L. G. Rudstam, T. Schaner, and T. J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970-2000). Can. J. Fish. Aquat. Sci. 60:471-490.

Mills, E. L., J.M. Casselman, R. Dermott, J.D. Fitzsimons, G. Gal, K.T. Holeck, J.A. Hoyle, O.E. Johannsson, B.F. Lantry, J.C. Makarewicz, E.S. Millard, I.F. Munawar, M. Munawar, R. O'Gorman, R.W. Owens, L.G. Rudstam, T. Schaner, and T.J. Stewart. 2005. A Synthesis of Ecological and Fish-Community Changes in Lake Ontario, 1970-2000. Technical Report 67, Great Lakes Fishery Commission, Ann Arbor, Michigan, USA.

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.

Naddafi, R., and L. G. Rudstam. 2014. Predation on invasive zebra mussel, *Dreissenapolymorpha*, by pumpkinseed fish, rusty crayfish, and round goby. Hydrobiologia 721:107-115.

Nalepa, T. F., S. A. Pothoven, and D. L. Fanslow. 2009. Recent changes in benthic macroinvertebrate populations in Lake Huron and impact on the diet of lake whitefish (*Coregonusclupeaformis*). Aquatic Ecosystem Health and Management 12:2-10.

Nalepa, T., D. W. Schloesser, S. A. Pothoven, D. W. Hondorp, D. L. Fanslow, M. L. Tuchman, and G. W. Fleischer. 2001. First finding of the amphipod *Echinogammarusischnus*and the mussel *Dreissena bugensis* in Lake Michigan. Journal of Great Lakes Research 27:384-391.

Palmer, M. E., and A. Ricciardi. 2005. Physical factors affecting the relative abundance of native and invasive amphipods in the St. Lawrence River. Canadian Journal of Zoology 82:1886-1893.

Patterson, M. W. R, J. J. R. Ciborowski, and D. R. Barton. 2002. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie. Journal of Great Lakes Research 31:223-237.

Pennuto, C. M., E. T. Howell, T. W. Lewis, and J. C. Makarewicz. 2012. *Dreissena* population status in Lake Ontario. Journal of Great Lakes Research 38:161-170.

Ozersky, T. D. Barton, and D. Evans. 2011. Fourteen years of dreissenid presence in the rocky littoral zone of a large lake: effects on macroinvertebrate abundance and diversity. Journal of the North American Benthological Society 30(4): 913-922.

Ray, W. J., and L. D. Corkum. 1997. Predation of zebra mussels by round gobies, *Neogobiusmelanostomus*. Environmental Biology of Fish 50:267-273.

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an "invasional meltdown" occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Science 58:2513-2525.

Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecology Letters 9:912-919.

Stewart, T. W. 1993. Benthic macroinvertebrate community changes following zebra mussel colonization of southwestern Lake Ontario. MS Thesis. The College at Brockport, State University of New York, Brockport, NY.

Stewart, T. W., and J. M. Haynes. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario following invasion of Dreissena. J. Great Lakes Res. 20:479–493.

Stewart, T. W., J. G. Miner, and R. L. Lowe. 1998a. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. Journal of the North American Benthological Society 17:81–94.

Stewart, T. W., J. G. Miner, and R. L. Lowe. 1998b. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of Dreissena. Journal of Great Lakes Research 24:868–879.

Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, E. L. Mills, K. T. Holeck, J. R. Liebig, I. A Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Science 59:1209-1228.

vanOverdijk, C. D. A., I. A. Grigorovich, T. Mabee, W. J. Ray, J. J. H. Ciborowski, and H. J. MacIsaac. 2003. Microhabitat selection by the invasive amphipod

*Echinogammarusischnus*and native *Gammarusfasciatus*in laboratory experiments and in Lake Erie. Freshwater Biology 48:567-578.

Walsh, M. G., D. E. Dittman, and R. O'Gorman. 2007. Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. J. Great Lakes Res. 33:83-92.

Ward, J. M., and A. Ricciardi. 2007. Impacts of *Dreissena*invasions on benthic macroinvertebrate communities: a meta-analysis. Diversity and Distributions 13:155-165.

Wilson, K. A., E. T. Howell, and D. A. Jackson. 2006. Replacement of zebra mussels by quagga mussels in the Canadian nearshore of Lake Ontario: the importance of substrate, round goby abundance, and upwelling frequency. International Association for Great Lakes Research 32:11-28.

Table 1. Abundance (SEM) of benthic macroinvertebrates (m^{-2}) collected in 2014 at the cobble and reef habitats.

	July		**September**	
Taxon	**Cobble**	**Reef**	**Cobble**	**Reef**
Annelida				
Oligochaeta	2163.4 (32.0)	1905.0 (60.8)	224.4 (4.5)	59.8 (3.5)
Turbellaria	1.2 (0.1)	62.2 (1.2)	0	20.7 (0.3)
Crustacea				
Isopoda				
Caecidotea	0	8.5 (0.3)	0	1.2 (0.1)
Decapoda				
Cambaridae				
Orconectes	0	11.0 (0.3)	0	0
Amphipoda				

Gammarusfasciatus	45.1 (0.5)	86.6 (1.4)	11.0 (0.54)	29.8 (0.3)
Echinogammarusischnus	169.5 (2.4)	1027.0 (13.8)	33.0 (1.7)	171.5 (3.2)
Hydracarina	68.3 (64.6)	92.7 (31.0)	123.2 (2.6)	90.2 (1.7)
Mollusca				
Bivalvia				
Dreissena	17.1 (0.5)	447.6 (5.8)	6.1 (0.3)	120.7 (1.8)
Insecta				
Trichoptera				
Hydroptilidae	2.4 (0.1)	17.1 (5.6)	0	3.7 (3.7)
Diptera				
Chironomidae	56.1 (26.0)	241.5 (18.5)	70.7(27.0)	190.2 (20.0)

Table 2a. Abundance (SEM) of benthic macroinvertebrates (m^{-2}) at the cobble site, 1983-2014.

Taxa	**1983**	**1991-1992**	**1999-2000**	**2014**
Turbellaria	14.5 (2.5)	21.4 (17.7)	0	0.6 (0.6)
Oligochaeta	26.5 (7.3)	492.2 (227.4)	15.8 (13.4)	1193.9 (969.5)
Hirudinea	0	0.6 (0.6)	12.1 (7.3)	0
Musculium	38.6 (2.5)	68.9 (14.0)	0	0
Dreissena	0	3452.0 (2169.3)	1113.1 (1113.1)	11.6 (5.5)
Gyraulus	0	8.7 (7.5)	4.9 (2.5)	0
Stagnicola	119.9 (99.4)	327.5 (167.7)	447.9 (432.1)	0
Physella	3.6 (3.6)	104.3 (48.2)	265.5 (257.0)	0
Valvata	0	36.6 (31.7)	0	0
Bithynia	0.6 (0.6)	0.6 (0.6)	0.6 (0.6)	0
Amnicola	1.8 (1.8)	638.4 (305.5)	35.2 (35.2)	0
Elimia	103.6 (1.2)	664.7 (515.9)	11.5 (8.0)	0
Gammarus	445.2 (212.7)	1002.5 (667.1)	994.6 (643.1)	28.0 (17.1)

Echinogammarus	0	0	180.0 (157.0)	101.2 (68.3)
Orconectes	1.8 (1.8)	37.2 (20.1)	1.2 (1.2)	0
Ephemeroptera	6.0 (6.0)	11.0 (6.1)	0	0
Trichoptera	18.1 (8.5)	28.1 (9.8)	1.2 (1.2)	1.2 (1.2)
Chironomidae	37.3 (37.3)	26.3 (21.4)	0	63.4 (7.3)
Other	0	25.6 (8.5)	1.2 (1.2)	95.7 (27.4)

Table 2b. Abundance (SEM) of benthic macroinvertebrates (m^{-2}) at the artificial reef, 1983-2014.

Taxa	**1983**	**1991-1992**	**1999-2000**	**2014**
Turbellaria	4.2 (3.0)	61.0 (36.6)	0	41.5 (20.7)
Oligochaeta	0	67.7 (54.3)	0	982.3 (922.6)
Hirudinea	0	0.6 (0.6)	1.2 (1.2)	0
Musculium	0.6 (0.6)	0	0	0
Dreissena	0	19411.9 (10227.6)	2092.0 (525.3)	284.1 (163.4)
Gyraulus	0.6 (0.6)	6.5 (5.0)	0.6 (0.6)	0
Stagnicola	40.4 (30.8)	103.0 (72.3)	337.0 (292.2)	0
Physella	30.7 (29.5)	59.7 (48.5)	160.6 (159.4)	0
Valvata	0	2.5 (2.5)	0	0
Bithynia	1.8 (1.8)	1.4 (0.2)	0	0
Amnicola	0	396.8 (252.0)	43.1 (43.1)	0
Elimnia	171.1 (8.5)	278.5 (182.5)	4.3 (4.3)	0
Gammarus	1106.7 (436.8)	2790.4 (1075.5)	605.5 (78.2)	58.2 (28.4)

Echinogammarus	0	0	536.4 (513.4)	599.1 (427.7)
Orconectes	1.2 (1.2)	3.1 (3.1)	1.2 (1.2)	5.5 (5.5)
Ephemeroptera	0	6.8 (6.8)	0	0
Trichoptera	3.0 (0.6)	61.0 (24.5)	0	10.4 (6.7)
Chironomidae	11.4 (11.4)	3.6 (2.4)	0	215.9 (25.6)
Other	0	1.2 (1.2)	1.2 (1.2)	96.3 (4.9)

Table 3a. Simpson's Diversity over four sampling periods, cobble and reef abundances combined (superscripts indicate whether or not Simpson's Diversity was significantly different from other years).

Year	Diversity
1983	0.475^{a}
1991-1992	0.686^{b}
1999-2000	0.613^{c}
2014	0.377^{d}

Table 3b. Simpson's Diversity of snails over four sampling periods, cobble and reef abundances combined (superscripts indicate whether or not Simpson's Diversity was significantly different from other years).

Year	Diversity
1983	0.525^{a}
1991-1992	0.695^{b}
1999-2000	0.536^{a}
2014	0.000^{c}

Table 4. Average Bray-Curtis similarities between pairs of years (1983, 1991-1992, 1999-2000, 2014), excluding *Dreissena* and *Echinogammarus.*

Year	**1991-1992**	**1999-2000**	**2014**
1983	63.15	54.94	34.68
1991-1992		51.24	40.50
1999-2000			24.50

Table 5. Percent contribution of benthic taxa to average dissimilarities between years (1983, 1991-1992, 1999-2000, 2014), excluding *Dreissena* and *Echinogammarus*. Taxa in bold were the three top contributors to differences between years. Dashes indicate taxa that contributed minimally (<3.0%) to differences between years.

Taxa	**1983 vs. 1991-1992**	**1991-1992 vs. 1999-2000**	**1983 vs. 1999-2000**	**1983 vs. 2014**	**1991-1992 vs. 2014**	**1999-2000 vs. 2014**
Turbellaria	6.25	9.03	**8.53**	6.59	-	5.73
Oligochaeta	**11.12**	**9.99**	-	**13.2**	3.83	**13.92**
Hirudinea	-	-	5.46	-	-	-
Musculium	-	4.75	7.6	5.91	4.32	-
Gyraulus	5.05	3.26	3.92	-	-	-
Stagnicola	4.93	4.48	8.22	11.05	**10.74**	**13.59**
Physella	**8.63**	6.2	**11.37**	5.2	8.79	9.81

Valvata	5.88	4.72	-	-	4.07	-
Bithynia	-	-	-	-	-	-
Amnicola	**18.72**	**10.66**	8.31	-	**13.04**	5.36
Elimnia	3.43	**11.03**	**15.17**	**14.47**	**12.31**	4.42
Gammarus	-	-	3.11	8.64	8.07	8.71
Orconectes	5.71	4.8	-	-	4.97	-
Ephemeroptera	4.53	4.67	-	-	3.9	-
Trichoptera	5.99	9.25	7.42	4.43	4.91	4
Chironomidae	6.08	5.32	7.94	8.83	5.94	**13.65**
Other (isopod and mites)	5.68	3.85	3.03	**13.45**	5.9	11.04

Table 6. Similarities of the benthic macroinvertebrate communities in the cobble and reef habitats in each study year and the two taxa contributing most to similarity, excluding *Dreissena* and *E. ischnus*.

Year	**Average similarity**	**Primary contributing taxon (% contribution)**	**Secondary contributing taxon (% contribution)**
1983	66.85	*Gammarus* (31.12)	*E. livescens* (24.58)
1991-1992	76.45	*Gammarus* (16.02)	*A. limosa* (13.18)
1999-2000	61.11	*Gammarus* (42.50)	*S. catascopium* (25.20)
2014	79.34	Oligochaeta (28.07)	Other (24.41)

Table 7. Analysis of Similarities (ANOSIM) R statistics (P = 0.029) between pairs of years (1983, 1991-1992, 1999-2000, 2014), excluding *Dreissena* and *Echinogammarus*.

Year	**1991-1992**	**1999-2000**	**2014**
1983	0.719	0.583	1.0
1991-1992		0.656	1.0
1999-2000			1.0

Table 8. Chironomid genera that contributed to community similarity in 1991-1992 and 2014, excluding unidentified taxa. Bolded numbers represent the top 3 genera in each community and year that contributed to community similarity.

Contributing genera	**1991-1992**	**2014**
Chironomus	-	10.93
Dicrotendipes	-	**24.18**
Micropsectra	-	5.14
Microtendipes	-	8.30
Orthocladius-Cricotopus	**67.56**	8.08
Paratanytarsus	-	7.32
Polypedilum	-	5.85
Procladiusholotanypus	-	5.62
Psectrocladius	**18.44**	**10.97**
Tanytarsus	-	**12.55**
*Thienemannimyia*group	**14.00**	**-**

Table 9. Mean (SEM) low, high, and average air temperatures (°F) and precipitation (cm/d) collected from the Buffalo Weather Station 30 d prior to sampling in July and September of each sampling year.

	Minimum Temperature		**Maximum Temperature**		**Average Temperature**		**Average Precipitation**	
	July	**Sept**	**July**	**Sept**	**July**	**Sept**	**July**	**Sept**
1983	64.3 (1.2)	53.5 (1.8)	84.1 (1.0)	73.8 (1.5)	74.2 (1.0)	63.7 (1.6)	0.2 (0.1)	0.2 (0.1)
1991-1992	60.5 (1.2)	58.2 (1.4)	80.9 (1.1)	79.7 (1.4)	70.7 (1.0)	69.0 (1.3)	0.2 (0.1)	0.1 (0.03)
1999-2000	59.9 (1.5)	57.7 (1.3)	79.2 (1.5)	75.9 (1.2)	69.5 (1.4)	66.8 (1.1)	0.1 (0.1)	0.4 (0.2)
2014	61.8 (1.1)	59.7 (1.1)	78.9 (0.9)	76.6 (1.3)	70.7 (0.9)	68.4 (1.1)	0.3 (0.1)	0.3 (0.1)

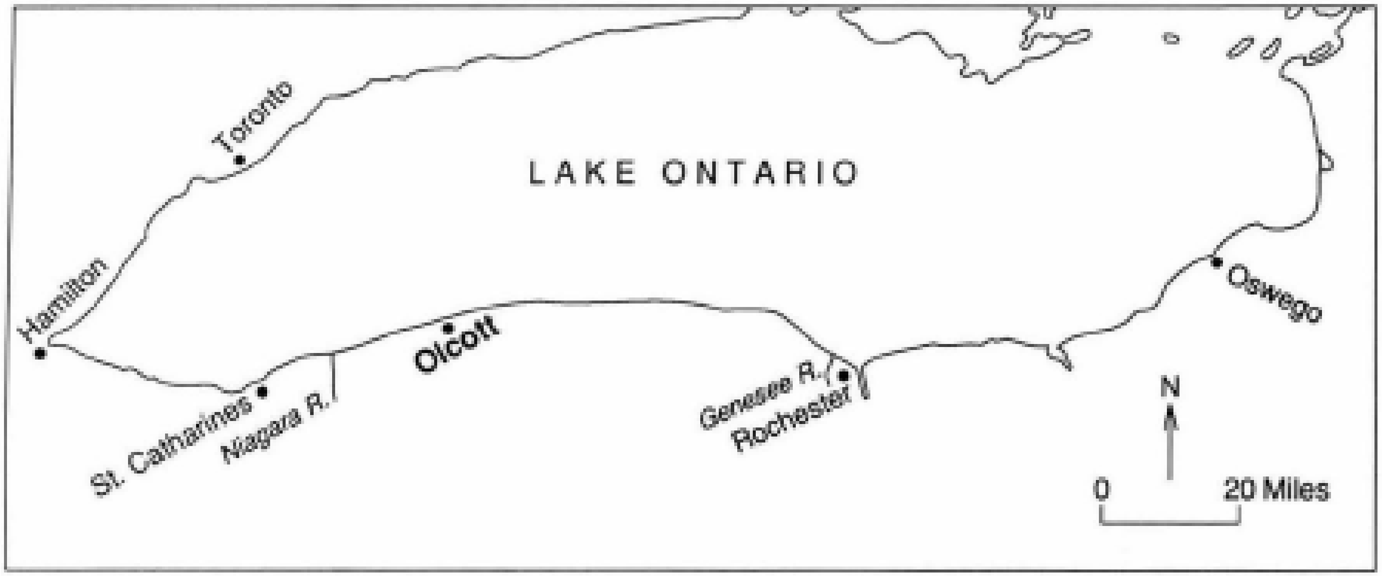

Figure 1. Map of Lake Ontario showing approximate location of the study area (Olcott, NY). Source: Stewart (1993).

Figure 2. Map of sampling locations in July and September 2014. In July the reef and cobble sites were sampled on consecutive days (vs. both on one day in September). On the second day in July a seiche put extremely cold water on the reef and long-term cobble site, so similar cobble habitat in warmer water closer to shore was sampled.

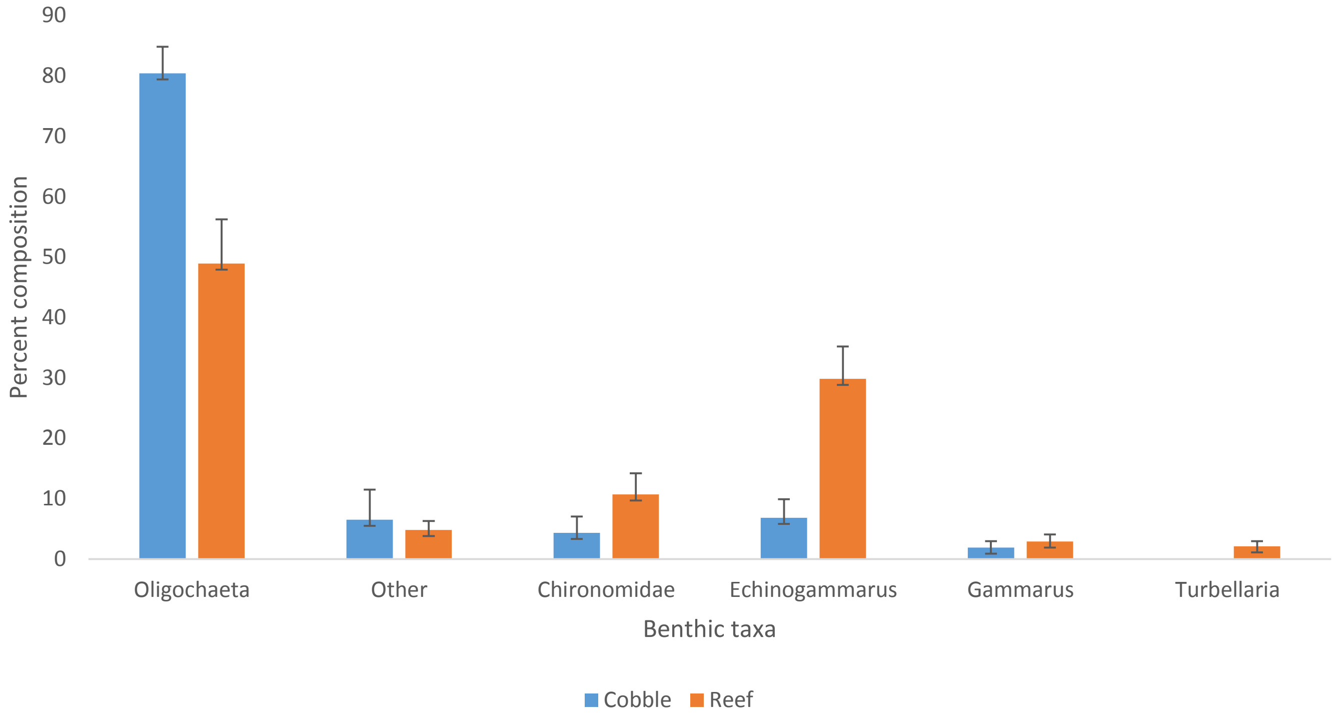

Figure 3. Percent composition (±1 SE) of non-dreissenid macroinvertebrate taxa at the cobble and artificial reef habitats in 2014.

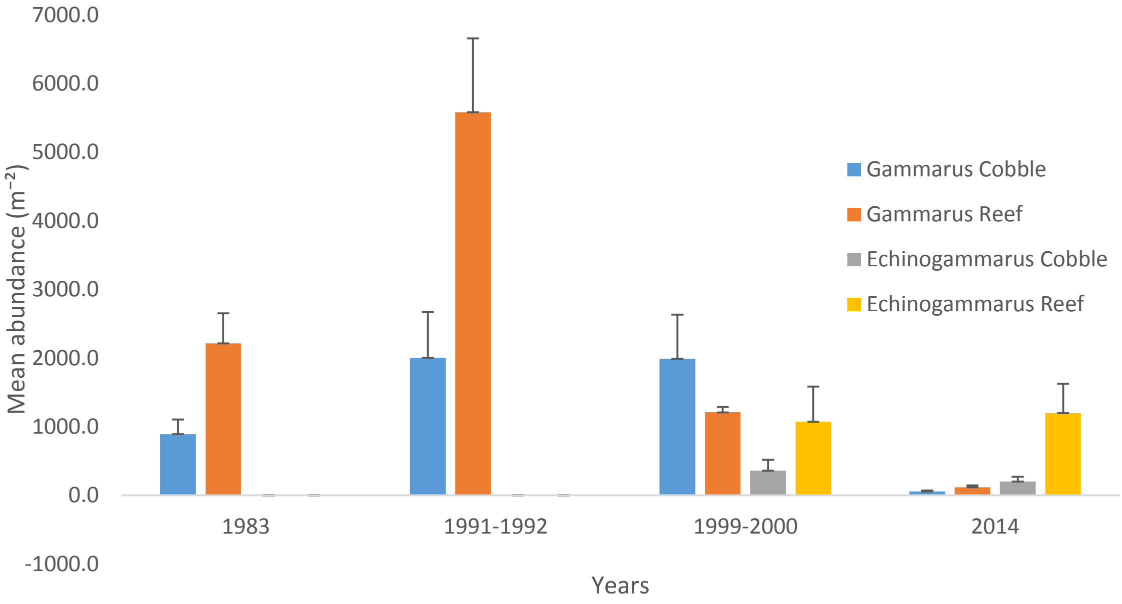

Figure 4. Mean abundance (±1 SE) of *G. fasciatus* and *E. ischnus* at the cobble and reef habitats, 1983-2014.

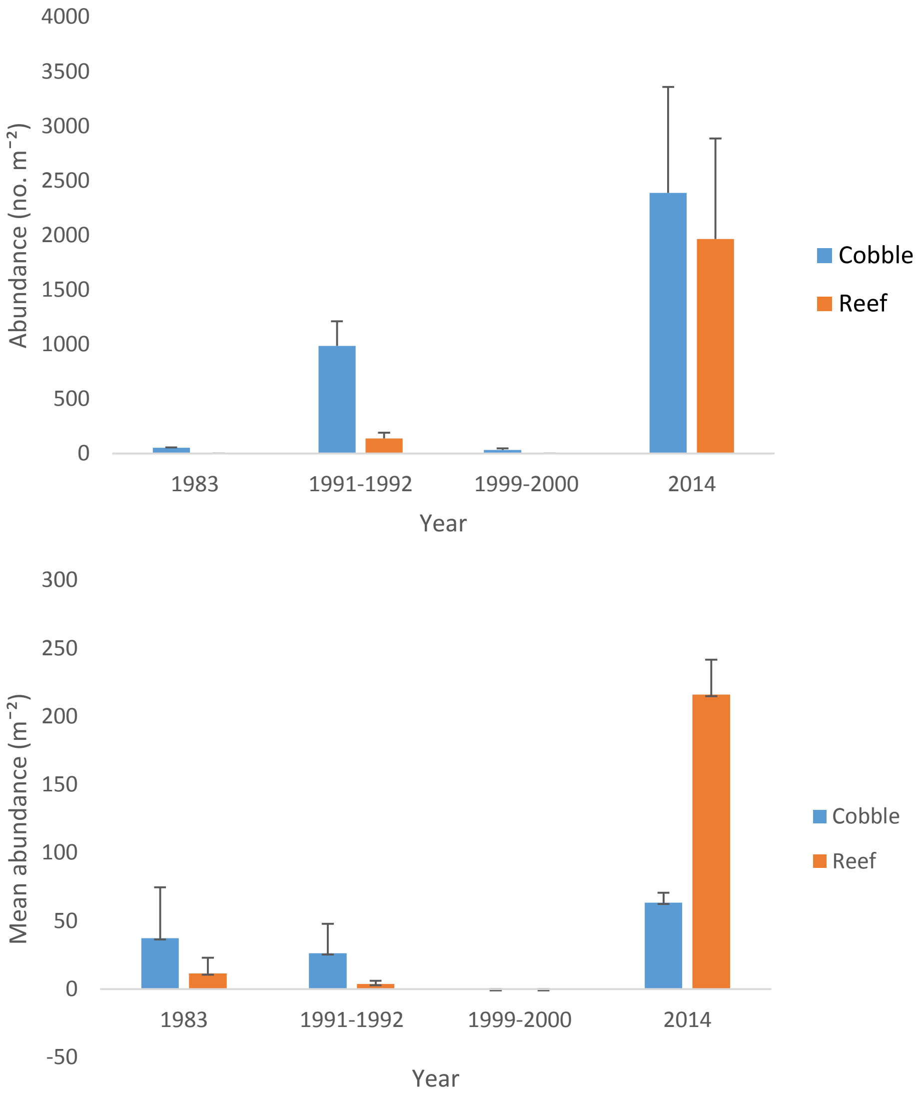

Figure 5. Mean abundance (±1 SE) of oligochaetes (top) and chironomids (bottom) at the cobble and reef habitats, 1983-2014.

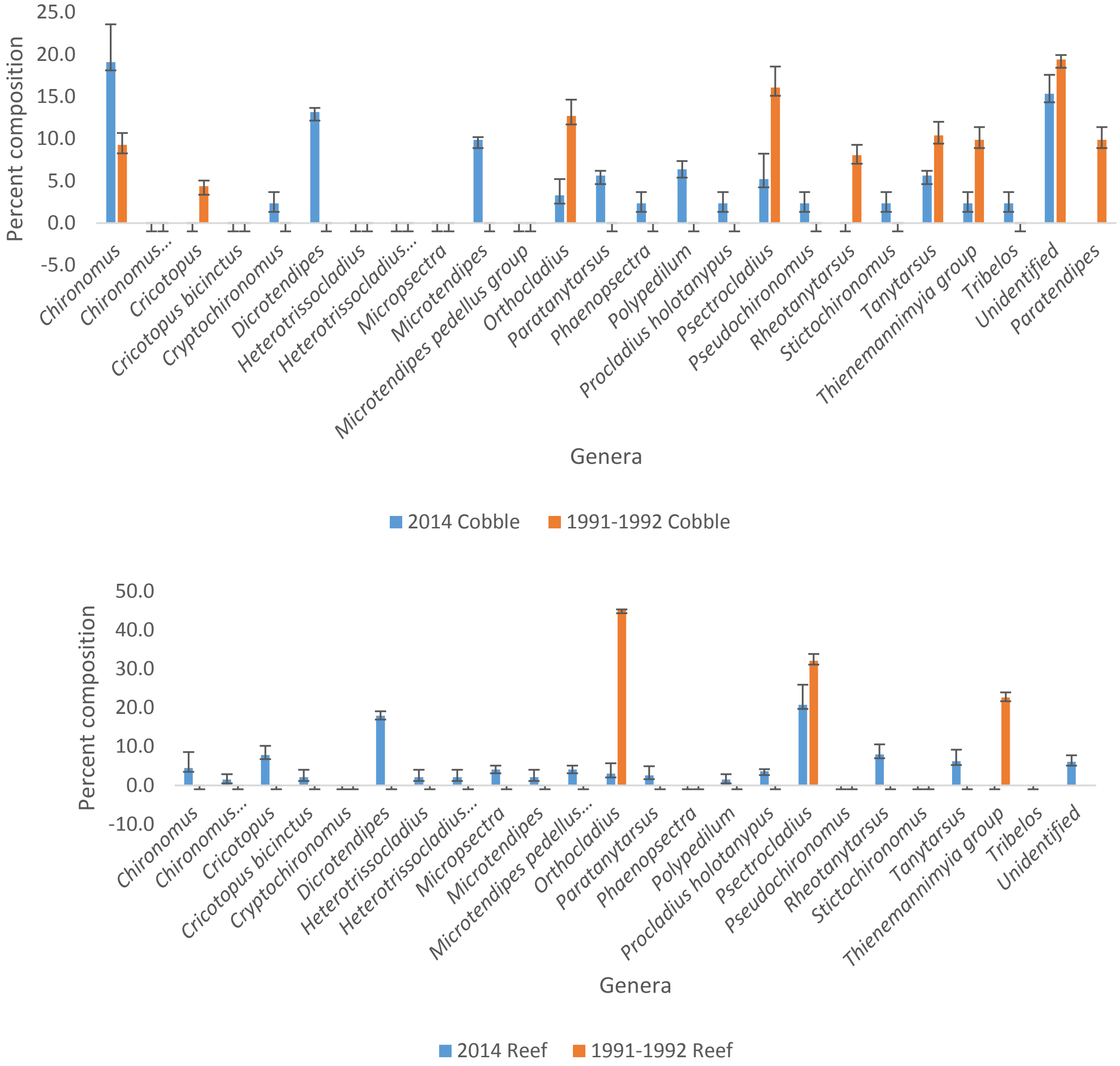

Figure 6. Percent composition (±1 SE) of chironomid genera at the cobble (top) and reef (bottom) habitats sampled in 1991-1992 and 2014.

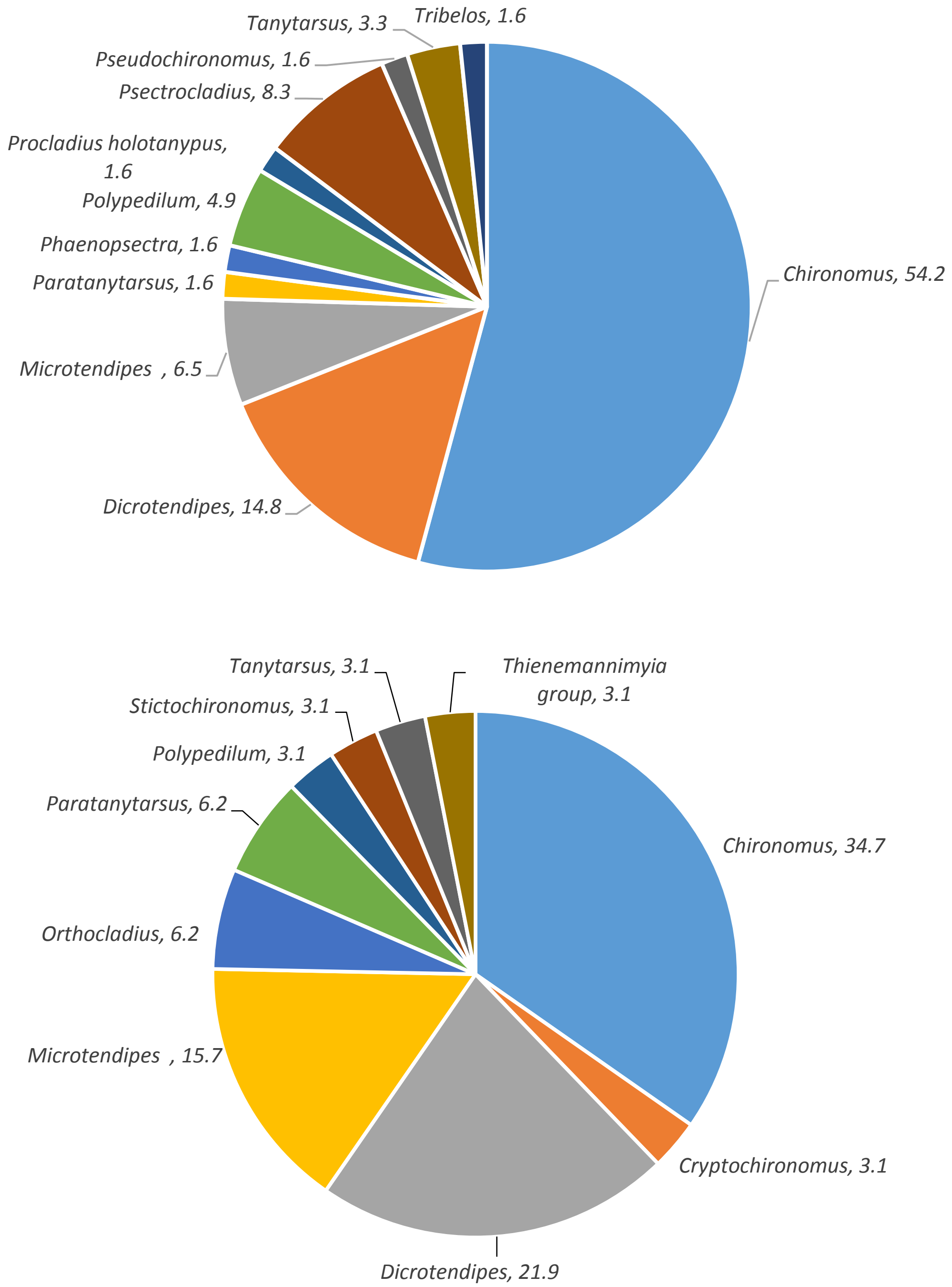

Figure 7. Percent composition of the chironomid genera at the cobble habitat on July 20 (top) and September 14, 2014 (bottom) (unidentified taxa excluded).

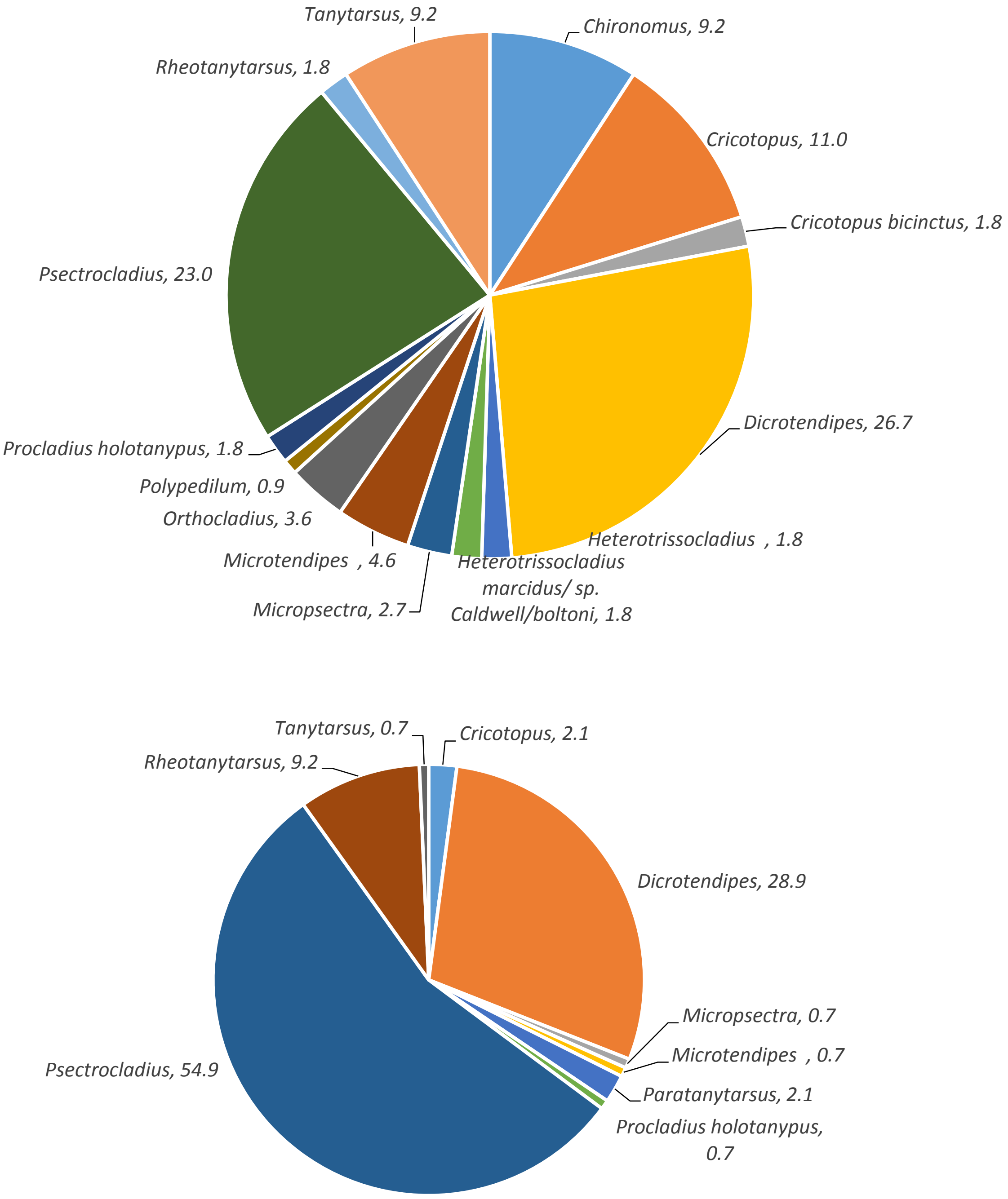

Figure 8. Percent composition of chironomid genera at the artificial reef on July 19, 2014 (top) and September 14, 2014 (bottom) (unidentified taxa excluded).

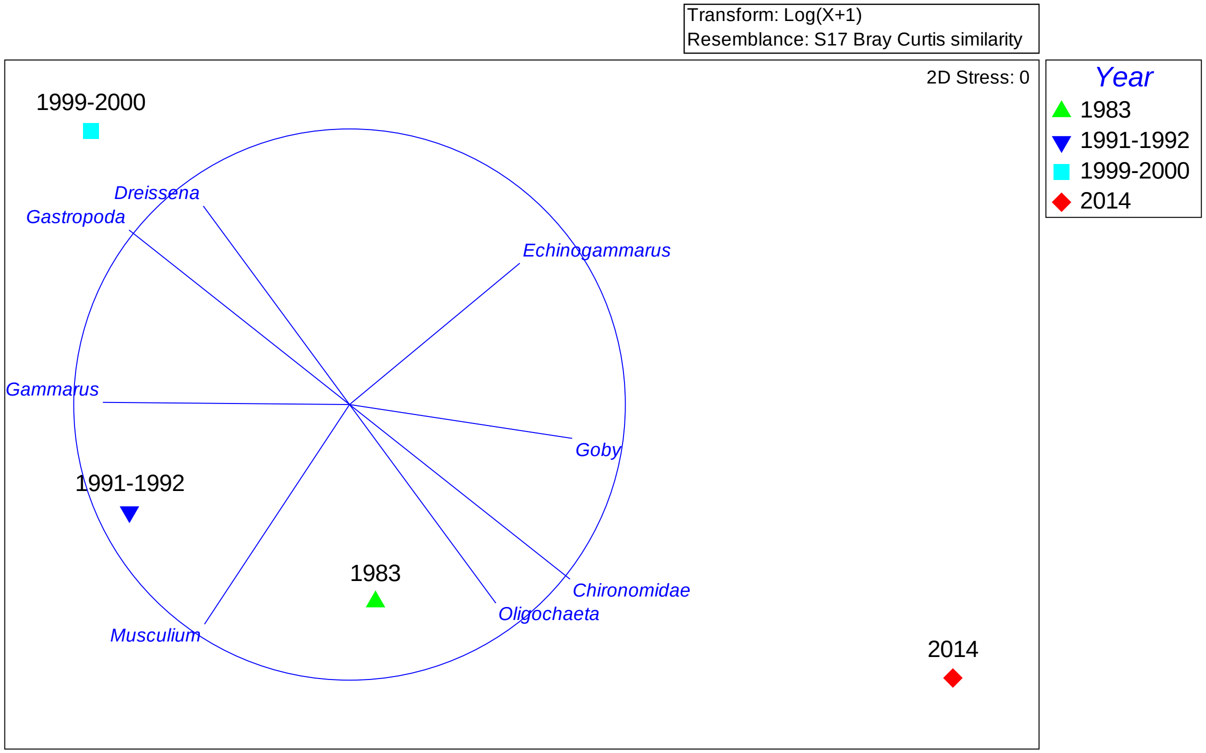

Figure 9. Nonmetric multi-dimensional scaling (nMDS) of the benthic macroinvertebrate communities, 1983-2014, with months and habitats combined, for a total of 4 data points in ordination space, and taxa as vectors on the ordination plot.

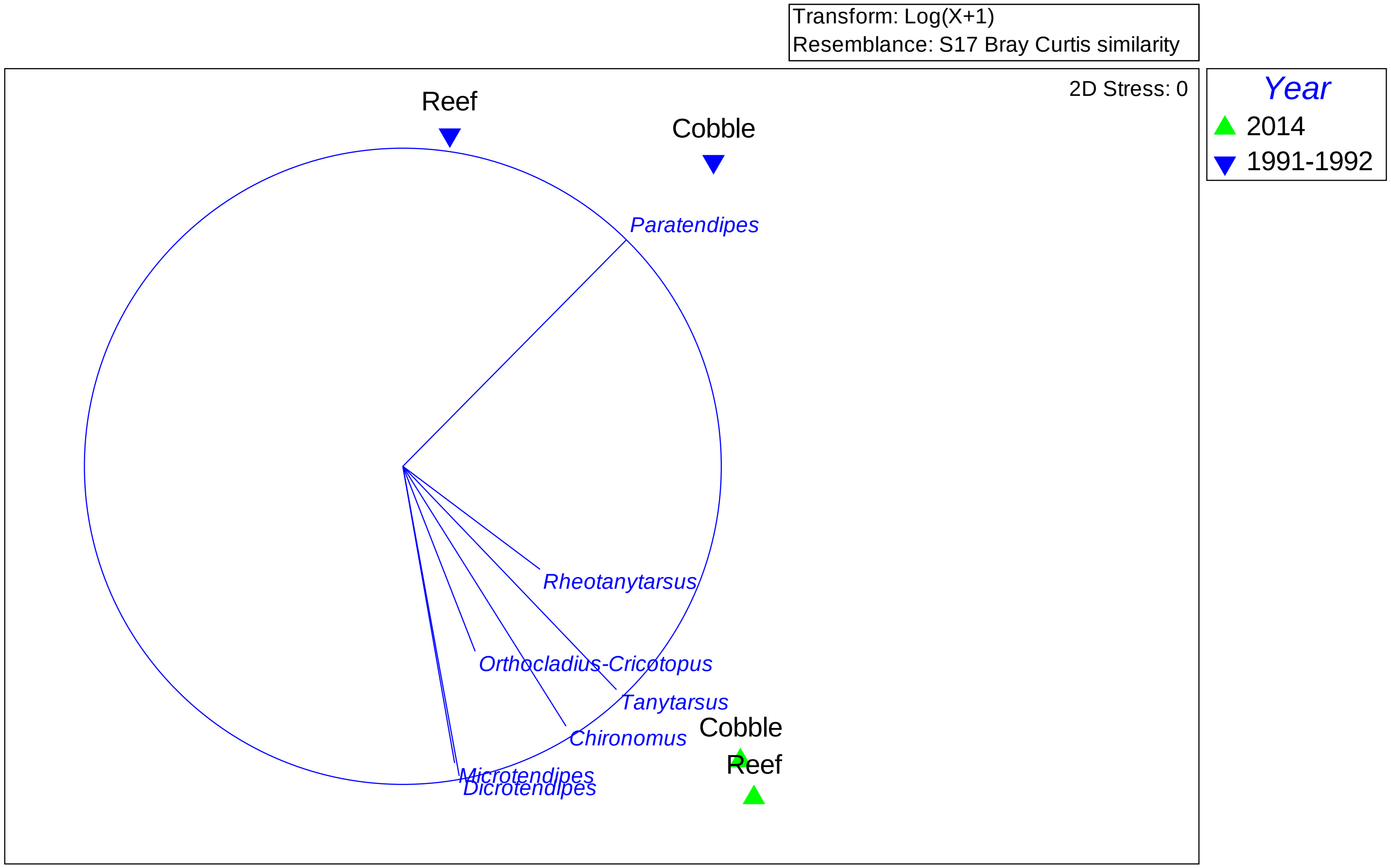

Figure 10. Nonmetric multi-dimensional scaling (nMDS) of the chironomid communities at the cobble and reef habitats in 1991-1992 and 2014, with selected genera as vectors on the ordination.

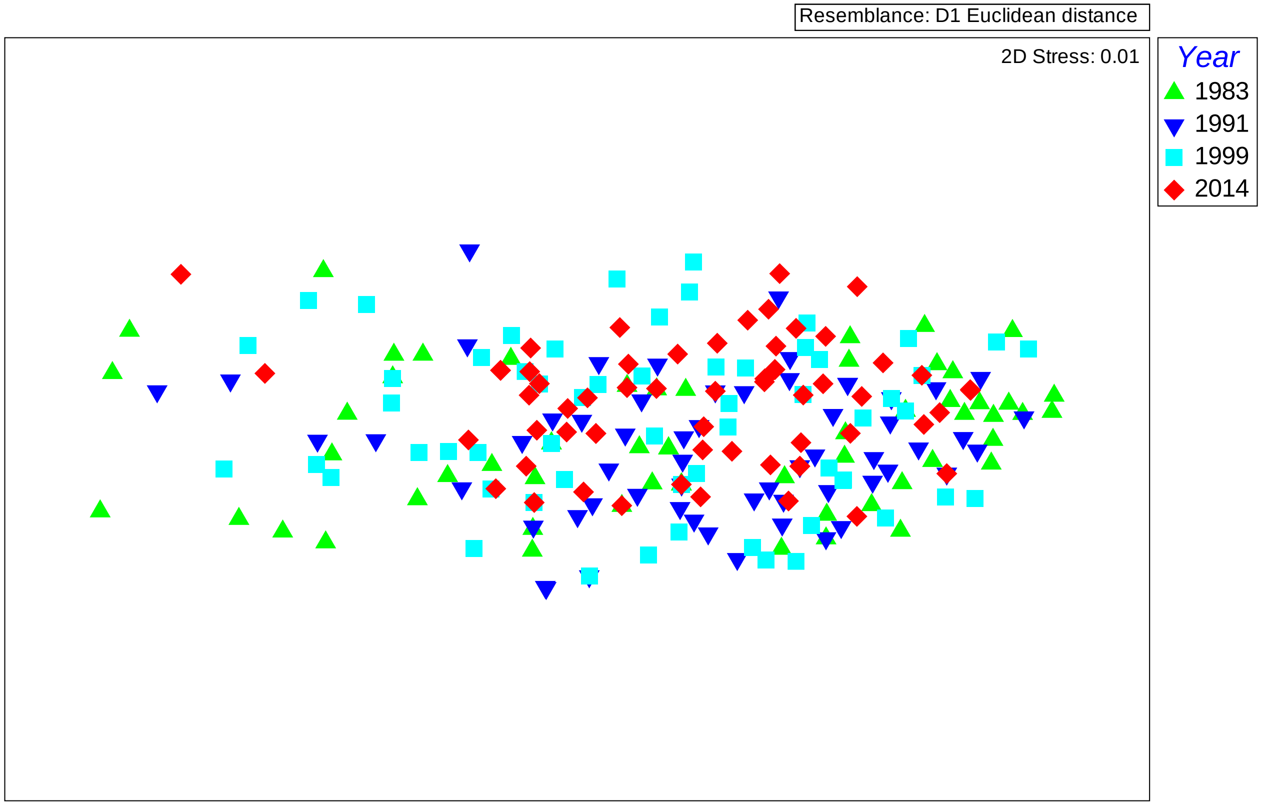

Figure 11. nMDS plot of air temperature and precipitation 30 d prior to sampling in July and September of each year, with July and September data combined in each year.

Appendices

Appendix 1a. Benthic macroinvertebrate abundances at the cobble site, July 20, 2014, by replicate sample.

Taxon	**Rep. 1**	**Rep. 2**	**Rep. 3**	**Rep. 4**	**Rep. 5**	**Mean (SEM)**
Annelida						
Oligochaeta	1091.5	1835.4	2567.1	1689	3634.1	2163.4(32.0)
Platyhelminthes						
Turbellaria	0	6.1	0	0	0	1.2(0.1)
Mollusca						
Bivalvia						
Dreissenidae						
Dreissena bugensis	0	18.3	6.1	30.5	30.5	17.1(0.5)
Arthropoda						
Crustacea						
Amphipoda						
Gammaridae						
Gammarus fasciatus	67.1	54.9	42.7	24.4	36.6	45.1(0.5)
Echinogammarus ischnus	158.5	292.7	164.6	103.7	128.04	169.5(2.4)
Isopoda						
Asellidae						
Caecidotea	0	0	0	0	0	0
Decapoda						
Cambaridae						
Orconectes	0	0	0	0	0	0
Hydracarina	24.2	54.5	36.4	42.4	181.8	67.9 (64.6)

Insecta						
Trichoptera						
Hydroptilidae	6.1	6.1	0	0	0	2.4(0.1)
Diptera						
Chironomidae						
Chironomus	0	0	12.2	0	24.4	13.5(2.3)
Chironomusriparius/crassicaudatus	0	0	0	0	0	0
Cricotopus	0	0	0	0	0	0
Cricotopusbicinctus	0	0	0	0	0	0
Cryptochironomus	0	0	0	0	6.1	1.2(0.55)
Dicrotendipes	0	12.2	12.2	0	18.3	8.5(1.6)
Heterotrissocladius	0	0	0	0	0	0
H. marcidus/sp. Caldwell/boltoni	0	0	0	0	0	0
Micropsectra	0	0	0	0	0	0
Microtendipes	0	0	6.1	0	24.3	6.1(2.1)
Orthocladius	0	6.1	0	0	6.1	2.4(0.67)
Paratanytarsus	0	12.2	0	0	0	2.4(1.2)
Phaenopsectra	0	0	0	0	0	0
Polypedilum	0	0	0	0	6.1	1.2(0.55)
Procladius holotanypus	0	0	0	0	0	0
Psectrocladius	0	0	0	0	0	0
Pseudochironomus	0	0	0	0	0	0
Rheotanytarsus	0	0	0	0	0	0
Stictochironomus	0	0	0	0	6.1	1.2(0.55)
Tanytarsus	0	6.1	0	0	0	1.2(0.55)
Thienemannimyia group	0	0	0	0	6.1	1.2(0.55)
Tribelos	0	0	0	0	0	0
Unidentified	36.6	0	6.1	36.6	24.3	20.6(3.4)

Appendix 1b. Benthic macroinvertebrate abundances at the cobble site, September 14, 2014, by replicate sample.

Taxon	**Rep. 1**	**Rep. 2**	**Rep. 3**	**Rep. 4**	**Rep. 5**	**Mean (SEM)**
Annelida						
Oligochaeta	396.3	97.6	311	79.3	237.8	224.4(4.5)
Platyhelminthes						
Turbellaria	0	0	0	0	0	0
Mollusca						
Bivalvia						
Dreissenidae						
Dreissena bugensis	0	0	18.3	12.2	0	6.1(0.3)
Arthropoda						
Crustacea						
Amphipoda						
Gammaridae						
Gammarus fasciatus	18.3	0	36.6	0	0	11.0(0.54)
Echinogammarus ischnus	6.1	0	122	12.2	24.4	33.0(1.7)
Isopoda						
Asellidae						
Caecidotea	0	0	0	0	0	0
Decapoda						
Cambaridae						
Orconectes	0	0	0	0	0	0
Hydracarina	152.4	48.8	48.8	237.8	128	123.2(2.6)
Insecta						

Trichoptera						
Hydroptilidae	0	0	0	0	0	0
Diptera						
Chironomidae						
Chironomus	72.7	36.6	30.3	24.3	36.6	40.0(3.8)
Cricotopus	0	0	0	0	0	0
Cricotopusbicinctus	0	0	0	0	0	0
Cryptochironomus	0	0	0	0	0	0
Dicrotendipes	42.4	0	0	0	12.2	11.0(3.7)
Heterotrissocladius	0	0	0	0	0	0
H. marcidus/sp. Caldwell/boltoni	0	0	0	0	0	0
Micropsectra	0	0	0	0	0	0
Microtendipes	18.3	6.1	0	0	0	4.8(1.6)
Orthocladius	0	0	0	0	0	0
Paratanytarsus	0	0	0	6.1	0	1.2(0.54)
Phaenopsectra	0	0	0	0	6.1	1.2(0.54)
Polypedilum	0	0	0	0	18.3	3.6(1.6)
Procladiusholotanypus	0	6.1	0	0	0	1.2(0.54)
Psectrocladius	12.2	0	12.2	0	6.1	6.1(1.2)
Pseudochironomus	0	0	6.1	0	0	1.2(0.54)
Rheotanytarsus	0	0	0	0	0	0
Stictochironomus	0	0	0	0	0	0
Tanytarsus	6.1	0	6.1	0	0	2.4(0.66)
Thienemannimyia	0	0	0	0	0	0
Tribelos	6.1	0	0	0	0	1.2(0.54)
Unidentified	24.4	6.1	0	0	6.1	7.3(2.0)

Appendix 1c. Benthic macroinvertebrate abundances at the artificial reef, July 19, 2014, by replicate sample.

Taxon	**Rep.1**	**Rep. 2**	**Rep. 3**	**Rep. 4**	**Rep. 5**	**Mean (SEM)**
Annelida						
Oligochaeta	463.4	664.6	1475.6	1859.8	5061	1904.9 (60.8)
Platyhelminthes						
Turbellaria	24.4	54.9	115.9	79.3	36.6	62.2(1.2)
Mollusca						
Bivalvia						
Dreissenidae						
Dreissena bugensis	286.6	298.8	487.8	445.1	719.5	447.6(5.8)
Arthropoda						
Crustacea						
Amphipoda						
Gammaridae						
Gammarus fasciatus	146.3	97.6	79.3	79.3	30.5	86.6(1.4)
Echinogammarus ischnus	567.1	780.5	9	1676.8	1146.3	1026.8(13.8)
Isopoda						
Asellidae						
Caecidotea	24.4	0	6.1	12.2	0	8.5(0.3)
Decapoda						
Cambaridae						
Orconectes	6.1	6.1	24.4	18.3	0	11.0(0.3)
Hydracarina	60.6	12.1	60.6	151.5	175.8	92.1 (30.7)
Insecta						

Trichoptera						
Hydroptilidae	18.3	6.1	18.3	6.1	36.6	17.1(0.4)
Diptera						
Chironomidae						
Chironomus	0	48.5	0	0	6.1	12.1(4.2)
Chironomusriparius crassicaudatus	0	0	0	0	6.1	1.2(0.55)
Cricotopus	48.5	12.2	6.1	0	6.1	14.5(3.9)
Cricotopus bicinctus	0	0	0	0	12.2	2.4(1.1)
Cryptochironomus	0	0	0	0	0	0
Dicrotendipes	66.7	24.4	7	0	18.3	35.1(8.2)
Heterotrissocladius	6.1	6.1	0	0	0	2.4(0.66)
H. marcidus/ sp. Caldwell/boltoni	0	0	0	1	0	2.4(1.1)
Micropsectra	0	0	6.1	0	12.2	3.6(1.1)
Microtendipes	12.2	12.2	6.1	0	0	6.0(0.66)
Orthocladius	0	0	12.2	6.1	6.1	4.8(1.01)
Paratanytarsus	0	0	0	0	0	0
Phaenopsectra	0	0	0	0	0	0
Polypedilum	0	6.1	0	0	0	1.2(0.5)
Procladiusholotanypus	6.1	0	0	0	6.1	2.4(0.55)
Psectrocladius	36.6	6.1	18.3	78.8	12.3	30.3(5.9)
Pseudochironomus	0	0	0	0	0	0
Rheotanytarsus	0	6.1	0	6.1	6.1	2.4(0.66)
Stictochironomus	0	0	0	0	0	0
Tanytarsus	6.1	12.2	0	18.3	24.4	12.1(1.9)
Thienemannimyia group	0	0	0	0	0	0
Tribelos	0	0	0	0	0	0
Unidentified	0	0	6.1	0	6.1	2.4(0.66)

Appendix 1d. Benthic macroinvertebrate abundances at the artificial reef, September 14, 2014, by replicate sample.

Taxon	**Rep. 1**	**Rep. 2**	**Rep. 3**	**Rep. 4**	**Rep. 5**	**Mean (SEM)**
Annelida						
Oligochaeta	0	42.7	250	0	6.1	59.8(3.5)
Platyhelminthes						
Turbellaria	42.7	6.1	30.5	18.3	6.1	20.7(0.5)
Mollusca						
Bivalvia						
Dreissenidae						
Dreissena bugensis	61	146.3	109.8	85.4	201.2	120.7(1.8)
Arthropoda						
Crustacea						
Amphipoda						
Gammaridae						
Gammarus fasciatus	30.5	26.8	18.3	36.6	36.6	29.8(0.3)
Echinogammarus ischnus	219.5	58.5	146.3	122	311	171.5(3.2)
Isopoda						
Asellidae						
Caecidotea	6.1	0	0	0	0	1.2(0.1)
Decapoda						
Cambaridae						
Orconectes	0	0	0	0	0	0
Hydracarina	128.05	48.8	164.6	54.9	54.9	90.2(1.7)
Insecta						
Trichoptera						
Hydroptilidae	0	0	0	0	18.3	3.7(0.3)

Diptera						
Chironomidae						
Chironomus	0	0	0	0	0	0
C. riparius/crassicaudatus	0	0	0	0	0	0
Cricotopus	12.2	0	0	0	6.1	3.6(1.1)
C. bicinctus	0	0	0	0	0	0
Cryptochironomus	0	0	0	0	0	0
Dicrotendipes	42.4	42.4	48.5	60.6	54.5	49.7(1.6)
Heterotrissocladius	0	0	0	0	0	0
H. marcidus/sp. Caldwell/boltoni	0	0	0	0	0	0
Micropsectra	0	0	0	0	6.1	1.2(0.54)
Microtendipes/pedellus group	0	0	0	0	6.1	1.2(0.54)
Orthocladius	0	0	0	0	0	0
Paratanytarsus	12.2	0	0	6.1	0	3.6(1.1)
Phaenopsectra	0	0	0	0	0	0
Polypedilum	0	0	0	0	0	0
Procladius	6.1	0	0	0	0	1.2(0.54)
Psectrocladius	115.1	97	72.7	48.5	139.4	94.5(7.1)
Pseudochironomus	0	0	0	0	0	0
Rheotanytarsus	18.3	24.4	18.3	0	18.3	15.8(1.8)
Stictochironomus	0	0	0	0	0	0
Tanytarsus	0	0	6.1	0	0	1.2(0.54)
Thienemannimyia group	0	0	0	0	0	0
Tribelos	0	0	0	0	0	0
Unidentified	0	6.1	0	18.3	18.3	8.5(1.8)

Appendix 2. Chironomid genera present at the cobble and reef sites in 1983, 1991-1992, and 2014. FFG refers to functional feeding guild (C-G, collector-gatherer; P, predator; C-F, collector-filterer; SCR, scraper; SHR, shredder).

Tribe	Genera	FFG	1983	1991-1992	2014
Chironomini	*Chironomus*	C-G	x	x	x
	Cryptochironomus	P			x
	Dicrotendipes	C-G, C-F	x		x
	Microtendipes	C-F, C-G	x		x
	Phaenopsectra	SCR	x		x
	Polypedilum	SHR			x
	Pseudochironomus	C-G			x
	Stictochironomus	C-G, SHR			x
	Tribelos	C-G			x
	Endochironomus	SHR, C-G, C-F	x		
	Glyptotendipes	SHR, C-G, C-F	x		
	Parachironomus	P, C-G	x		
	Paratendipes	C-G	x	x	
Orthocladiinae	*Heterotrissocladius*	C-G	x		x
	Orthocladius/Cricotopus	C-G, SHR	x	x	x
	Psectrocladius	C-G, SHR	x	x	x
	Nanocladius	C-G	x		
	Synorthocladius	C-G	x		
Tanypodinae	*Thienemannimyia group*	P	x	x	x
	Procladiusholotanypus	P	x		x
Tanytarsini	*Micropsectra*	C-G	x		x
	Paratanytarsus	?	x		x
	Rheotanytarsus	C-F	x	x	x
	Tanytarsus	C-F, C-G	x	x	x

Appendix 3. Replicate sample and mean *Dreissena* abundance estimates at the cobble and artificial reef sites, 2014.

			Cobble			
Date	**Rep. 1**	**Rep. 2**	**Rep. 3**	**Rep. 4**	**Rep. 5**	**Mean (SE)**
7/20/2014	0	18.3	6.1	30.5	30.5	17.1 (6.22)
9/14/2014	0	0	18.3	12.3	0	6.1 (3.9)
			Reef			
7/19/2014	286.6	298.8	487.8	445.1	719.5	447.6 (78.6)
9/14/2014	61.0	146.3	109.8	85.4	201.2	120.7 (24.6)

Appendix 4. Replicate sample and mean *Dreissena* biomass estimates at the cobble and reef sites, 2014.

			Cobble			
Date	**Rep.1**	**Rep. 2**	**Rep. 3**	**Rep. 4**	**Rep. 5**	**Mean (SE)**
7/20/2014	0	7.2	3.5	11.4	1.1	4.6 (2.1)
9/14/2014	0	0	8.5	5.7	0	2.8 (1.79)
			Reef			
7/19/2014	54.7	57.03	93.1	85.0	137.3	85.4 (15.0)
9/14/2014	10.4	25.02	36.4	26.8	34.4	26.6 (4.59)