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Thirty years of change in a benthic macroinvertebrate community of southwestern Lake Ontario after invasion by four Ponto-Caspian species

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Abstract: Beginning in the mid-1980s, the Laurentian Great Lakes underwent successive invasions by Ponto-Caspian species. We quantified major changes in the diversity and relative abundance of pre-invasion benthic macroinvertebrates at the same study site in southwestern Lake Ontario from 1983–2014. The zebra mussel *Dreissena polymorpha* Pallas arrived at the study site before 1991, the quagga mussel *Dreissena rostriformis bugensis* Andrusov and the amphipod *Echinogammarus ischnus* Stebbing arrived before 1999, and the Round Goby *Neogobius melanostomus* Pallas arrived about 2004. The macroinvertebrate community in 2014 was very different from 3 earlier communities in 1983, 1991, and 1999. In 2014, pulmonate and prosobranch snails and sphaeriid bivalves were absent, *D. r. bugensis* replaced *D. polymorpha*, *E. ischnus* replaced *Gammarus fasciatus* Say as the dominant amphipod, and a previously diverse community of benthic fish was replaced by abundant *N. melanostomus*. From 1983 to 1999, the relative abundance of prosobranchs and pulmonates declined 10-fold and rose 2-fold, respectively. From 1991 to 2014, the relative abundance of oligochaetes and chironomids increased 32- and 78-fold, respectively. The shifts we report probably are attributable to nutrient enrichment of the nearshore of Lake Ontario during the 1990s leading to a thick carpet of macroalgae, a change in the base of the benthic food web from dreissenid feces and pseudofeces to macroalgal detritus, and predation by *N. melanostomus* on snails.

Key words: benthic macroinvertebrates, *Dreissena*, *Echinogammarus ischnus*, *Neogobius melanostomus*, invasion ecology, temporal change, Lake Ontario.

Successive invasions by Ponto-Caspian species in the Laurentian Great Lakes have long been a concern, especially when such invasions affect the structure or function of benthic macroinvertebrate communities (Mills et al. 1993). As the number of invasive species in the Great Lakes has increased, short- and long-term effects on pre-invasion Great Lakes ecosystems have been noted (Ricciardi 2001). Following their introduction to Lake Ontario in the late 1980s, zebra (*Dreissena polymorpha* Pallas) and quagga (*D. rostriformis bugensis* Andrusov) mussels dramatically changed the nearshore benthos of Lake Ontario physically and biologically, and these changes profoundly influenced macroinvertebrate communities (Mills et al. 2005, Ozersky et al. 2011).

Within a few years of the zebra mussel invasion of the nearshore of Lake Ontario, the amphipod *Gammarus fasciatus* Say and snails increased in abundance (Stewart and Haynes 1994). Such increases of pre-invasion taxa were attributed to modification by zebra mussels of habitat by shell-building and nutrient-enrichment from feces and pseudofeces (Vanderploeg et al. 2002). Dense dreissenid colonies provide attachment surfaces for algae and foraging space and refuge for amphipods, turbellarians, and oligochaetes (Stewart et al. 1998, Vanderploeg et al. 2002). However, the immediate benefits of dreissenids coincided with the decline of pre-invasion unionid and sphaeriid bivalves, probably because dreissenids have high rates of filtration of suspended food particles (Lauer and McComish 2001). The

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combined increase in benthic habitat complexity and food supply consequent to ecosystem engineering by dreissenids led to positive changes in macroinvertebrate diversity from 1991 to 2000 at one nearshore site in southwestern Lake Ontario (Stewart 1993, Stewart and Haynes 1994, Haynes et al. 1999, 2005).

Zebra and quagga mussels also provide ideal habitat and foraging space for the exotic euryhaline amphipod (*Echinogammarus ischnus* Stebbing), which coevolved with dreissenids in the Ponto-Caspian region of eastern Europe (Dermott et al. 1998). *Echinogammarus ischnus* entered Lake Erie in 1994 and is now commonly associated with dreissenid colonies in the Laurentian Great Lakes (González and Burkart 2004). In its introduced habitat, especially at the outlet of the Niagara River, *E. ischnus* became the dominant amphipod within a 1-y period (Dermott et al. 1998), and van Overdijk et al. (2003) suggested that *E. ischnus* would replace *G. fasciatus* as the dominant amphipod in the nearshore elsewhere in the Great Lakes. The establishment and expansion of *E. ischnus* in the Great Lakes may be facilitated by zebra and quagga mussels because dreissenids occur with *E. ischnus* in their native Ponto-Caspian habitats (van Overdijk et al. 2003). In turn, the establishment of *E. ischnus* and dreissenids may have facilitated the invasion of the Round Goby (*Neogobius melanostomus* Pallas), which coevolved with dreissenids and *Echinogammarus* in the Ponto-Caspian region (DeVanna et al. 2011).

The Round Goby, first reported in the St. Clair River in 1990 (Lederer et al. 2006), probably arrived in Lake Ontario in 2003 (Walsh et al. 2007). Their rapid spread in the Great Lakes probably was facilitated by the presence of dreissenid mussels, a favored prey item (Vanderploeg et al. 2002). A generalist predator, the Round Goby possesses molariform pharyngeal teeth that allow it to consume an increasing proportion of zebra and quagga mussels as it matures (Ray and Corkum 1997, French and Jude 2001, Brush et al. 2012, Kipp and Ricciardi 2012).

In the Great Lakes, the Round Goby has been implicated in reducing macroinvertebrate abundance and changing predator feeding behavior (Kuhns and Berg 1999, Barton et al. 2005, Lederer et al. 2006). Dermott et al. (2012) suggested that the Round Goby probably was responsible for the decline in epibenthic species in the Bay of Quinte (northeastern Lake Ontario) because it exploits nonshelled taxa, such as chironomid midges (Chironomidae) and gammarid amphipods (Gammaridae) (Brush et al. 2012). Steep population declines of abundant Mottled Sculpin (*Cottus bairdi* Girard) and Johnny Darter (*Etheostoma nigrum* Rafinesque) in the early 2000s coincided with the expansion of the Round Goby in southern Lake Michigan (Lauer et al. 2004). Round Gobies may negatively affect Mottled Sculpins by out-competing them for food, habitat, and spawning sites (Lauer et al. 2004). From 1983 to 2000 before the Round Goby arrived in the early 2000s, Mottled Sculpins and Johnny Darters were common at our Lake Ontario study site (Haynes 1995).

Previous investigations of Round Goby effects on Great Lakes macroinvertebrate communities were done without the benefit of site-specific, long-term data sets. Here, we compare the macroinvertebrate community at a location in southwestern Lake Ontario that was first sampled in 1983 before invasions by 4 Ponto-Caspian species. The objective of our study was to describe changes in the macroinvertebrate community after the zebra mussel invasion (before 1991), after invasions by *E. ischnus* and the quagga mussel (between 1995 and 1999), and after invasion by the Round Goby (about 2004).

METHODS

Study area

Our study site is an artificial reef (lat 43°20'10.5"N, long 78°45'25"W) and adjacent natural cobble habitat (lat 43°19'84"N, long 78°45'49"W) in southwestern Lake Ontario situated ~0.8 km offshore and ~1.6 km west of Olcott, New York, at depths ranging from 5 to 7 m. The cobble site is a mixture of cobble, sand, and silt, and is representative of the nearshore benthic environment along the southwestern Lake Ontario shore. The artificial reef, constructed in 1982 to attract spawning Lake Trout (*Salvelinus namaycush* Walbaum) and other sport fishes, consists of siltstone, shale boulders, and cinder blocks. Both habitats provide favorable microhabitat for epifauna and infauna, but pore size is much greater on the reef.

Sample collection

Our sampling methods in 2014 were consistent with those of past studies (Bader 1985, Stewart and Haynes 1994, Haynes et al. 2005). In July and September, SCUBA divers laid out one 30-m transect on each of the cobble and artificial reef habitats and then used a dome suction sampler (Gale and Thompson 1975) to collect 5 replicate benthic samples spaced equidistantly along each transect. The sampler was a stainless steel ring that enclosed an area of 0.164 m², a bilge pump connected to a 12-V motorcycle battery, and a Plexiglas® cover with 2 armholes. A hose (with a nozzle containing steel rods spaced 1.27 × 1.27 cm apart to reduce clogging of the pump) was attached to the pump. Samples were collected by vacuuming the substrate enclosed within the circumference of the dome suction sampler for ~3 min, after which each 500-μm-mesh collecting bag was transferred to our boat on the surface.

On the boat, samples were rinsed through a 600-μm sieve to retain macroinvertebrates, which were transferred to jars containing carbonated water to relax organisms. Before samples were returned to the laboratory, carbonated water was decanted and replaced with 10% buffered formalin. After 24 to 48 h in the laboratory, the formalin solution was replaced with 70% ethanol stained with rose Bengal to make the organisms more visible.

Organisms were separated from macroalgae and debris under a dissecting microscope using magnifications of 10 to 40 \times . Macroinvertebrates were counted only if a shell was intact or the head was attached to a body. All organisms were identified to the lowest practical taxonomic resolution then combined into higher taxonomic levels to enable comparisons with levels reported in previous sampling years. To allow for separate comparisons of gilled vs lunged snails, we grouped *Physa*, *Stagnicola*, and Planorbidae into the subclass Pulmonata (lunged snails; hereafter referred to as pulmonate snails), and *Bithynia*, *Amnicola*, *Valvata*, and *Elimia* into the subclass Prosobranchia (gilled snails; hereafter referred to as prosobranch snails).

Daily temperature (average, low, high) and precipitation data for 30 d before each monthly sampling date in each year (1983–2014) were obtained from the Buffalo, New York, airport weather station. These measurements, standardized based on *z*-scores, were compared with nonmetric multidimensional scaling (NMDS) in the multivariate software Plymouth Routines in Multivariate Ecological Research (PRIMER 6; Clarke and Gorley 2006) to examine whether presampling weather conditions were correlated with the macroinvertebrate community among years and months.

Data analysis

We calculated sample mean abundances (organisms/m²) and their standard deviations for each artificial reef and cobble taxon for each sampling month in 2014, 1999, 1991, and 1983, and Simpson's diversity for combined (habitats and months) yearly samples. We assessed differences in Simpson's diversity between 6 pairs of sampling years with *t*-tests (Brower and Zar 1984), and we used a Bonferroni correction to adjust α ($\alpha_{\text{adj}} = 0.05/6 = 0.0083$).

We used a generalized linear model (GLM) implemented with the *manyglm* function in the *mvabund* package of R statistical software (version 3.3.0; R Project for Statistical Computing, Vienna, Austria; Warton et al. 2012) to test for differences in overall benthic community composition among years, months, and habitats. Our long-term abundance data had a strong mean–variance relationship (inherent in abundance data) which, when analyzed using distance-based routines, such as SIMPER and PERMANOVA, confound location (between-group; mean) and dispersion (within-group; variance) effects (Warton et al. 2012). The *manyglm* function (Wang et al. 2016), which assumes a mean–variance relationship, is an analysis of deviance for fitting multivariate GLMs to high-dimensional multivariate data, such as abundance data (Wang et al. 2016). We used *manyglm*, but our choice of analysis of our data set was not especially critical because trends in taxon abundances across years were so striking that they appeared in both distance-based and GLM analyses. We ran the *manyglm* using habitat, month, and year as factors. The response variables were the raw count data for each taxon in each tran-

sect replicate of each year, month, and habitat ($n = 79$, 5 replicates \times 2 habitats \times 2 mo \times 4 y – 1 lost sample).

We first fit a main effects model using the formula, “invertFit = manyglm(inverts~Habitat*Month*Year,data = X, offset = log(apply(inverts,1,mean)).”

We used an offset, which is a term added to a predictor variable and has a coefficient of 1, to account for possible differences in sampling intensity across samples (Wang et al. 2016). We then ran a univariate analysis of variance (ANOVA) for each taxon and adjusted the *p*-value for multiple testing with a step-down resampling procedure (Wang et al. 2016). We used 999 bootstrap iterations from the *manyglm*.

We analyzed our multivariate abundance data with 2 ordination methods to show the detailed and overall changes in the benthic community over the 4 sampling years. First, we used the latent variable unconstrained ordination method in the package *boral* in R (Hui 2015) to visualize in detail the relationships between the 79 macroinvertebrate replicate counts in terms of benthic taxon abundance and the taxa associated with the 4 sampling years. Unconstrained ordination is used to visualize multivariate data in low-dimensional space, and the interpretation of the resulting plot is similar to that of nonmetric multidimensional scaling (Hui 2015). To illustrate the major changes in the benthic community among the 4 sampling years, we used nonmetric multidimensional scaling (NMDS) in PRIMER. This multivariate method is based on a triangular resemblance matrix of Bray–Curtis similarities among all pairs of samples. (Bray–Curtis is the standard method for assessing community similarity of data like ours.) NMDS represents samples as points in 2-dimensional space so that the relative distances of all points are in the same rank order as the relative Bray–Curtis similarities of the samples. Points close together on the ordination represent communities similar in % composition (relative abundance) of benthic taxa, whereas points far apart correspond to communities that differ in taxonomic composition. We chose a GLM to describe significant changes in the macroinvertebrate community quantitatively, but the latent variable ordination and the NMDS produced qualitatively clear visualizations of what the *manyglm* output showed quantitatively.

RESULTS

Changes in % composition of the macroinvertebrate community

Macroinvertebrate community composition in 2014 differed strongly from composition in 1999, 1991, and 1983 (Table 1). Pulmonate and prosobranch snails and sphaeriid bivalves were absent, quagga mussels replaced zebra mussels, and *E. ischnus* had replaced *G. fasciatus* as the dominant amphipod (Fig. 1A, Table 1). From 1983 to 1999, the relative abundance of prosobranch snails declined nearly 10-fold and that of pulmonate snails rose 2-fold (Fig. 1B,

Table 1. Mean (SE) abundance (individuals/m²) of benthic macroinvertebrates in southwestern Lake Ontario in 1983, 1991, 1999, and 2014. Month (July, September) and habitat (cobble, reef) data (Bailey 2015) were combined within study years.

	1983	1991	1999	2014
Platyhelminthes				
Turbellaria	37.3 (1.5)	164.7 (9.0)	0	84.2 (6.5)
Annelida				
Oligochaeta	52.9 (3.7)	1119.7 (69.5)	31.5 (3.2)	4352.0 (246)
Hirudinea	0	2.4 (0.2)	26.6 (2.0)	0
Mollusca				
Bivalvia				
Sphaeriidae	78.3 (4.9)	137.8 (9.3)	0	0
<i>Dreissena polymorpha</i>	0	28088.3 (1035.7)	1456.8 (131.0)	0
<i>Dreissena rostriformis bugensis</i>	0	0	4953.2 (445.0)	591.5 (46.1)
Gastropoda				
Pulmonata				
Planorbidae	1.2 (0.1)	30.2 (1.7)	10.9 (0.7)	0
<i>Stagnicola</i>	320.5 (21.6)	860.9 (44.2)	1569.7 (96.3)	0
<i>Physella</i>	68.6 (6.5)	327.9 (13.7)	852.1 (56.8)	0
Prosobranchia				
<i>Valvata</i>	0	78.1 (7.3)	0	0
<i>Bithynia</i>	4.8 (0.4)	3.9 (0.2)	1.2 (0.1)	0
<i>Ammicola</i>	3.6 (0.4)	2070.4 (78.7)	156.4 (10.2)	0
<i>Elimia</i>	549.3 (8.9)	1886.3 (111.7)	31.5 (1.9)	0
Crustacea				
<i>Gammarus fasciatus</i>	3103.6 (123.1)	7585.6 (326.6)	3200.0 (128.5)	172.4 (7.2)
<i>Echinogammarus ischnus</i>	0	0	1432.7 (108.3)	1401.0 (102)
<i>Orconectes</i> spp.	6 (0.4)	80.5 (5.76)	4.8 (0.31)	11.0 (1.2)
Insecta				
Ephemeroptera	12 (1.3)	35.5 (1.8)	0	0
Trichoptera	42.1 (2.5)	178.0 (6.4)	2.4 (0.3)	23.2 (1.7)
Chironomidae	97.4 (7.9)	59.7 (4.9)	0	558.5 (20.3)

Table 1). From 1991 to 2014, the relative abundances of oligochaetes and chironomids increased 32- and 78-fold, respectively (Fig. 1C, Table 1).

Weather data (low, mean, and high daily temperature; daily precipitation) for the 30 d before each monthly sampling date in 1983, 1991, 1999, and 2014 showed no distinct groupings in NMDS space. Points associated with the weather variables on the 2-dimensional ordination overlapped considerably among sampling years (Bailey 2015). These results indicate that presampling weather (a surrogate for lake physical conditions) was not a significant factor in changes observed in the macroinvertebrate communities sampled from 1983 to 2014.

GLMs

Month, habitat, year, and the interactions among these factors produced many significant results, but the strongest

factor by far was year. Significant differences in relative abundances between months (3/23 taxa) and habitats (5/23 taxa) were far fewer than significant differences among years (22/23 taxa), and differences related to month and habitat probably were related to species biology, not invasive taxa. The models (Table 2) revealed significant changes (adjusted for multiple comparisons) among years (1983, 1992, 1999, 2014) for all benthic taxa analyzed, perhaps with the exception of the crayfish *Orconectes* ($p = 0.052$). Differences between months (July vs September) were significant for the snails *Stagnicola* ($p = 0.013$) and *Valvata* ($p = 0.019$) and for the decapod *Orconectes* ($p = 0.019$). Differences between habitats (cobble vs reef) were significant for oligochaetes ($p = 0.001$), sphaeriids ($p = 0.001$), zebra mussels ($p = 0.001$), the snail *Valvata* ($p = 0.008$), and prosobranch snails in general ($p = 0.036$).

Significant habitat \times month interactions (Table 2) occurred for *Orconectes* ($p = 0.031$) and for pulmonate

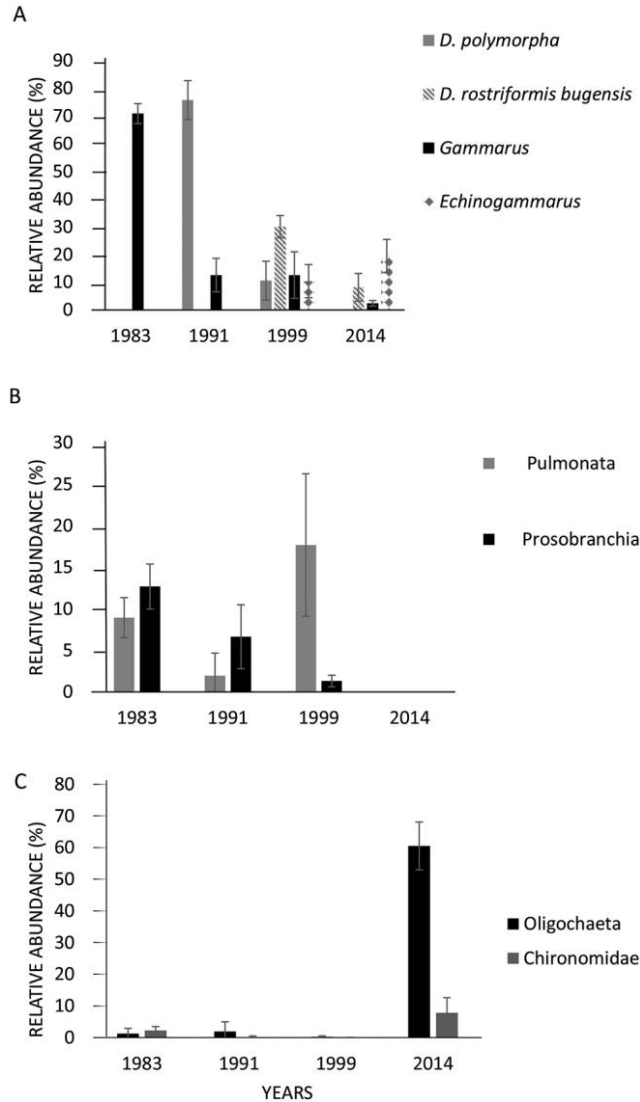


Figure 1. Mean (\pm SE) annual relative abundance (% composition) of *Gammarus fasciatus*, *Echinogammarus ischnus*, *Dreissenapolyomorpha*, and *Dreissena rostriformis bugensis* (A), Pulmonata and Prosobranchia (B), and Oligochaeta and Chironomidae (C) at the study site from 1983 to 2014.

($p = 0.001$) and prosobranch snails ($p = 0.001$). Significant habitat \times year interactions occurred for oligochaetes ($p = 0.012$), turbellarians ($p = 0.001$), the snails *Stagnicola* ($p = 0.024$) and *Elimia* ($p = 0.013$), *Orconectes* ($p = 0.002$), caddisflies (Trichoptera, $p = 0.012$), and chironomids (Chironomidae, $p = 0.003$). Significant month \times year interactions occurred for oligochaetes ($p = 0.001$); the snails *Stagnicola* ($p = 0.002$), *Physa* ($p = 0.001$), *Ammicola* ($p = 0.001$), and *Elimia* ($p = 0.031$); the amphipod *Gammarus* ($p = 0.003$); caddisflies ($p = 0.014$), chironomids ($p = 0.001$); zebra mussels ($p = 0.001$); quagga mussels ($p = 0.001$); the amphipod *Echinogammarus* ($p = 0.004$); and pulmonate ($p = 0.014$) and prosobranch snails ($p = 0.001$).

The central question of our study was whether benthic macroinvertebrate community changes were associated with the establishment of 4 Ponto-Caspian species. The remainder of our paper will focus on how the composition of the benthic macroinvertebrate community differed among the 4 sampling years and potential causes for observed changes.

Temporal changes in macroinvertebrate community similarity and taxonomic diversity

Excluding invasive taxa, the benthic communities sampled in 1983, 1991, and 1999 were more similar (Bray–Curtis) to one another than to the community sampled in 2014 (Table 3). Changes in Simpson's diversity over time were heavily influenced by changes in snail diversity, which were highest in 1991 (0.695) and lowest in 2014 (0.000) (Table 4). Snail diversity was significantly different ($p < 0.001$) between all pairs of years except 1983 and 1999 ($p = 0.7$). Simpson's diversity of all benthic taxa, excluding dreissenid mussels, was lowest in 2014 (0.377) and highest in 1991 (0.686), and taxon diversity differed significantly ($p < 0.001$) among all pairs of years (Table 4).

Determinants of community change

The 4 distinct community groupings (sampling years) coincided with successive invasions: 1983, pre-invasion; 1991, early post-invasion of zebra mussels; 1999, early post-invasion of quagga mussels and the amphipod *E. ischnus*; and 2014, disappearance of zebra mussels, late post-invasion of quagga mussels and *E. ischnus*, and strong establishment of the Round Goby at our study site. Unconstrained 2-dimensional ordination with the latent variable method presented the 79 benthic samples collected from 1983–2014, and all replicates were clustered by year group (Fig. 2). The 1983 and 1991 sample groups were closer to each other in ordination space than to the 1999 and 2014 sample groups. In 1983 and 1991, the communities were characterized by relatively high abundances of gammarid amphipods, *Elimia*, *Orconectes*, Trichoptera, Ephemeroptera, sphaeriid bivalves, Planorbidae snails, and *Bithynia*. Zebra mussels were present in 1991 and 1999, which may explain why this taxon is situated roughly equidistant between 1999 and 1991 in ordination space. The 2014 samples were characterized by *Echinogammarus*, Acari (water mites), oligochaetes, and chironomids, and occupied the upper right portion of the ordination space, distinctly separate from the rest of the sample groups.

The NMDS ordination of % composition for all 4 sampling years (2-dimensional stress = 0; Fig. 3) showed a pattern similar to that observed in Fig. 2. The stress value indicated that the arrangement of the 4 communities (years with habitats and months combined) was the best representation of the true Bray–Curtis similarities (Table 3) among those communities. The 1983, 1991, and 1999 communities clustered more closely to each other than to the 2014

Table 2. Generalized Linear Model *manyglm* results (Deviation test statistic, *p*-value) of abundance (individuals/m²) of taxa sampled in 1983, 1991, 1999, and 2014. *D.* = *Dreissena*, *df* = degrees of freedom. Bold indicates *p* < 0.05.

Source	df	Oligochaeta	Hirudinea	Turbellaria	Sphaeriidae	Planorbidae	Stagnicola	Physa	Valvata	Bitrynia	Ammicola	Elimia
Habitat	74	4.7, 0.001	4.3, 0.202	0, 0.900	17.4, 0.001	1.7, 0.747	2.3, 0.635	0.01, 0.202	15.2, 0.008	1.03, 0.096	6.8, 0.116	0.22, 0.986
Month	73	5.9, 0.835	1.8, 0.898	0.1, 0.320	1.0, 0.878	2.1, 0.767	11.5, 0.013	0.9, 0.898	10.8, 0.019	1.3, 0.957	0.15, 0.957	0.02, 0.898
Year	70	71.7, 0.001	12.8, 0.038	48.1, 0.012	72.8, 0.001	23.7, 0.012	61.5, 0.001	47.3, 0.001	28.2, 0.001	14.8, 0.016	69.9, 0.001	129.9, 0.001
Habitat × month	66	3.0, 0.955	0.2, 0.955	0.0, 0.285	4.1, 0.506	0.13, 0.955	0.07, 0.990	0.16, 0.918	0.4, 0.955	2.3, 0.467	2.4, 0.854	1.8, 0.151
Habitat × year	62	16.2, 0.012	0.5, 0.918	29.0, 0.001	4.7, 0.542	6.2, 0.827	13.0, 0.024	5.4, 0.400	0.0, 0.898	3.4, 0.918	5.4, 0.918	15.0, 0.013
Month × year	59	26.3, 0.001	0.0, 0.272	21.3, 0.435	2.1, 0.721	4.2, 0.272	33.2, 0.002	76.4, 0.001	0.0, 0.721	3.3, 0.721	51.0, 0.001	17.4, 0.031

Table 2 (extended)

<i>Gammarus</i>	<i>Orconectes</i>	Ephemeroptera	Trichoptera	Chironomidae	<i>D. bugensis</i>	<i>D. polymorpha</i>	<i>Echinogammarus</i>	Pulmonata	Prosobranchia	Isopoda	Acari
0.07, 0.995	6.9, 0.096	0.09, 0.995	5.9, 0.152	0.98, 0.895	12.4, 0.096	42.8, 0.001	11.6, 0.096	10.9, 0.138	16.5, 0.036	2.4, 0.635	0.75, 0.903
6.3, 0.157	12.2, 0.019	1.9, 0.898	0.27, 0.767	1.0, 0.935	5.5, 0.266	0.0, 0.998	2.0, 0.815	7.0, 0.129	0.0, 0.078	0.02, 0.994	6.2, 0.157
100.8, 0.001	8.8, 0.052	54.0, 0.001	37.6, 0.001	69.0, 0.001	71.5, 0.001	78.4, 0.001	95.0, 0.001	69.1, 0.001	119.0, 0.001	13.0, 0.020	112.0, 0.001
8.1, 0.134	11.5, 0.031	0.25, 0.151	0.006, 0.387	2.1, 0.467	1.6, 0.955	2.1, 0.955	10.0, 0.241	40.2, 0.001	35.3, 0.001	3.4, 0.742	3.8, 0.686
9.3, 0.117	25.2, 0.002	1.2, 0.918	26.8, 0.012	13.0, 0.003	0.0, 0.827	0.0, 0.914	0.0, 0.827	0.0, 0.858	0.0, 0.946	4.2, 0.404	2.6, 0.573
24.5, 0.003	2.0, 0.435	0.31, 0.721	17.8, 0.014	56.7, 0.001	39.8, 0.001	28.6, 0.001	13.5, 0.004	9.7, 0.014	17.5, 0.001	0.0, 0.778	1.9, 0.642

Table 3. Bray–Curtis % similarities of the benthic macroinvertebrate community for year pairs: 1983–2014. Larger values indicate greater similarity based on numerical densities of taxa.

Year	1991	1999	2014
1983	61.09	52.99	11.16
1991		46.41	17.77
1999			6.82

community, indicating that the 2014 community (post-Round Goby invasion) had undergone greater change than had earlier communities after invasions by dreissenid mussels and *E. ischnus*. Taxa associated with sampling period communities ($r \geq 0.6$) are represented as vectors on the NMDS ordination. For instance, pulmonate snails were associated with 1999, prosobranch snails and zebra mussels were associated with 1991, quagga mussels were associated with 1999 and 2014, and *E. ischnus* was associated with 1999 and 2014. The oligochaete and chironomid vectors were associated with 1991 and 2014 (they were abundant in both years), whereas *G. fasciatus* was associated with 1983, 1991, and 1999 communities (when it was still abundant).

DISCUSSION

The effects of species introductions on pre-invasion community structure or ecosystem function may be few or many, short- or long-term, as evidenced by successive invasions of aquatic species in the Great Lakes (Mills et al. 1993, Haynes et al. 2005). Despite invasion by 3 Ponto-Caspian invertebrates, the benthic invertebrate community at our study site changed in a major way only after invasion by a Ponto-Caspian fish, the Round Goby. GLM univariate results showed significant differences in several taxa between months and habitats, but we were most interested in significant changes in macroinvertebrate taxa among years because 3 of the years in which we sampled followed the introduction of new Ponto-Caspian species. Several trends in macroinvertebrate community structure were apparent from 1983 to 2014: 1) a decline in overall taxonomic diversity, 2) disappearance of snails, 3) increase in densities and relative abundance of small, soft-bodied oligochaetes and chironomids, and 4) replacement of *G. fasciatus* by *E. ischnus* (amphipods) and zebra mussels by quagga mussels.

An overview of the macroinvertebrate community: 1983–2014

In 1983, the pre-invasion ‘control’ for our data set, the benthic invertebrate community was dominated by *G. fasciatus* and a diverse assemblage of snails (Bader 1985). In 1991, one year after invasion by the zebra mussel, the macroinvertebrate community had the same pre-invasion members, but the abundances of several pre-invasion taxa, including *G. fasciatus*, increased nearly 2-fold probably be-

cause of the short-term ecosystem-engineering effects of zebra mussels (Stewart 1993, Haynes et al. 2005). In addition, the 1991 community had higher Simpson’s diversity than did the 1983, 1999, or 2014 communities. In 1999, quagga mussels and *E. ischnus* were present at the cobble and reef habitats, but the quagga mussel had replaced the zebra mussel as the dominant dreissenid by a factor of 3.4 (Haynes et al. 2005). Many taxa, including *G. fasciatus*, sphaeriid bivalves, several prosobranch snails, and aquatic insects, that had increased strongly in abundance in 1991 had declined to pre-invasion or lower levels by 1999. In 2014, ~10 y after the establishment of Round Goby, the benthic community was less diverse than in previous years and was dominated by oligochaetes (60%) and *E. ischnus* (19%).

Factors contributing to lower taxonomic diversity in 2014

The high Simpson’s diversity in 1991 coincided with the highest zebra mussel abundance and snail diversity during the study period. In contrast, Simpson’s diversity was lowest in 2014, in large part, because of the absence of snails. The differences in Simpson’s diversity for snails and the macroinvertebrate community between 1983 and 2014 highlight short-term positive (1983–1991) and long-term negative (1991–2014) effects of invasions.

Our diversity results are similar to 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). From 1991 to 2014, Ephemeroptera disappeared and Trichoptera decreased in abundance, but Hydrptilidae (algae-piercing Trichoptera) increased in abundance. A decline in the biodiversity of the macroinvertebrate fauna, including the disappearance of previously abundant Ephemeroptera and Trichoptera and increased importance of snails also was observed in northeastern Lake Erie from 1974 to 2001 (Ratti and Barton 2003). However, changes in Lake Erie from 1974 to 1985 cannot be attributed to the Ponto-Caspian invasions, which began with zebra mussels in 1986. Ratti and Barton (2003) reported 3 abundant exotic species (Round Goby, quagga mussel, and *E. ischnus*), and suggested that the quagga mussel was responsible for the overall decline in invertebrate diversity. We observed

Table 4. Simpson’s diversity of benthic macroinvertebrates and snails in each year (months and habitats combined). Values with the same superscript are not significantly different.

Year	Macroinvertebrate diversity (all taxa)	Snail diversity
1983	0.475 ^c	0.525 ^b
1991	0.686 ^a	0.695 ^a
1999	0.613 ^b	0.536 ^b
2014	0.377 ^d	0.000 ^c

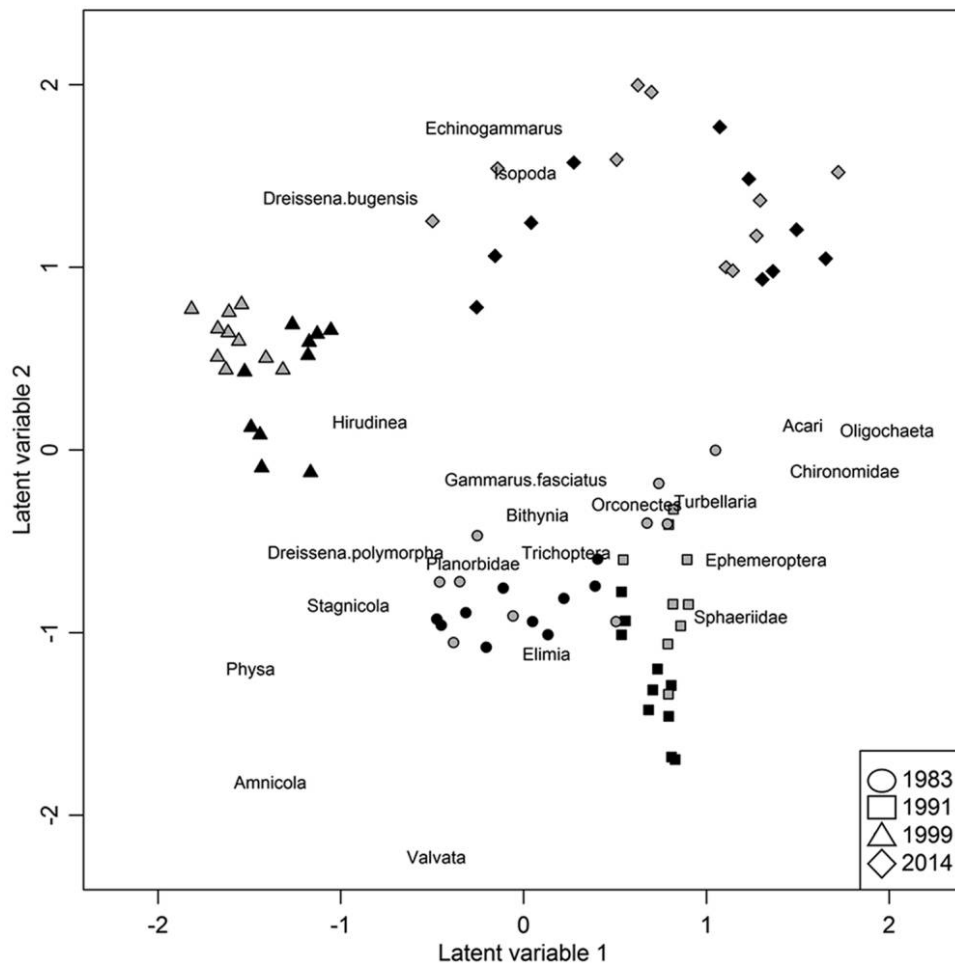


Figure 2. Unconstrained ordination of 79 benthic macroinvertebrate replicate counts based on the latent-variable method. Gray and black shapes represent cobble and reef samples, respectively. Benthic taxa on the ordination are associated with the samples and year groups in which they were important.

a decline in quagga mussel abundance, a stable abundance of *E. ischnus*, and many Round Gobies/m² while sampling in 2014. Therefore, we hypothesize that the Round Goby is most responsible for the decline of macroinvertebrate diversity at our study site.

Shifts in body-size predominance of nondreissenid taxa

Relative abundances of oligochaetes, chironomids, and prosobranch snails were low and of pulmonate snails were high in 1999 (Haynes et al. 2005). In 2014, relative abundances of oligochaetes and chironomids were high, and no snails were observed. Round Goby density was positively correlated with chironomid biomass and negatively correlated with snail body size and abundance in the St Lawrence River (Kipp and Ricciardi 2012). Where Round Goby was present in the upper St Lawrence River, the median size and taxon richness of snails declined; only small Hydrobiidae and large Pleuroceridae (both prosobranchs) persisted. Presumably, small snails could escape Round Goby

predation by living in crevices, and Round Gobies could not eat large snails (Kipp et al. 2012).

Burlakova et al. (2014) reported a 50% increase in oligochaete and chironomid densities at their Lake Erie study sites during the first decade after the dreissenid invasion and lower abundance of the same taxa from 2009 to 2012. In contrast, by 2014, the relative abundances of oligochaetes and chironomids had increased by 32- and 78-fold, respectively, at our study site. Varying oligochaete and chironomid abundances between western Lake Erie and our site may have been a result of different sampling gear (Ponar grab vs dome suction) or differences in macroalgae, dreissenid, or Round Goby density or substrate type.

In a lake-wide, Ponar-grab survey of benthic macroinvertebrates in Lake Ontario, oligochaetes were the 2nd-most abundant taxonomic group sampled in 2008–2009 with a relative abundance of 24% (Birkett et al. 2015). Oligochaetes were the most abundant group in the western basin of Lake Ontario at a depth of 11 m, consistent with the large increases in oligochaetes at our 5- to 7-m-deep

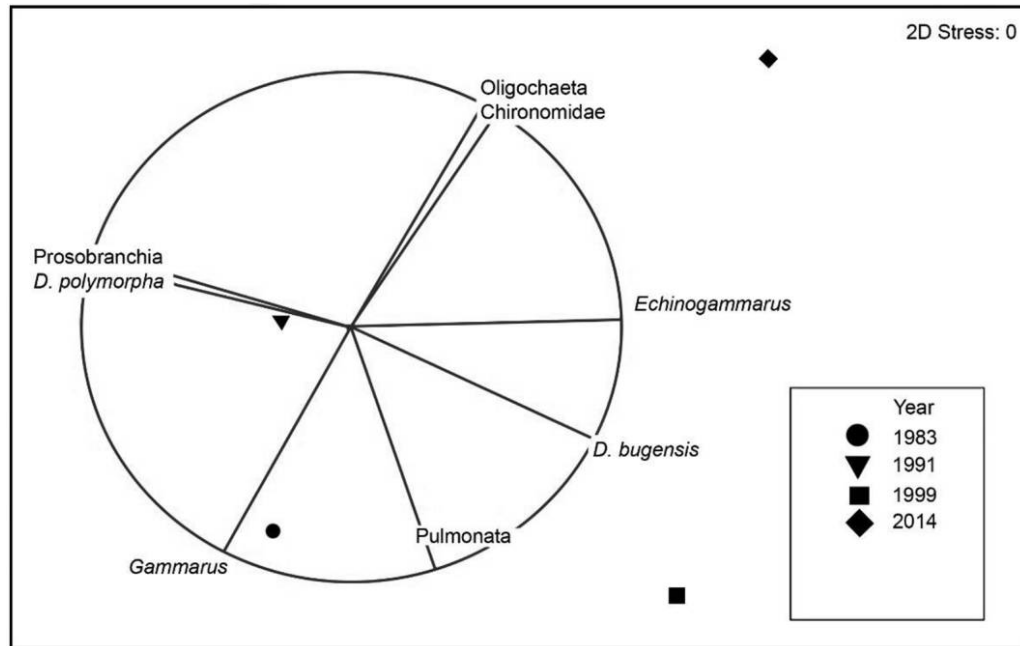


Figure 3. Nonmetric multidimensional scaling (NMDS) ordination of arcsine-transformed relative abundance (% composition) of benthic macroinvertebrate taxa in 1983, 1991, 1999, and 2014. The vectors on the ordination represent benthic taxa that were significantly correlated ($r \geq 0.6$) with the 4 sampling years: Prosobranchia and *Dreissena polymorpha* (1991), Pulmonata and *Dreissena rostriformis bugensis* (1999), *Echinogammarus ischnus* (between 1999 and 2014), Oligochaeta and Chironomidae (2014), and *Gammarus fasciatus* (1983). The circle on the NMDS represents the 100% correlation limit for the vectors.

site in 2014. Increasing *Cladophora* abundance also has been reported at nearshore sites in Lake Ontario, probably because of increased light penetration to the benthos consequent to ongoing filter-feeding by dreissenids. Increased abundance of algal detritus may support higher abundances of oligochaetes and chironomids than before the dreissenid invasions (Higgins et al. 2012). We hypothesize that the dense macroalgal mats at our study site provide refuge from Round Goby predation for oligochaetes and chironomids because the algae hide these taxa from this visual predator and could potentially interfere with Round Goby feeding (Barton et al. 2005).

The Round Goby probably exerts top-down control on benthic macroinvertebrates, which has led to a trophic cascade. Consistent with our observations of thick macroalgal mats on the artificial reef in 2014, Kuhns and Berg (1999) hypothesized that Round Goby predation on herbivorous snails would release *Cladophora* and other macroalgae from grazing pressure, allowing them to proliferate, thereby increasing microhabitat, feeding opportunities, and refugia for oligochaetes and chironomids.

Trends in snail abundance

Patterns of change from 1983 to 2014 differed between prosobranch and pulmonate snails. Prosobranch snails decreased and pulmonate snails increased from 1983 to 1999 and both were absent in 2014. Round Gobies probably preyed

heavily on snails between 2004 and 2014 (Barton et al. 2005, Naddafi and Rudstam 2014), but degradation of benthic water quality in the southwestern nearshore area of Lake Ontario since 2000 (Makarewicz and Howell 2012) also may have affected snails. Prosobranchs are more sensitive to water quality than pulmonates, which tolerate nutrient enrichment and lower dissolved O_2 (Peckarsky et al. 1990). We did not measure water quality at our site during the study period, but recent water-quality analyses in the nearshore area of southwestern Lake Ontario suggested beneficial use impairment caused by elevated nutrients (Makarewicz and Lewis 2015). Also, Eighteen Mile Creek and the Niagara River, 2 International Joint Commission Areas of Concern, are in the southwestern coastal zone of Lake Ontario near our study site. Anthropogenic inputs of NO_3^- and PO_4^{3-} (Makarewicz and Howell 2012) might be influencing nearshore water chemistry at the Olcott reef. If water quality was impaired before and during the invasion Round Goby, the different extirpation trajectories of prosobranch and pulmonate snails at our study site may be the result of a combination of nutrient enrichment, lower benthic dissolved O_2 , and Round Goby predation.

Trends in species replacements at the cobble and reef habitats

Echinogammarus ischnus Expansion of *E. ischnus*, declines of populations of *G. fasciatus*, and replacement of zebra

mussels by quagga mussels have occurred in several Laurentian Great Lakes (Nalepa et al. 2001, Wilson et al. 2006, Kestrup and Ricciardi 2009). *Echinogammarus ischnus* is smaller but produces larger broods than pre-invasion gammarids (Grabowski et al. 2007). It is a rocky substrate specialist that uses its uropods and antennae for stabilization while moving along substrates (Palmer and Ricciardi 2005). Dreissenids may have facilitated the expansion of *E. ischnus* and decline of *G. fasciatus* because *E. ischnus* coevolved with dreissenids in the Ponto-Caspian region. *Echinogammarus ischnus* may be able to use habitat spaces in dreissenid colonies (e.g., as refugia from predators) more effectively than pre-invasion gammarids in the Great Lakes (Nalepa et al. 2001, González and Burkart 2004).

Echinogammarus ischnus was first collected at our study area in 1999 (Haynes et al. 2005), and its abundance exceeded that of *G. fasciatus* by 2014. However, its overall abundance did not increase dramatically after 1999, especially in the cobble habitat (Bailey 2015), where areas of silt and sand sediment were unsuitable for *E. ischnus* (Palmer and Ricciardi 2005). Gammarid density increased >50% in both habitats soon after the invasion of the zebra mussel, but had declined >50% at the reef by 1999. *Gammarus fasciatus* was less abundant at both cobble and reef in 2014 than during predreissenid sampling in 1983. Although *E. ischnus* occurred in higher numbers than *G. fasciatus* in 2014, total *E. ischnus* abundance was <50% of that recorded for *G. fasciatus* during the 3 previous sampling periods, suggesting that *E. ischnus* does not use detrital resources as efficiently as *G. fasciatus*. Perhaps relatively small numbers of both *E. ischnus* and *G. fasciatus* have left more detritus available for oligochaetes and chironomids, which were much more abundant in 2014 than in previous years.

González and Burkart (2004) proposed that dreissenids may have facilitated invasion of *E. ischnus* by providing better food resources. The quality of food for benthic taxa probably differs between dreissenid colonies (biodeposition of relatively nutrient-rich feces and pseudofeces) and macroalgal mats (relatively nutrient-poor detritus). Since 1991, dreissenid mussel abundance and benthic community diversity have declined, whereas macroalgal abundance has increased at our study site. *Echinogammarus ischnus* and *G. fasciatus* potentially use different habitats and may not be competing directly for the same food resources. For example, Limén et al. (2005) used stable-isotope analysis to show that *E. ischnus* did not consume dreissenid feces and pseudofeces, whereas *G. fasciatus* did.

Gammarus fasciatus has become rare in many near-shore areas of the Laurentian Great Lakes (Dermott et al. 1998). Factors contributing to the persistence of *G. fasciatus* in some nearshore areas in the presence of *E. ischnus* may include local genetic variation or phenotypic plasticity, such as euryhalinity and generalist foraging behavior, which may increase success in disturbed habitats (Derry et al. 2013).

In addition, microhabitats such as the dense macroalgae mats observed at the Olcott reef in 2014 may provide opportunities for pre-invasion gammarid amphipods to coexist with *E. ischnus* (Palmer and Ricciardi 2005, Derry et al. 2013). Last, in laboratory experiments, Round Gobies ate both *E. ischnus* and *G. fasciatus* (González and Burkart 2004), so predation may reduce numbers of both species enough that they do not compete for resources, thereby enabling coexistence.

Dreissena rostriformis bugensis The quagga mussel had become the dominant dreissenid mussel at our study site by 1999, a situation that parallels reports from 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 for suspension feeders to amounts at which the quagga mussel was the better competitor (Ricciardi 2001). Other factors that may have contributed to success of the quagga mussel include its higher filtration rate in warmer water, faster growth rate in the presence of predators, and longer siphons and byssal threads, which allow it to thrive on soft sediments (Birkett et al. 2015). Our GLMs showed that quagga mussel abundance did not differ between cobble and reef habitats, but zebra mussel abundance did. The apparently wider ecological niche of the quagga mussel may have enabled it to replace the zebra mussel at our study site.

By 2006, zebra mussels were nearly gone from the near-shore of Lake Ontario, and quagga mussel densities were similar to zebra mussel densities documented during the first decade of the dreissenid invasion (Wilson et al. 2006). The quagga mussel was the dominant dreissenid at our study site in 2014, but its abundance and biomass were <50% of those reported for all dreissenids in past sampling periods (Stewart and Haynes 1994, Haynes et al. 1999, 2005). We underestimated dreissenid abundance in 1999 and 2014 because the dome suction sampler did not remove all dreissenids from the substrate, whereas in 1991, we scraped zebra mussels from rocks transported to the boat. Nevertheless, Pennuto et al. (2012) reported that divers scraping the surfaces of rocks in the nearshore of Lake Ontario found fewer total dreissenids in 2008 than in 1999, and both Barton et al. (2005) and Naddafi and Rudstam (2014) reported that Round Gobies reduced dreissenid biomass.

Changes in the fish community

Sixteen fish species, including Lake Trout, White Bass (*Morone chrysops* Rafinesque), and Yellow Perch (*Perca flavescens* Mitchell), were collected with gill nets at the reef and cobble sites in 1983 before the dreissenid invasions (Merritt 1985). In 1999, before the Round Goby invasion, the assemblage of fishes had not changed from that reported

for 1983 (Haynes 1995, Haynes et al. 2005). Fish were not quantified in 2014, but we observed high densities (5–10 individuals/m²) of Round Gobies, especially at the reef, and no other fish except a few pelagic Alewife (*Alosa pseudoharengus* Wilson). Aggressive behavioral interactions between Round Gobies and Mottled Sculpins and Johnny Darters may have contributed to population declines in Lake Michigan from 1984 to 2002 (Lauer et al. 2004). Johnny Darters and Slimy Sculpins (*Cottus cognatus* Richardson) were common at our study site (Haynes 1995) and on the nearshore benthos of southern Lake Ontario (Mills et al. 2005) before the Round Goby invasion. Our observation of many Round Gobies and no pre-invasion fish taxa in 2014 suggests that the Round Goby, perhaps in conjunction with the thick macroalgal mat, displaced the pre-invasion fish community and drove changes in the macroinvertebrate community (Kornis et al. 2012).

Concluding remarks

The Olcott reef was constructed in 1982 to provide spawning habitat for Lake Trout and to improve coastal fisheries. Through 1999, the assemblage of fish in our study area remained unchanged after the original fish survey in 1983 (Merritt 1985, Haynes 1995, Haynes et al. 2005). We did not survey fish in 2014, but we saw many Round Gobies, a few pelagic Alewives, no other benthic fish, and a thick carpet of macroalgae on the reef. Thus, we have quantified changes in the macroinvertebrate community over 30 y, but also illustrated how intentions to provide better conditions for species of human interest can be foiled by an introduced species. The Round Goby appears to have set in motion a trophic cascade (Carpenter et al. 1985) at our study site that has eliminated snails and allowed thick macroalgal growth on Lake Trout spawning habitat at the Olcott reef. Subsequent ecological effects appear to be displacement of a diverse assemblage of native fishes and creation of unsuitable habitat for Lake Trout embryos and larvae. Algal mats in late autumn and winter would prevent eggs from falling into the cracks between reef rocks, the natural habitat for embryonic development, and decrease dissolved O₂ concentrations critical for Lake Trout development. Our findings have implications for future fish habitat restoration projects in the Laurentian Great Lakes and other geographic regions where community- or habitat-altering species invade.

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Author contributions: KBB organized the study, participated in all field collections, identified all invertebrates, did all statistical analyses, and wrote the first draft of the manuscript, which arose from her MS Thesis. JMH was KBB's major advisor, led collecting of invertebrates by SCUBA, consulted on statistical findings, and played a major role during revisions of the manuscript. DIW pro-

vided KBB with instructions and code to implement the appropriate multivariate tests in the *mvabund* package of R.

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