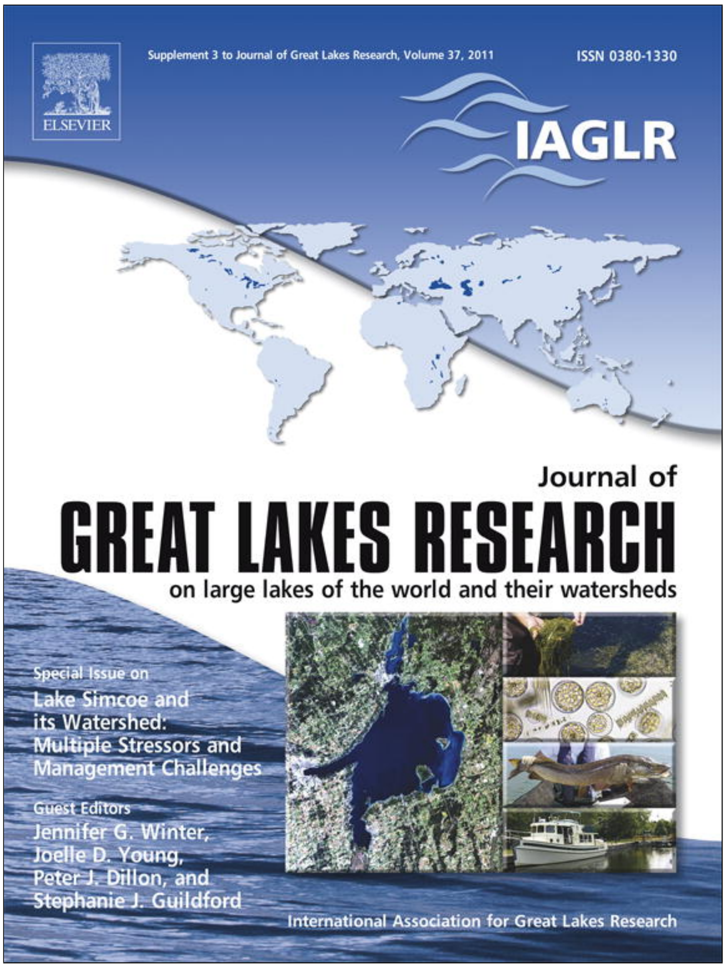
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Temporal changes in the benthic invertebrate community of Lake Simcoe, 1983–2008

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The Lake Simcoe ecosystem has been subjected to multiple stressors during the past century, including changes in nutrient loads and the introduction of non-native species. To evaluate the effects of these changes on the Lake Simcoe offshore benthic community, we collected benthic samples in 2008 at sites allowing statistical comparisons with detailed surveys in 1983 and qualitative comparisons with others focussing more on nearshore collections in 2005 and 1926. Total abundance of benthic invertebrates declined significantly from 1983 to 2008, and correspondence analyses revealed major changes in community composition. Typical of the overall pattern, three of the major benthic taxa (Nematoda, Oligochaeta and Ostracoda) declined from 1983 to 2008, particularly at depths greater than 10 m. Chironomids showed little change in abundance from 1983 to 2008 but their biomass increased because body length nearly doubled during this period. Oligochaete abundance declined but biomass remained the same due to increases in body length from 1983 to 2008. Ostracod abundance and biomass both declined because body size distributions did not change from 1983 to 2008. In contrast to total invertebrate abundance, that of dreissenid mussels, amphipods, isopods, gastropods and sphaeriids increased and these taxa also occupied greater depths (up to 30 m) in 2008 compared with historical surveys. Our results suggest a strong effect of both water quality changes and dreissenid establishment in shaping the contemporary Lake Simcoe benthic invertebrate community.

Introduction

Benthic invertebrate communities of many lakes throughout the world have changed as a result of increasing contaminant (and/or nutrient) loading and the introduction of invasive species. It has been suggested that declining phosphorous loading and the introduction and spread of *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel) are two of the main factors causing changes in benthic communities in the Great Lakes region (Nalepa et al., 2007). Benthic invertebrate communities are good indicators of recent changes in environmental conditions related to habitat quality and lake productivity (Carter et al., 2006). In lakes where phosphorous loads have been reduced (e.g., Lakes Michigan, Ontario and Erie), overall benthic abundance decreased despite an increase in the abundance of species that are sensitive to poor water quality (Carter et al., 2006). Lower phosphorous concentrations reflect a decrease in lake productivity and may lead to a reduction in organic matter settling in the benthos, a critical source of food for many benthic taxa, particularly in profundal ecosystems (Nalepa et al., 2007).

The introduction and spread of dreissenids have also affected the composition and distribution of benthic communities in the Great Lakes and inland lakes of North America. *Dreissena* are filter-feeding organisms that form dense populations on most shallow, near shore regions (Hecky et al., 2004). Mussels can be found in deep soft substrate but favour harder substrates in near shore zones where they can be responsible for high rates of particle removal due to the renewal of suspended particles by strong currents (Dermott and Kerec, 1997). The most consistent pattern observed in Great Lakes benthic communities upon the establishment of dreissenids is the decline of the deepwater amphipod, *Diporeia*, and the increase of the amphipod *Gammarus* in shallow waters (Nalepa et al., 2009). *Dreissena* appear to divert food and energy from the water column to the benthos, shifting productivity from pelagic to benthic regions through their filtering activities (Nalepa and Fahnenstiel, 1995). Invasion of these mussels has benefited certain benthic species by increasing food availability in the form of mussel biodeposits and increasing the structural complexity of the benthic region (Ricciardi et al., 1997). Additional changes resulting from dreissenid invasion include increased

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competition with benthic organisms for organic material settling in the benthic zone and an increase in water clarity (Nalepa et al., 2007).

Although several researchers have documented changes in benthic invertebrate communities in the Great Lakes associated with dreissenid invasion, none has provided detailed descriptions of long-term changes in the benthic communities of inland lakes such as Lake Simcoe. The Lake Simcoe ecosystem has been subjected to multiple stressors during the past century, including changes in nutrient loads and the introduction of invasive species such as dreissenid mussels. Lake Simcoe is one of the largest freshwater bodies in southern Ontario and is home to coldwater fisheries of great socioeconomic importance (Kilgour et al., 2008) that generates approximately $112 million annually (Eimers et al., 2005). Historically, the major concern for Lake Simcoe has been increases in phosphorus loads from inflowing tributaries and sewage treatment plants (Eimers et al., 2005). Prior to agriculturalization and urbanization of the basin, phosphorous concentrations were relatively uniform across the lake (Johnson and Nicholls, 1989). In the early 1970s Lake Simcoe experienced rapid urbanization and increases in phosphorous loading associated with land use changes (Evans et al., 1996). By the mid 1980s phosphorous loading rates had reached about 90 tonnes per year (Johnson and Nicholls, 1989). The coldwater fishery began to decline due to the loss of habitat as a result of eutrophication of the lake (Evans et al., 1996). The Lake Simcoe Environmental Management Strategy was initiated in the early 1990s to address coldwater fishery declines. Since then, the water quality of the lake has improved and total phosphorous loads have declined to 72 tonnes per year on average (LSRCA and MOE, 2009). However, dreissenid mussels invaded the lake in 1992 (Evans et al. 2011) and the rapid rate of urbanization remains a concern as it continues to affect nutrient inputs to Lake Simcoe (Stantec Consulting Ltd., 2006).

In this study we document changes in the taxonomic composition, abundance and body size of the offshore benthic community of Lake Simcoe associated with changes in nutrient loads and invasive species by comparing data collected in 2008 to previous surveys conducted in 1926 (Rawson, 1930), 1983 (Lake Simcoe Fisheries Assessment Unit; Griffith, 1991) and 2005 (Stantec Consulting Ltd., 2006). If the benthic community of Lake Simcoe has responded primarily to phosphorous abatement, a decline in overall benthic abundance and shifts in taxonomic composition (indicative of improved trophic state, such as a reduction in oligochaete abundance; Nalepa et al., 2003) would be expected. However, if the benthic community responded primarily to dreissenid colonization, we expected declines in sphaeriids and chironomids in the pelagic zone, possibly as a result of modified nutrient pathways (Nalepa et al., 1998; Ricciardi et al., 1997). In addition, increases in amphipods (*Gammarus*) and filter feeders that appear to benefit from the added structural complexity of lake bottoms resulting from the dreissenid shell deposition are expected (Hecky et al., 2004). We had no expectations regarding changes in invertebrate body size when initiating the study.

Methods

Field locations and sampling

Depth-stratified benthic samples were collected at 40 sites across Lake Simcoe between August 13–15 and 26–27, 2008 including nine sites from 1.5 to 38 m deep in Kempenfelt Bay surveyed in 1926 (Rawson, 1930), 25 sites in the main basin along five transects at depths of 10, 15, 20, 25 and 30 m sampled in 1983 (Lake Simcoe Fisheries Assessment Unit; Griffith, 1991) and at six sites from 6 to 40 m deep sampled in 2005 in both Kempenfelt Bay and the western section of the main basin (Stantec Consulting Ltd., 2006) (Fig. 1). We also had access to benthic counts collected in 2005 from seven of the 25 main basin sites corresponding to those reported in Griffith (1991) from depths of 20 and 30 m (M. Rennie, unpubl., Fig. 1).

In 2008 an Eckman grab (area of opening = 0.0225 m^2) was used at sites deeper than 15 m and a petite Ponar grab (area of opening = 0.023 m^2) was used at shallower sites where high abundance of mussels prevented the proper operation of the Eckman grab. Duplicate benthic samples were collected at each of the 40 sites and combined into a single composite sample. Sediments were placed in buckets and returned to the lab for sieving with tap water to prevent sample contamination. Grab samples were passed through a sieve box with sequential screens of 500- and 250-µm mesh. Material trapped on each sieve was separately transferred into jars, labelled and preserved with 10% formalin. Eckman grabs of 0.05 m^2 and 0.024 m^2 were used in 1926 and 1983 respectively and in 2005 triplicate samples were taken with a petite Ponar grab of 0.023 m^2 (Kilgour et al., 2008). Samples in 1983 were taken at each site (1–3 replicates per site) with an Eckman grab identical to the one used in 2008. Sediments were placed in buckets and preserved with 10% formalin. Samples were later sorted in the lab using methods described in Griffiths (1991). Triplicate samples from 2005 reported in Kilgour et al. (2008) were taken with a petite Ponar grab identical to the one used in 2008. 2005 samples from the seven main basin sites (Rennie, unpubl.) were from a single grab taken at each site during late July.

Sorting, enumeration and size estimates

All organisms collected in 2008 were counted, identified and sorted into broad taxa (Polychaeta, Nematoda, Ephemeroptera, Anomopoda, Oligochaeta, Ostracoda, Chironomidae (non-tanypodinae), Tanypodinae, Copepoda, Sphaeriidae, Gastropoda, Planaria, Amphipoda, Isopoda, *Dreissena*, Decapoda, Hydracarina, Turbellaria, Trichoptera) using a dissecting microscope at 6–12× magnification. Organism counts, the sums of individuals counted in the 250-µm and 500-µm mesh sieves, were divided by the area of the sampling device to give areal abundance (no/m^{-2}) at all 40 sampling sites.

Body lengths (mm) of preserved Chironomidae, Oligochaeta and Ostracoda (up to 30 individuals per sample) from three sites each at depths of 10, 20 and 30 m common to 1983 and 2008 were measured along the longest body axis from digitized images of the organisms using ImageJ software (version 1.33u; http://rsbweb.nih.gov/ij/). These three taxa were the only ones measured by the agency that collected them in 1983 that were also present in 2008. When more than 30 individuals were present in a sample, they were selected at random for measurement. Individual body mass for these three taxa was determined by weighing to 0.1 mg a known number of preserved individuals patted dry with a kim-wipe, and dividing the total mass by the number of individuals. Individual mass was converted to dry mass using published conversion factors (Cook, 1975).

Two methods were used to estimate biomass concentration for chironomids, oligochaetes and ostracods. We utilized two methods since both rely on simplifying assumptions, which may introduce uncertainty in our estimates. Therefore, agreement in patterns between both methods provides stronger evidence for real patterns, and helps discount spurious results based on simplifying assumptions. In method A the mean masses of individuals measured in 1983 and 2008 (Table 1) were multiplied by abundance to give biomass concentration (mg/m^2) at sampling sites common to 1983 and 2008. However, this method assumes size distributions of individuals are normally distributed, which is often not the case. For method B, all organism lengths measured for a given taxon at the three sites within a depth stratum and year were combined into a single relative size distribution with 1-mm size bins for chironomids and oligochaetes, and 0.1-mm size bins for ostracods. Body masses at the mid-points of each size interval were determined from length-mass equations (Table 2), multiplied by the relative frequency, then summed and

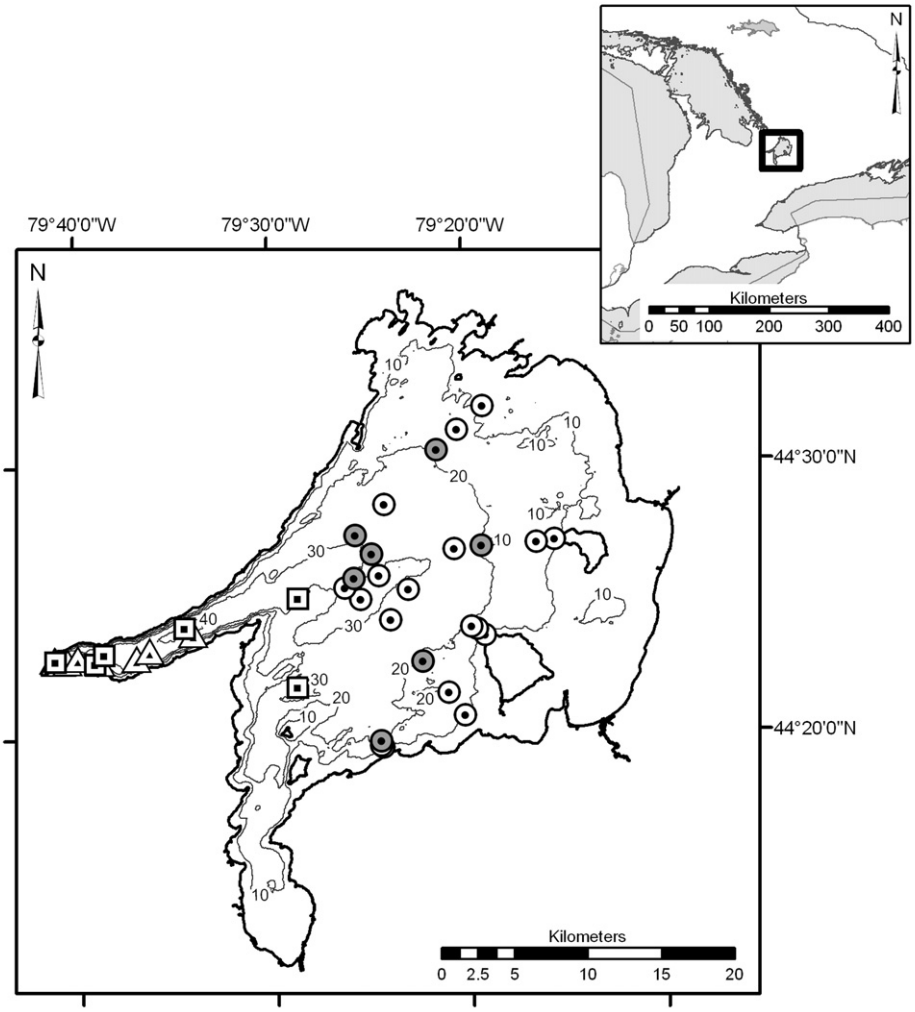

Fig. 1. Location of sampling sites in Lake Simcoe, August 2008. Depth contours are in meters. △ = sites replicated from 1926 survey; ⊙ = sites replicated from 1983 survey; ▣ = sites replicated from 2005 survey, ⊙(shaded) = sites also sampled in 2005 (M. Rennie, unpubl.).

scaled to abundance to give biomass concentration (mg/m^2) at each of the sampling sites common to 1983 and 2008. This method, while based on actual size distributions from the lake, relies on length-weight relationships from other systems.

Statistical analysis

Statistical comparisons were only feasible between invertebrate communities in 1983 and 2008 that had a relatively large number of common stations (Fig. 1). Numerical concentration values were $\log_{10}(n+1)$ transformed prior to analysis where appropriate to help homogenize variances and normalize distributions. Minitab 15 software (Minitab Inc, State College, Pennsylvania) was used for statistical analyses. To facilitate multivariate analysis, relatively coarse taxonomic resolution was used to generate an appropriate ratio of taxa (15) to sites (25 common to 1983 and 2008 = 50). Taxa that were found in fewer than 10% of samples over both years (e.g., Decapoda, Hydracarina and Trichoptera) were assumed to be very rare and were excluded from analysis. To generate biplots, we performed correspondence analysis (CA) on transformed areal abundances. As a measure of spatial variation in community structure *within* years we computed multivariate distances between the positions of all possible station pairs within each depth zone (i.e., controlling for depth effects) for

Table 1
Mean individual weights (dry mass, mg) at various depth strata for benthic invertebrates in Lake Simcoe, Canada. Means presented are averages from values at three sites per depth stratum (10, 20, 30 m).

Year	Depth stratum (m)	Chironomidae	Oligochaeta	Ostracoda
1983	10	0.0099	0.0146	0.0196
	20	0.0120	0.0101	0.0117
	30	0.1100	0.0471	0.0131
2008	10	0.4051	0.1982	0.0109
	20	0.3321	0.1024	0.0096
	30	0.2240	0.1815	0.0100

Table 2
Equations used to estimate weight at length for benthic invertebrate taxa in Lake Simcoe, Canada. L is length (mm), W is mass (mg), *N* is number of organisms measured, and R^2 is the variance explained by the regression. Equations for Chironomidae and Oligochaeta are for dry mass. Equation for Ostracoda is for wet (fresh) mass. Values were converted afterwards to dry mass using a published conversion factor for this taxon (0.108, Cook 1975). n/r = not reported in original text.

Taxon	Equation	*N*	R^2	Source
Chironomidae	$W = 0.00215{*}L^{2.71}$	38	0.84	Johnston and Cunjak (1999)
Oligochaeta	$W = 0.025{*}L$	n/r	n/r	Nalepa and Quigley (1980)
Ostracoda	$W = 0.81058{*}L^{2.4755}$	26	0.90	Ron Dermott, unpublished data; Based on *Cadona spp.* collected in Lake Erie

each year sampled (1983 and 2008). To measure variation in community structure *between* years, we determined the multivariate distances between the 1983 and the 2008 positions of each station. We chose chord distance as our measure of dissimilarity as it deals effectively with zero counts and best describes changes in relative abundance (Orloci, 1967). This value ranges between a maximum dissimilarity of $\sqrt{2}$ and a minimum of zero (i.e., total similarity). A two-factor ANOVA, followed by Tukey's post-hoc comparisons, was used to contrast the magnitude of spatial versus temporal variation with chord distance as the dependent variable and depth (10, 15, 20, 25 and 30 m) and scale (within 1983, within 2008, between 1983 and 2008) as independent variables.

To evaluate temporal and spatial changes in invertebrate abundance more closely, two-factor ANOVAs were used with log-transformed taxon abundance as the dependent variable and water depth (10, 15, 20, 25, 30 m) and year (1983, 2008) as independent variables. Seven separate ANOVAs were used, one for total invertebrate abundance and one for each of the benthic taxa from the CA that had non-zero observations at the majority of stations. Critical probability values were Bonferroni corrected to $0.05/7 = 0.0071$. Due to potential methodological concerns regarding the enumeration of ostracods from the 1983 survey (Griffith 1991), we examined community patterns in the CA and in total invertebrate abundance with and without ostracods included.

Similar ANOVAs were used to evaluate temporal changes in log-transformed biomass concentration. Three separate ANOVAs were used, one each for chironomids, oligochaetes and ostracods (the only taxa for which we had size data in both years), and critical probability values Bonferroni corrected to $0.05/3 = 0.0167$. Separate two-factor ANOVAs were also used to evaluate changes in body size of each of chironomids, oligochaetes and ostracods with log-transformed body length (mm) of individual organisms as the dependent variable, depth (10, 20, 30 m) and year (1983, 2008) as the independent variables, and critical probabilities Bonferroni adjusted to $0.05/3 = 0.0167$.

Some taxa did not meet the parametric assumptions of ANOVA, however ANOVA is robust to departures from parametric assumptions especially when statistical designs are balanced as in our study (Zar, 1999; Zolman, 1993).

Qualitative comparisons to previous surveys

To qualitatively examine long-term changes in the Lake Simcoe benthic community, we compared the 2008 survey data to those reported in the three previous benthic community surveys. Data collected in 1926 and 2005 were from 500-μm sieves only, and were compared to 2008 data from the 500-μm sieves. Because organism counts from the 1983 survey were a combination of individuals found in the 250-μm and 500-μm meshes, we adjusted these counts by using taxon-specific proportions of individuals collected on the 500-μm sieve in 2008. Due to variation in sampling depth among historical surveys, we assigned sites to six depth zones in order to facilitate qualitative comparisons among years: 0–9.9 m, 10–14.9 m, 15–19.9 m, 20–24.9 m, 25–29.9 m and >30 m, respectively. Densities of all invertebrates combined, and of nine taxa (those comprising approximately 93% of all invertebrates over all years) were graphed and visually compared to examine trends among years or depth zones.

Results

Abundance at common stations, 1983 and 2008

Biplots from the CA demonstrated a clear separation of sites between 1983 and 2008, indicating substantial community change during this time (Fig. 2A). The first two axes described 52.4% of the total variation in benthic invertebrate abundance. Nematodes and dreissenids explained the greatest proportion of variation in the first axis (25% and 22% respectively), followed by amphipods (13%), gastropods (12%) and isopods (10%). Variation in axis 2 was primarily attributed to Planaria (26%), Ephemeroptera (14%) and sphaeriids (14%). Ostracods did not explain any major component of variation (<3%) on any of the first four axes. While 1983 sites clustered together, site scores in 2008 were more structured by depth along both the first and second axes, with 10-m sites being distinct from sites at 20–30 m, and 15-m sites being intermediate (Fig. 2A). Spatial differences among transects were minor since sites did not group by transect in either year (Fig. 2B). CA results on the data with ostracods removed were nearly identical to those with ostracods; the first two axes described 52% of the total variation in benthic invertebrate abundance. Again, nematodes and dreissenids explained the most variation on the first axis, followed by amphipods and gastropods. Axis 2 was best explained by variation in Turbellaria, Sphaeriids and Ephemeropterans. Patterns of clustering were also similar.

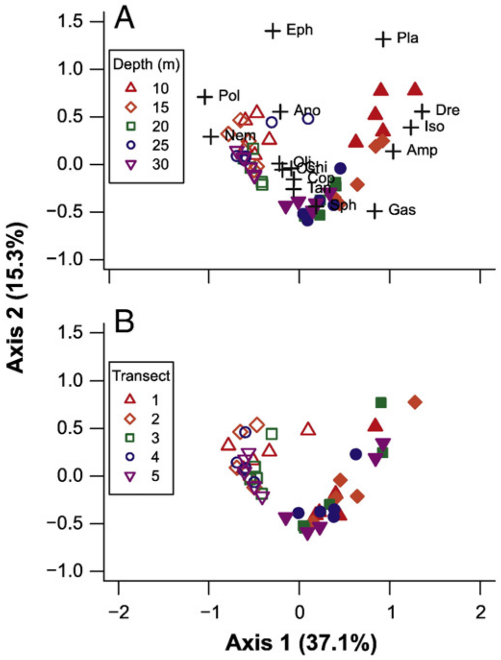

Fig. 2. Biplot of correspondence analysis showing scores of taxa (+) and sites (open symbols are 1983 and closed are 2008) along the first two axes by (A) depth and (B) transect. The percentage of total variation explained by each axis is shown. Taxon abbreviations are **Pol**ychaeta, **Nem**atoda, **Eph**emeroptera, **Ano**mopoda, **Oli**gochaeta, **Ost**racoda, **Chi**ronomidae (non-tanypodinae), **Tan**ypodinae, **Cop**epoda, **Sph**aeriidae, **Gas**tropoda, **Pla**naria, **Amp**hipoda, **Iso**poda and **Dre**issena.

The two-factor ANOVA of chord distances showed significant effects of scale, depth and interaction ($F_{2,210} = 230$, $F_{4,210} = 19.4$, $F_{8,210} = 3.9$, respectively, all p-values <0.0003), hence we analyzed all treatment combinations with the post-hoc Tukey's test. Chord distances between site pairs within each depth zone were similar in 1983 and 2008 (Tukey's test, 1983 vs. 2008, $p = 0.98$), and did not vary systematically with depth (Fig 3). Values were approximately 0.45 on average for both years. We considered this to represent within-year variation among sites. In comparison, chord distances of individual sites between 1983 and 2008 were 0.82 on average, nearly double within-year variation and were statistically distinct from within-year chord distances for both 1983 and 2008 (Fig. 3; Tukey's test, $p<0.0001$). Chord distances between 1983 and 2008 sites were also greater at shallower depths (Fig. 3), suggesting greater changes in the benthic invertebrate community have occurred in shallow zones than in deep, offshore areas. Patterns in chord distances with ostracods removed were identical (scale, $F_{2,210} = 236$; depth

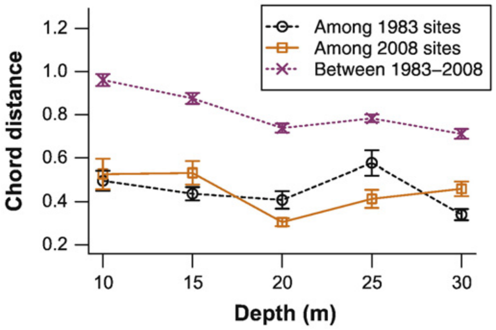

Fig. 3. Chord distances for each depth zone from biplots (Fig. 1) between site pairs (squares and solid lines: 2008, circles and dashed lines: 1983) and between the same sites in 1983 and 2008 (X, dotted line). Chord distance of √2 = most different, 0 = exact similarity. Values are means ± standard error of mean.

$F_{4,210} = 10.5$; interaction, $F_{8,210} = 3.9$, all $p < 0.0003$), though distance measures for all taxa were slightly lower (0.08 on average).

Total invertebrate abundance was lower in 2008 than 1983 except at the shallowest depth. Though total abundance varied more with depth in 1983 than in 2008, there was no significant interaction between year and depth (Fig. 4, Table 3). With ostracods removed, the interaction between year and depth was significant (Fig. 4, Table 3); total invertebrate abundances at depths > 20 m were 50% to 25% of those in 1983, though invertebrate abundance at shallower depths was similar between years. In contrast to patterns in total abundance, gastropods, amphipods, and isopods were virtually absent in 1983 (amphipods were found only in one sample) but were abundant in 2008. Sphaeriid abundance was significantly greater in 2008 than 1983, and despite lower 2008 abundance at the shallowest depth, did not statistically vary with depth in either year; there was also no interaction between depth and year (Table 3, Fig. 4). Similar to patterns in total abundance, nematodes were extremely rare in 2008 despite being common and abundant in 1983. Polychaetes, which were patchily distributed in 1983 at depths of 10–15 m, were undetected in 2008. Oligochaete and ostracod abundance was significantly lower in 2008 than in 1983 (Table 3). Oligochaete abundance did not vary with depth, while ostracod abundance increased significantly with depth (Table 3). While there were no significant interactions between year and depth for either taxon, differences in abundance between years appeared to be greatest in deeper zones while minor changes were observed at 10 m (Fig. 4). Total chironomid abundance did not differ statistically between 2008 and 1983 (Table 3), though abundance at 30 m were about four times lower in 2008 (Fig. 4). Neither did non-predaceous chironomid abundance differ between years, but it did vary with depth (Fig 4). Predaceous chironomid (Tanypodinae) abundance varied neither with

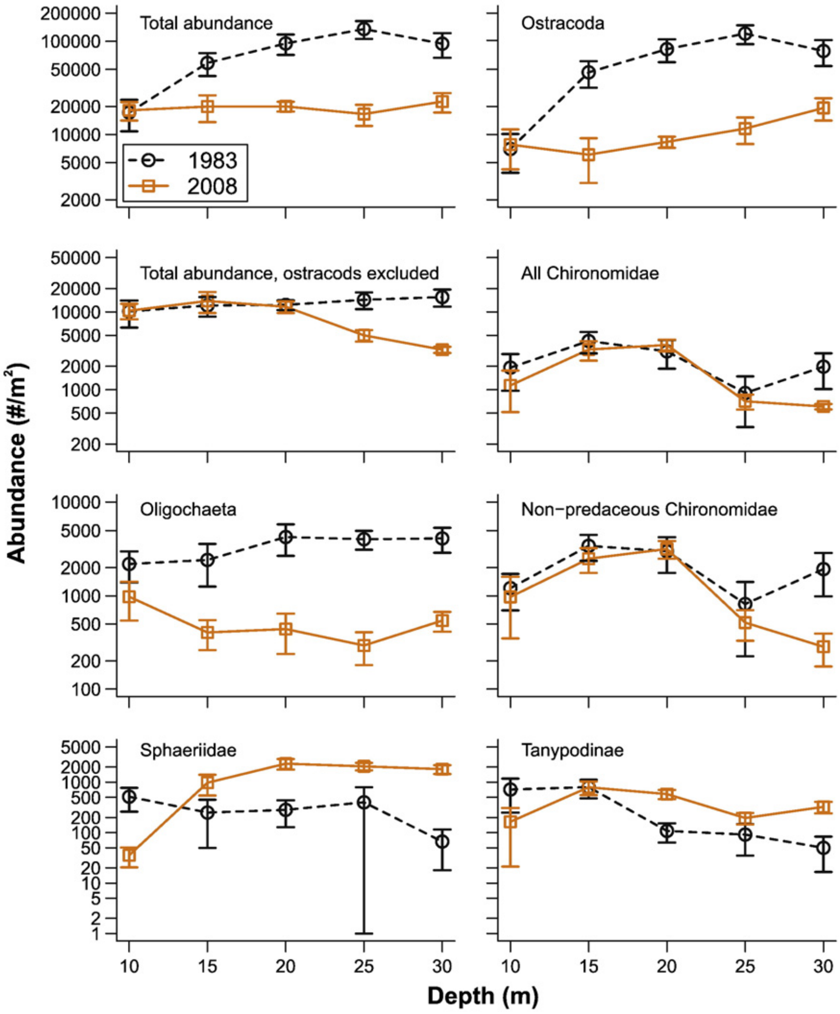

Fig. 4. Comparison of abundance (No/m^2 ± standard error) for total and major benthic taxa (those that had non-zero observations at the majority of stations) over depth in the main basin of Lake Simcoe in 1983 (circles and dashed lines; Griffith, 1991) and 2008 (squares and solid lines; this study).

Table 3

F-values and probabilities from results of two-factor ANOVAs on log- transformed abundance and biomass compared between 1983 and 2008 and among depths. Abundance degrees of freedom associated with year, depth, interaction and error were 1, 4, 4 and 40 respectively (1, 2, 2 and 24 for biomass). Biomass (A) are biomass estimates using mean dry weights for each depth zone, Biomass (B) utilize length distributions and length-weight equations (Table 2). Critical *p*-values are Bonferroni corrected to 0.0071 for abundance and 0.017 for biomass estimates. Values in bold are statistically significant.

Taxon		Abundance		Biomass (A)		Biomass (B)	
	Factor	*F*	*p*	*F*	*p*	*F*	*p*
Total abundance	Year	24.9	<**0.0001**				
	Depth	4.67	**0.0035**				
	Year × Depth	3.94	0.0087				
Total abundance (ostracods removed)	Year	2.865	0.0971				
	Depth	0.81	0.3729				
	Year × Depth	10.18	**0.0025**				
Total Chironomidae	Year	0.0003	0.9866	27.85	<**0.0001**	18.17	**0.0003**
	Depth	3.56	0.0142	3.94	0.0330	7.84	**0.0024**
	Year × Depth	0.75	0.5661	6.11	**0.0071**	0.34	0.7141
Non-predaceous Chironomidae	Year	0.37	0.5469				
	Depth	4.36	**0.0050**				
	Year × Depth	0.90	0.4749				
Tanypodinae	Year	1.72	0.1968				
	Depth	1.78	0.1518				
	Year × Depth	2.77	0.0404				
Sphaeriidae	Year	23.76	<**0.0001**				
	Depth	1.21	0.3206				
	Year × Depth	3.68	0.0121				
Oligochaeta	Year	26.78	<**0.0001**	0.094	0.7615	5.25	0.0311
	Depth	0.58	0.6796	2.67	0.0894	1.27	0.2969
	Year × Depth	0.22	0.9231	1.35	0.2788	0.66	0.5260
Ostracoda	Year	17.34	**0.0002**	5.71	0.0251	2.77	0.1088
	Depth	6.53	**0.0004**	7.13	**0.0037**	10.37	**0.0006**
	Year × Depth	2.22	0.0837	1.41	0.2631	2.52	0.1012

year nor depth although did tend to be lower at the shallowest depths in 2008, and higher at depths greater than 15 m (Fig. 4).

Size distributions and biomass, 1983–2008

The mean lengths of chironomids and oligochaetes more than doubled from 1983–2008 (Table 4, Fig. 5). Increases in size were greatest at shallow depths, and less dramatic at deeper sites (Fig. 5). Size distributions of ostracods were similar between years, but varied significantly with depth (Table 4, Fig. 5).

Patterns of invertebrate biomass differed from abundance in two of three taxa for which size data were available. While chironomid abundance was not significantly different between years, biomass was significantly greater in 2008 no matter which method of computing biomass was used (Table 3, Fig. 6). Although oligochaete abundance was significantly lower in 2008 than 1983, biomass did not differ between years based on either computation method (Table 3, Fig. 6). Ostracod biomass tended to increase with depth. Apparently lower biomass in 2008 was not statistically significant despite differences of an order of magnitude at 20 and 30 m (Table 3, Fig. 6).

Table 4

F-values and probabilities from results of two-factor ANOVAs for log- transformed lengths compared between 1983 and 2008 and across 10, 20 and 30 m depth strata. Critical *p*-values are Bonferroni corrected to 0.017. Values in bold are statistically significant.

Taxon		Length		
	Factor	*df*	*F*	*p*
Total chironomidae	Year	1	207.81	<**0.0001**
	Depth	2	11.14	<**0.0001**
	Year × Depth	2	7.74	**0.0005**
	Residual	295		
Oligochaeta	Year	1	130.96	<**0.0001**
	Depth	2	7.42	<**0.0001**
	Year × Depth	2	9.47	<**0.0001**
	Residual	341		
Ostracoda	Year	1	0.03	0.8587
	Depth	2	9.57	<**0.0001**
	Year × Depth	2	1.07	0.3434
	Residual	453		

Qualitative long term trends and comparisons

Qualitative comparisons of abundance across all years for which data were available indicate that total invertebrate abundance in 2005 and 2008 was intermediate between 1926 and 1983. *Dreissena* were present only in 2005 and 2008 (Fig. 7). Similarly, amphipods and isopods were rare before 2005 and occupied all depths (up to 30 m) by 2008 (Fig. 7). Although present in the lake at most depths since 1926, sphaeriids have generally increased in abundance, particularly at greater depths, and by 2008 occupied all depth zones (Fig. 7). Gastropods were present in most depth zones in 1926, were absent in 1983, but then became more abundant at most depths by 2005 and 2008 (Fig. 7). In contrast to these patterns, ostracods and nematodes were rare in 1926 but abundant in all but the shallowest depth in 1983. Since then nematode abundance decreased gradually until they were quite rare in all but >30 m in 2008, while ostracods decreased at mid-water depths in 2005 but increased again by 2008 (Fig. 7). Chironomid abundance in 2008 appears to be lower than those in 1983 and 2005, but greater than those in 1926.

Discussion

The Lake Simcoe offshore benthic invertebrate community composition has changed dramatically in years following phosphorous abatement and dreissenid colonization. Community composition shifted from high abundances of nematodes and low abundances of isopods, amphipods and gastropods in 1983 to the opposite pattern in 2008 along with the additional appearance of dreissenid mussels. Within-year variation in community composition was quite low in both years compared to much greater change in composition at the same site between years, particularly at shallow sites.

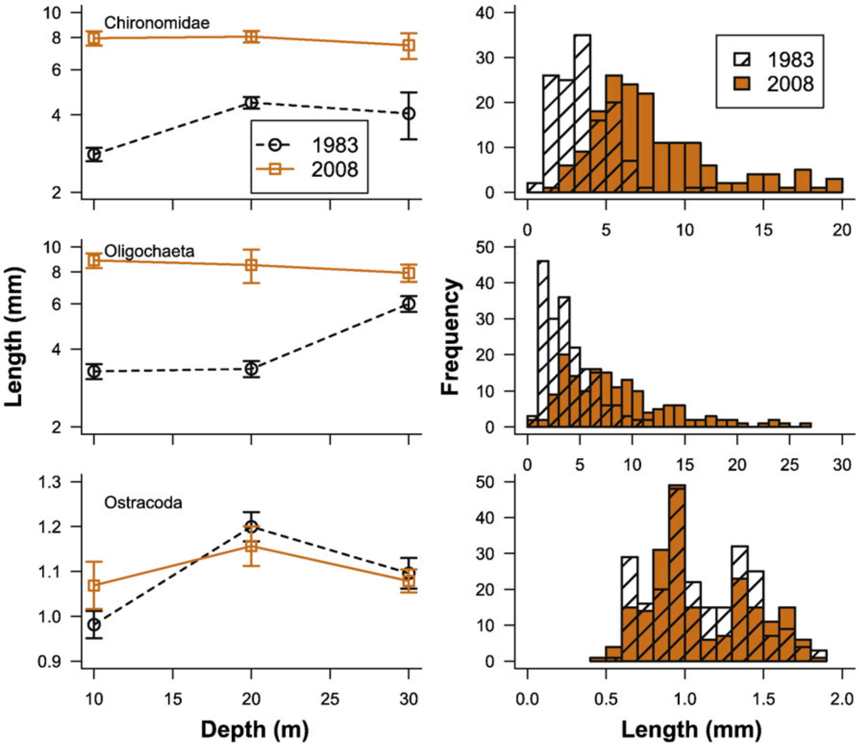

Fig. 5. Relation between mean length (± standard error) and depth of chironomids, oligochaetes and ostracods (taxa for which length data were available) for 1983 and 2008 (left panel, symbols as in Fig. 4), and size-frequency distributions of all measured individuals (right panel, 1983 cross-hatched open bars, 2008 are shaded bars).

In contrast to previous studies in which increases in total invertebrate abundances were reported following *Dreissena* invasion (Griffiths, 1993; Stewart and Haynes, 1994), total invertebrate abundance in Lake Simcoe was lower in 1983 than 2008 by nearly an order of magnitude due particularly to lower abundances of ostracods, nematodes and oligochaetes. When ignoring ostracod abundance, total invertebrate abundance was lower only at depths greater than 20 m. One of the most consistent changes in benthic

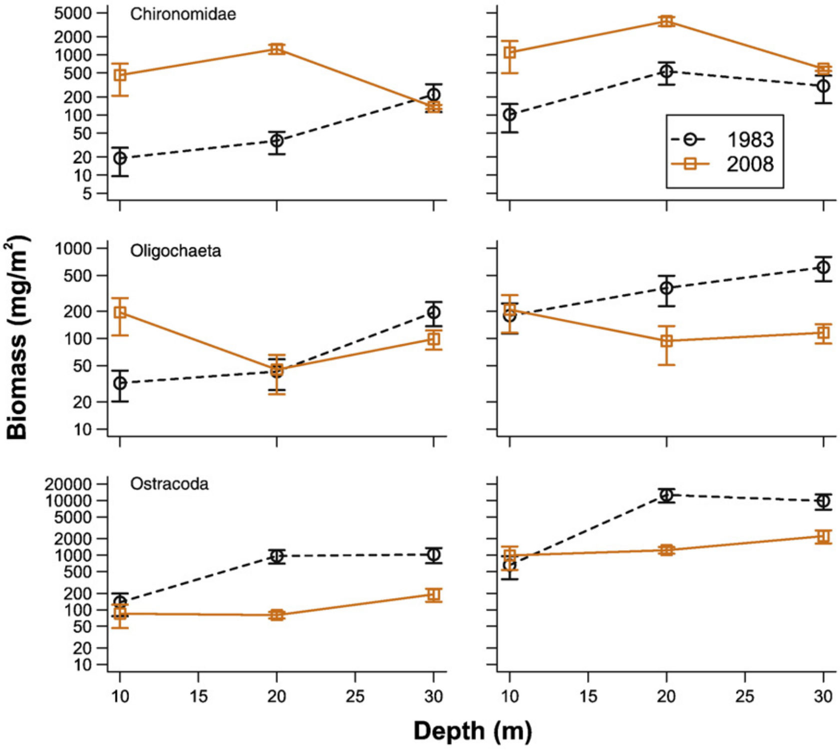

Fig. 6. Biomass (mg dry weight/m^2) of Lake Simcoe benthic invertebrates for which length data were available (chironomids, oligochaetes and ostracods), 1983-2008. Left panels show biomass estimated using method A (based on mean invertebrate weights; see text for details). Right panels show biomass estimated using method B (based on distributions of length and length-weight relationships; see text for details). Symbols as in Fig. 4.

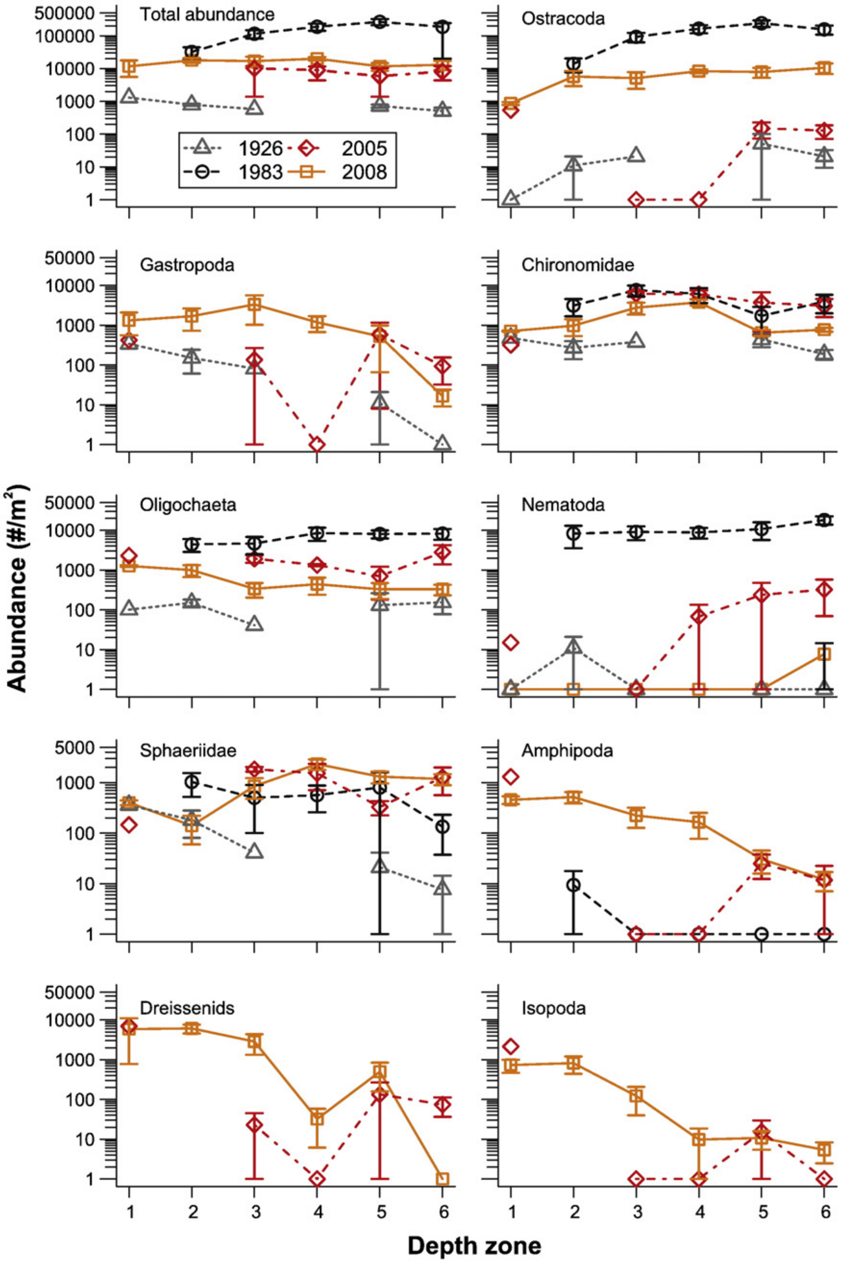

Fig. 7. Numerical abundance (mean no/m^2 ± standard error) from 500-μm mesh of total invertebrate abundance and major benthic invertebrate taxa (those comprising 93% of the invertebrate community in the 1983–2008 correspondence analysis) for all years with data. Depth zone 1 corresponds to depths 0–9.9 m, depth zone 2 to 10–14.9 m, depth zone 3 to 15–19.9 m, depth zone 4 to 20–24.9 m, depth zone 5 to 25–29.9 m and depth zone 6 to > 30 m. Densities were based on surveys in 1926 (Rawson, 1930; Triangles, dotted lines), 1983 (Griffith, 1991; circles, dashed lines), 2005 (Stantec Consulting Ltd., 2006; diamonds, dot-dash lines) and 2008 (this study; squares, solid lines). Depth zone 4 was missing in 1926, as were zones 1 and 2 in 1983 and 2005, respectively.

invertebrate communities in the Great Lakes has been the decline in *Diporeia*, but this genus has never been documented in Lake Simcoe (Rawson, 1930; this study).

Lower nematode abundance in 2008 in Lake Simcoe compared to 1983 contrasts with results for Lake Erie from Dermott and Kerec (1997) who found that abundance of nematodes increased due to increases in food sources such as organic matter and bacteria in the faeces and pseudofaeces deposited by *Dreissena*. Some species of nematodes can tolerate anoxia, and this may explain relatively high Lake Simcoe abundance in 1983, a year with relatively low mean volume weighted oxygen (Evans et al., 1996). Decreases in phosphorous concentrations and associated increases in oxygen levels from 1983 to 2008 may have led to the decline in nematodes while favouring other taxa requiring higher oxygen concentrations.

Ostracod abundance and biomass increased from 1926 to 2008, but the decline in abundance between 1983 and 2008 may be at least partially methodological. Griffith (1991) reported that high abundance found 1983 may have resulted from discrepancies in sorting and counting procedures and suggested that ostracods recorded in 1983 might have been confused with shells of dead individuals. A second possibility was that empty half-shells of ostracods may have been counted as whole animals. While we therefore have to be cautious in our interpretations, ostracods were nevertheless still abundant in 2008 with an overall mean abundance of 5031/m^2, an increase of two orders of magnitude from 1926 when no methodological problems were reported (Rawson, 1930). Others have noted positive effects of *Dreissena* on ostracod abundance (Dermott and Kerec; 1997, Ricciardi et al., 1997). Bially and MacIsaac (2000) found ostracods to benefit from increased organic matter and complex substrata associated with *Dreissena*.

Total benthic invertebrate abundance was lower in 2008 than 1983 despite higher abundance for a number of other taxa, such as dreissenids, gastropods, isopods and amphipods that were absent or rare in 1983. The absence of certain taxa in 1983 may reflect the effects of eutrophication and low oxygen in the deep waters of the lake associated with higher phosphorous loads during the 1980 s (Eimers et al., 2005; Evans et al., 1996). Krieger and Ross (1993) suggested nutrient increases in Lake Erie led to oxygen depletion in the late 1970s that severely reduced the distribution and abundance of many benthic invertebrates. Carter et al. (2006) also found that anthropogenic increase of nutrients and organic inputs into Muskegon Lake severely degraded benthic communities in the 1970s. It is possible that gastropods and amphipods were present in 1983 but at depths shallower than 10 m that were not sampled. Rawson (1930) reported the highest abundances of gastropods at 3–8 m and amphipods at 4 m.

The reappearance of gastropods in 2005 and 2008 may be a response to an increase in food supply and structural complexity of lake bottoms associated with *Dreissena*. In littoral regions, nutrient release by dreissenids and increased light penetration from filtering activities can result in higher benthic algal growth that in turn provides a food source for gastropods (Bially and MacIssac 2000; Griffiths, 1993; Ricciardi et al., 1997; Stewart and Haynes, 1994).

The increases we observed in the abundance of deposit feeding taxa such as amphipods and isopods following the dreissenid invasion have been noted in several studies (Gonzalez and Downing, 1999; Nalepa et al., 2003; Ricciardi et al., 1997; Stewart and Haynes, 1994). In addition, the first occurrence of high abundances of the amphipod *Echinogammarus ischnus* in Lake Simcoe was reported in the 2005 survey, a species often associated with *Dreissena* (Kilgour et al., 2008). These increases in amphipod and isopod abundance coincided with increases in dreissenid abundance at greater depths by 2005 and 2008. They may be associated with greater substrate complexity at depth when dreissenids colonize by settling on accumulations of their own shells (Hecky et al., 2004; Ricciardi et al., 1997). Increases in amphipods can have positive effects since they are prey for fish of commercial and recreational importance in Lake Simcoe such as yellow perch (*Perca flavescens;* Gonzalez and Downing, 1999; Hayward and Margraf, 1987; Roseman et al., 1996).

Our data indicated that sphaeriids were significantly more abundant in 2008 than 1983 at depths greater than 20 m despite previous findings showing declines in response to phosphorus reductions (e.g., Lake Michigan: Nalepa et al., 1998, Nalepa et al., 2003). It has been argued that an increase in sphaeriids in response to nutrient enrichment is typical for large, deep lakes such as Lake Michigan, where the volume of the hypolimnion is much greater than that of the epilimnion, and oxygen never becomes limiting (Krieger and Ross, 1993; Saether, 1980). However, in smaller shallower lakes, such as Lakes Erie and Simcoe, oxygen can become limiting as a result of nutrient enrichment and restrict the abundance of certain benthic groups (Krieger and Ross, 1993). In the case of Lake Simcoe, higher sphaeriid abundance may be in response to reductions of nutrient enrichment, increase in summer oxygen levels and overall improvements in the quality of benthic habitats compared to conditions reported in the 1980 s. The relatively low contemporary abundance of sphaeriids at depths more shallow than 20 m, where dreissenids are found in greatest abundance, may result from an increase in competition for food, or physical attachment by *Dreissena* that may limit the mobility of sphaeriids and disrupt their reproductive habits. This may also limit their ability to avoid predators or force them to occupy unfavorable environmental conditions (Nalepa et al., 2003; Van Appledorn and Bach, 2007).

While our data on size distributions were limited, we observed significantly larger sizes of both chironomids and oligochaetes in 2008 compared to 1983, two taxa for which abundance either declined or was relatively unchanged from 1983. For chironomids, the shift in size distribution was so large that biomass was an order of magnitude higher in 2008 than 1983 whereas patterns in abundance between these years were not statistically different. This pattern is opposite to observations from Lake Erie, where, after declines in nutrient loading and dreissenid invasion, chironomid biomass *declined* despite very little change in chironomid abundance (Dermott and Kerec, 1997). For oligochaetes, the increase in length and mean size was large enough to either counter or reverse declines in abundance. Such dramatic shifts in body size are almost certainly associated with species changes within these broad taxa between years, possibly associated with changes in water quality. These observations stress how interpretations regarding ecosystem change can differ whether based on abundance or biomass data.

It is unlikely that the necessary use of a petite Ponar (vs. Ekman) grab to sample shallow depths in 2008 affected our general conclusions. While some studies suggest differences in the sediment penetration between these samplers, others report them to generate similar estimates of invertebrate abundance and community composition (Elliott and Drake, 1981; Schloesser and Nalepa, 2002). Another study reported very little effect of sediment penetration between 5 and 10 cm depth on chironomid biomass estimates (Sherfy et al., 2000).

Since the reduction of phosphorus loads into Lake Simcoe, there have been some shifts in communities that are indicative of improved conditions. Despite having increased in body size, oligochaetes declined significantly through time, a change more likely associated with decreases in nutrient loads than with dreissenid invasion (Nalepa et al., 1998). This is consistent with studies on eastern Lake Erie where oligochaete abundance also declined during a period of oligotrophication and dreissenid invasion (Dermott and Kerec, 1997). It has been suggested that oligochaetes may actually increase in abundance in response to *Dreissena* feces and pseudofaeces that provide additional food (McNickle et al., 2006; Stewart and Haynes, 1994). Therefore, lower oligochaete abundance in 2008 than 1983 is more likely to be attributed to the reduction of phosphorous loads and productivity of Lake Simcoe. Although there was no statistical interaction between year and depth for either chironomids or oligochaetes, there was nevertheless a slight tendency for the abundance of both taxa to be lower at greater depths in 2008 compared to 1983 (depths greater than 20 m for oligochaetes, and 25 m for chironomids). It has been suggested that initial filtering, interception and retention of nutrients by *Dreissena* in littoral regions deprives deep water regions of nutrient inputs resulting in a decline of these two taxa at greater depths (Hecky et al., 2004; Nalepa et al., 2003). Declines in these taxa and in the total abundance of offshore invertebrates in general may reflect this interception of energy otherwise destined for the profundal community.

In summary, our data indicated a shift in benthic taxa indicative of an improved trophic state and quality of the benthic environment of Lake Simcoe. In addition, changes in the abundances and distributions of certain taxa, such as amphipods, isopods and gastropods community, are consistent with the effects of invasive dreissenids. However, it is difficult to assign specific responses of the benthic community to either environmental variables or biological interactions because of the complex nature of the changing food web. Further monitoring and integrated studies on all food web components of the lake will provide a better understanding of the complex changes and interactions occurring in the Lake Simcoe ecosystem.

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