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Decadal changes in benthic invertebrate biomass and community structure in Lake Simcoe

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Abstract. Total benthic invertebrate biomass in shallow offshore waters (depths 10–15 m) increased 17-fold on average following the invasion of dreissenid mussels and implementation of P controls in Lake Simcoe, Ontario, despite a 50% overall decrease in total invertebrate density during the same time period. The increase in total invertebrate biomass at 10- and 15-m depths was primarily dreissenid biomass. Patterns of biomass with depth and dreissenid invasion for individual taxa were typically similar to those for density. Biomass of chironomid and nondreissenid bivalves declined at shallow (10–15 m) sites but increased at the deepest (20–30 m) sites, whereas biomass of oligochaetes declined at all sites. Density and biomass of Amphipoda, Isopoda, and Gastropoda increased at depths $\geq$10 m, and these taxa were found more frequently in deeper sites after dreissenid invasion than before. Increased habitation of deeper sites by these taxa may be mediated by increased habitat complexity caused by deposition of dreissenid shells, nutrient enrichment of substrate occupied by dreissenids, and improvements in hypolimnetic dissolved O_2 and water clarity observed during dreissenid invasion. Increased length and biomass of profundal chironomids after dreissenid invasion may be the result of taxonomic changes in the chironomid community, which in turn appear to be closely associated with improvements in deep-water O_2 concentrations. Changes in the benthic community described here probably have important consequences for the degree of coupling between nearshore and offshore habitats in Lake Simcoe.

Key words: Lake Simcoe, *Dreissena polymorpha*, benthic invertebrates, benthic–pelagic coupling, ecosystem engineering, productivity, community composition.

The dreissenid mussels (zebra mussel, *Dreissena polymorpha*; quagga mussel, *Dreissena rostriformis bugensis*) are among the more problematic invasive taxa in North America. These mussels have affected production (and related processes) in aquatic ecosystems. In a recent meta-analysis, Higgins and Vander Zanden (2010) described some of the far-reaching effects these species have had on water chemistry and lower trophic components of aquatic ecosystems. Consistent with predictions of the nearshore P shunt model (Hecky et al. 2004), dreissenids appear to redirect a significant component of primary production in aquatic ecosystems toward the nearshore (Higgins and Vander Zanden 2010). This redirection can lead to increased nearshore–offshore coupling in traditionally offshore consumer species (Rennie et al. 2009b), potentially as a result of reduced offshore production that has been linked to dreissenids (Fahnenstiel et al. 2010). Dreissenids negatively affect growth, condition, and feeding ecology of benthivorous fishes (French and Bur 1996, Rennie et al. 2009a, b).

Extensive research in the Great Lakes has documented effects of dreissenids on benthic invertebrate communities (e.g., Dermott and Kerec 1997, McNickle et al. 2006, Nalepa et al. 2009), but far less is known about their effects on inland North American lakes (but see Miehls et al. 2009a). Inland lakes may show a more pronounced response to dreissenid establishment because of their smaller size, typically shallower

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depths, and higher ratio of littoral area to volume compared with the Great Lakes.

Urban development has intensified in the watershed of Lake Simcoe (Ontario, Canada) over the past 50 y, and basin-wide P-reduction strategies have been in place since the early 1980s (Nicholls 1995, Evans et al. 1996, Winter et al. 2007). Despite reductions in P loading, in-lake ice-free total P (TP) concentrations have changed little, and show no clear directional trend toward TP reduction (Young et al. 2011). Natural recruitment of zebra mussels was first detected in Lake Simcoe in 1994, and the species was well established by 1996 (Evans et al. 2011). Changes in Lake Simcoe water clarity and algal biovolumes coincided with reductions in P loading and the appearance of zebra mussels (Eimers et al. 2005). Jimenez et al. (2011) showed that the Lake Simcoe benthic invertebrate community was markedly different in 1983 than in 2008. However, Jimenez et al. (2011) compared only 2 points in time. Thus, the degree to which the observed patterns were a result of environmental conditions specific to those particular years or characterized the pre- and postinvasion benthic communities in Lake Simcoe could not be assessed.

With a few exceptions (Dermott and Kerec 1997, Karatayev et al. 1997, Mercer et al. 1999), responses of lentic benthic invertebrate communities to dreissenid invasion have been measured in terms of changes in density (Higgins and Vander Zanden 2010). Density responses can indicate overall change but, unlike biomass, provide little information regarding how these changes might affect energy transfer from the sediments to the benthic invertebrate community or from benthic invertebrates to secondary consumers (including fishes). Furthermore, patterns of biomass often cannot be inferred from patterns in density (e.g., Jimenez et al. 2011). Whole-community estimates of benthic biomass in Lake Simcoe are currently lacking.

We addressed the effects of dreissenids on the benthic invertebrate community of Lake Simcoe by comparing trends in density and biomass of benthic invertebrates over a period from 1982 to 2009 with regard to the timing of dreissenid invasion. We also interpreted published data (Eimers et al. 2005, Winter et al. 2011, Young et al. 2011) to evaluate the degree to which changes in water quality unrelated to dreissenids might influence our results as well as the potential indirect effects of dreissenids on benthos via effects on water quality.

Methods

Sampling

Benthic invertebrates were sampled along a nearshore–offshore transect on Lake Simcoe, Ontario (Fig. 1) during 1982, 1983, 1986, 2008, and 2009. The transect originated at Sibbald Point Provincial Park and continued toward an Ontario Ministry of Environment long-term sampling station, K45 (Nicholls 1995). Sites were sampled on the transect at 5, 10, 15, 20, 25, and 30 m depths. In most years, sampling was done in late summer (July–September). However, in 1986 samples were collected under the ice in March. Depending on the year of the survey, 3 to 7 replicate samples were taken at each site (Table 1). Samples were taken at 5 m only in 1983, 1986, and 2009. Sampling was done with a 15.24-cm Ekman dredge. In 2008 and 2009, a 15.24-cm mini-Ponar dredge was used in areas where dreissenids interfered with the operation of the Ekman dredge. Organisms were collected on a 500-μm sieve and preserved in 10% buffered formalin.

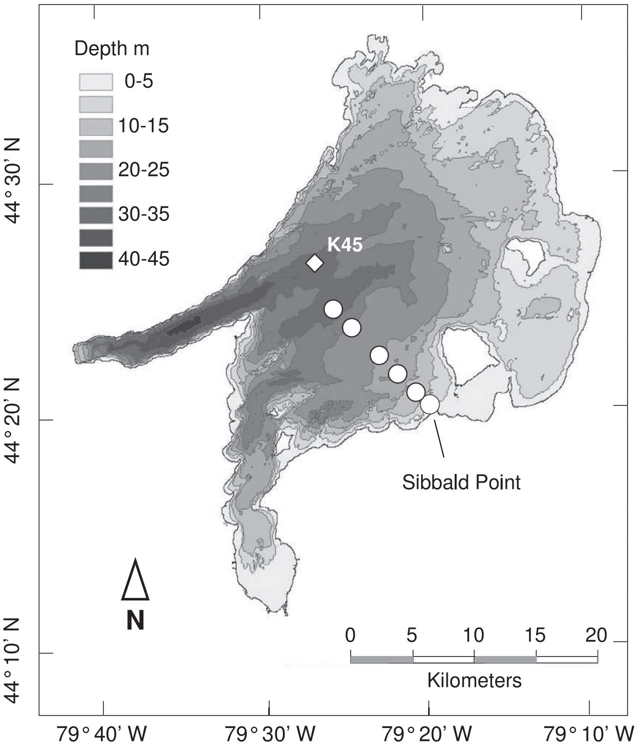

Fig. 1. Map of Lake Simcoe showing location of sites along the transect sampled and lake bathymetry. K45 is an Ontario government water sampling site, shown for reference.

Sorting and measurement

Samples were sorted in the laboratory and separated into broad taxonomic groups (mostly order, except Chironomidae and *Dreissena* spp.; Table 2), enumerated, and returned to 10% buffered formalin. We revisited preserved samples in 2009 to measure

TABLE 1. Number of replicate samples taken on offshore transects at each depth strata.

	Year				
	Preinvasion			Postinvasion	
Depth (m)	1982	1983	1986	2008[a]	2009
5	–	6	3	–	3
10	6	6	3	3	3
15	7	6	3	3	3
20	7	6	3	3	3
25	4	6	3	3	3
30	7	6	3	3	3

[a] Data from 2 adjacent transects in 2008 survey included to increase sample sizes

lengths and masses needed to develop length–mass regressions. When densities of a taxon were high, we randomly selected up to 25 individuals (from replicate samples where possible) from each site in each year (subsampling occurred in 12% of 252 site × year × taxon combinations investigated). We measured lengths as the distance along the longest axis of the organism. We also weighed a subset of organisms from 1982 and 2008 samples (Table 2). We dabbed each organism with a clean laboratory wipe and weighed it to the nearest 0.01 mg. We estimated proportions of soft tissues vs whole organisms (shells and soft tissues) for shelled organisms (*Dreissena*: 19% of total mass, Gastropoda: 34%, Ostracoda: 29%, nondreissenid Bivalvia: 34%; sample sizes for proportions of soft tissues were as in Table 2 for these taxa).

Length distributions

We inspected mean lengths of organisms from all years visually for differences across sites (depths) and between years pre- (1982, 1983, 1986) and post- (2008, 2009) dreissenid invasion where data were sufficient. Length data at all sites in all years were not available for any taxon, so we estimated mean lengths for each taxon for pre- and postinvasion years to permit estimation of biomass. This procedure allowed us to select the appropriate level of detail in length-frequency distributions to estimate biomass of each taxon. Length-frequency distributions for Amphipoda, Chironomidae, Gastropoda, and Oligochaeta corresponded to mean values estimated for each depth and time period (pre- and postinvasion). Insufficient data on Ephemeroptera and nondreissenid Bivalvia were available from all depths and both

TABLE 2. Length–mass relationships for taxa examined in this study. Lengths (L) are in mm. Relationship for mass is for 10% formalin-preserved wet mass (mg). Preservation correction factors are presented as % mass loss relative to unpreserved samples as reported in the literature. n = sample size, n/a = not applicable. Bold indicated significant difference in parameter among years.

Taxa	n	Years examined	Difference in slopes among years	Difference in intercepts among years	Mass (mg)	Preservation correction factors (source reference)[g]
Amphipoda	43	1982, 2008	$p = 0.214$	$p = 0.675$	$0.01936L^{2.9869}$	30[1]
Chironomidae	89	1982, 2008	$p =$ **0.008**[a]	n/a	1982: $0.00232L^{3.1660}$ 2008: $0.01969L^{2.2425}$	28.1[2,3]
Ephemeroptera	16	1982, 2008[b]	n/a	n/a	$0.0546L^{2.2798}$	4.75[4]
Gastropoda	47	1982, 2008	$p = 0.44$	$p = 0.07$	$0.23652L^{3.0385}$	24[5]
Isopoda	30	2008	n/a	n/a	$0.02661L^{2.8848}$	12[6]
Oligochaeta	60	1982, 2008	$p <$ **0.0001**[a]	n/a	1982: $0.00866L^{2.2646}$ 2008: $0.08010L^{0.8596}$	23[2]
Ostracoda[c,d]	39	1982, 1993	$p = 0.07$	$p = 0.24$	$0.15028L^{4.0400}$	12[6]
Nondressenid Bivalvia[e,f]	54	1982, 2008	$p = 0.78$	$p =$ **0.038**[a]	1982: $0.11559L^{3.5179}$ 2008: $0.15392L^{3.5179}$	9[7]
Dreissena	35	2008	n/a	n/a	$0.16865L^{2.9222}$	9[7]

[a] See Fig. 2 for data plots

[b] Only 1 observation from 2008, preventing statistical comparisons among years

[c] Additional data from 1993 samples (Division of the Environment, Ontario Ministry of Natural Resources, unpublished data) included to improve sample sizes for this taxon

[d] No mass data were available from 2008 samples; relationship from 1982, 1993 data applied to all years

[e] Used common slope from analysis of covariance model

[f] Category is all nondreissenid pelecypods (Psididae and Sphaeriidae; no unionids were collected in the samples)

[g] 1 = Wetzel et al. (2005), 2 = Howmiller (1972), 3 = Donald and Paterson (1977), 4 = Heise et al. (1988), 5 = value reported for *Lymnaea* spp. in Pakhomov (2003), 6 = value reported for crustaceans in Pakhomov (2003), 7 = value reported for *Mytilus edulis* in Pakhomov (2003); correction factors are presented as reported % mass loss caused by preservation

time periods. Thus, we generated length-frequency distributions for each depth with sufficient data and applied them to both time periods. For Isopoda, Ostracoda, and dreissenids, length-frequency distributions were similar across depths and time periods, so we used length-frequency distributions over all depths and time periods.

Length–mass regressions

Where data were sufficient, we compared regressions of log-transformed lengths and masses for all taxa among years using tests for heterogeneity of slopes and analysis of covariance (ANCOVA). We were most interested in significant differences between years when dreissenids were absent (1982–1986) vs those when dreissenids were present (2008–2009). All statistical analyses and figures were generated in R (R Development Core Team, Vienna, Austria).

Estimation of biomass

We estimated preserved biomass for each taxon from length–mass regressions (Table 2) and the appropriate length-frequency distributions (see above). For each depth and time period, we estimated preserved mass (mg) at the mid-point of each size class (length; mm) in the length-frequency distribution with the appropriate length–mass regression (Table 2) and multiplied by the relative frequency of the size class observed at the site. We used 1-mm size classes for all taxa except ostracods, for which we used 0.5-mm size classes. We summed masses over all size classes to obtain preserved biomass (mg), which we standardized to the area of the dredge used for collection and expressed /m^2. We converted estimates of preserved biomass to fresh biomass with published conversion factors (Table 2). We held all samples in preservative for ≥130 d to permit stabilization of specimen masses (Donald and Paterson 1977). We converted biomass to g/m^2 for graphical presentation.

Evaluating changes in invertebrate density and biomass

We excluded rare taxa or those for which length or mass could not be determined reliably from our analysis. On average, the 9 taxa included in our study (including dreissenids) represented 91% (by density) of all benthic organisms identified in our samples. Total density and biomass estimates reported here are sums based on these 9 taxa.

We used general linear mixed-effects models to evaluate changes in the total density and biomass (shell-free, fresh mass) of the benthic invertebrate community. Site depth and invasion status were fixed effects and year was a random effect nested within invasion status. The general linear model (GLM) was expressed as:

$$y = \text{depth} + \text{invasion} + \text{invasion}(\text{year}) + (\text{depth} \times \text{invasion}) + (\text{depth} \times \text{invasion}(\text{year})) + \varepsilon$$

where invasion(year) is read as year nested within invasion status. Similar statistical model formulations have been used elsewhere to describe invertebrate community patterns during dreissenid invasion (McNickle et al. 2006).

Our invertebrate count data conformed to a Poisson distribution. We specified this distribution in our GLM with a logarithmic-link function, where the area sampled was included in our model formula as a link function (Zuur et al. 2009, O'Hara and Kotze 2010). O'Hara and Kotze (2010) recently demonstrated that GLMs using negative-binomial- or Poisson-based distributions when applied to count data out-performed traditional log(x)- or $\sqrt{(x)}$-transformation methods. We ran analyses with the *glmer* function in the *lme4* package in R and fitted models using a maximum-likelihood approximation. We back-transformed counts from parameters for each invasion period and depth from the model. Standard errors for counts were estimated by applying the delta method to the parameter estimates and variance/covariance matrix for the model (function *deltamethod* in the *msm* package). We standardized back-transformed counts to the area sampled by the dredge used for collection and expressed them /m^2.

The statistical model (above) applied to untransformed total invertebrate biomass density was distributed with a constant coefficient of variation (slope of a plot of squared absolute residuals vs predicted values = 1), indicating that a log(x)-transformation to invertebrate biomass was appropriate. To permit log(x)-transformations on 0 biomass estimates, we added a correction factor equal to ½ the minimum value observed to all observations in the data set. We back-transformed parameter estimates for each invasion period and depth (minus the correction factor) and estimated 95% confidence intervals with the method outlined in Krishnamoorthy and Mathew (2003), which is an appropriate method for estimation of confidence intervals around means with small sample sizes (i.e., $n < 20$). Upper values of back-transformed confidence intervals are often greatly inflated for sample sizes <5 (Krishnamoorthy and Mathew 2003), as was the case for our postinvasion samples (Table 1). Therefore, analyses of invertebrate biomass

TABLE 3. Results (p-values) of goodness-of-fit comparisons evaluating the significance of terms involving dreissenid invasion in general vs reduced models (see text for details). n/a = not appropriate given a priori model specification or significance of interaction term. Bold indicates $p \leq 0.05$.

		Density (5–30 m)		Biomass (10–30 m)[a]	
Organism	Model constraints	Depth × invasion	Invasion	Depth × invasion	Invasion
Total invertebrates		**0.0042**	n/a	**0.023**	n/a
Nondreissenids		**0.014**	n/a	0.058	0.99
Amphipoda	5–20 m only	**<0.0001**	n/a	**0.048**	n/a
Chironomidae		**0.05**	n/a	0.163	n/a[c]
Dreissenidae[b]	2008–2009, 5–25 m only	n/a	n/a	n/a	n/a
Ephemeroptera	5–10 m only	0.39	0.13	n/a	0.301
Gastropoda		**0.0058**	n/a	0.561	**0.037**
Isopoda	5–10 m only	**0.0085**	n/a	n/a	**0.012**
Oligochaeta		**0.014**	n/a	0.113	0.159
Ostracoda		**0.031**	n/a	0.233	0.164
Bivalvia	15–30 m only	**0.012**	n/a	**0.010**	n/a

[a] Models for invertebrate density are for all depths, whereas 5-m depths are excluded from models fit to biomass (see text for details)

[b] Models were constrained to obtain parameter estimates for density, biomass at depth over both postinvasion years (Figs 3, 4)

[c] Invasion term not investigated given evidence against additive effects as seen in data plots

did not include our 5-m depth sites, where the sample sizes for estimates of back-transformed means in postinvasion years ($n = 3$) were insufficient to provide reasonable error estimates. We present annual means at 5 m from 2009 for graphical comparison.

For both density and biomass, we compared the general statistical model with simpler reduced models using goodness-of-fit tests to determine: 1) whether the depth × invasion status interaction terms contributed significantly to the overall model, and if not 2) whether including the invasion status term explained more variation than a reduced model with only site depth as a fixed factor and a year × depth interaction as a random factor. We compared models with a likelihood-ratio test (e.g., Pinheiro and Bates 2000, page 83). The likelihood of the more general model (L_g) should be greater than that of the simpler models (L_s), so the likelihood-ratio test statistic was $2\log(L_g/L_s) > 0$. The asymptotic distribution of this test statistic (under the null hypothesis that the simpler model is sufficient) follows a χ^2 distribution with a and b degrees of freedom, where a is the number of parameters in the general model and b is the number of parameters in the restricted model. This test is carried out in R using the *anova* function on the 2 *lmer* models being compared.

In each case, the full model was compared with a simpler one where the interaction between depth and invasion status was excluded:

$$y = \text{depth} + \text{invasion} + \text{invasion}(\text{year}) + (\text{depth} \times \text{invasion}(\text{year})) + \varepsilon$$

A nonsignificant p-value from this comparison indicated that inclusion of the interaction term in the more general model did not provide a better fit to the data than the simpler model and that the simpler model should be chosen based on parsimony. If the simpler model was sufficient, we compared it with the model where the fixed effect of invasion status was excluded:

$$y = \text{depth} + \text{year}(\text{depth} \times \text{year}) + \varepsilon$$

A nonsignificant p-value indicated that inclusion of a fixed factor describing dreissenid invasion did not provide a better fit than year-to-year random variation of sites at depth and that the simpler model should be chosen based on parsimony.

We applied similar approaches to density and biomass data for individual taxa where appropriate. In certain cases, we limited analyses to depths at which taxa were typically found in all years. We excluded the invasion term when evaluating depth-specific patterns of dreissenids in 2008 and 2009. Constraints of all model applications and statistical results are reported in Table 3. We ran general linear hypothesis post hoc tests on the full model formulations to identify significant differences among relevant combinations of depth and invasion status. Back-transformed means and errors estimated from model parameters were plotted.

Benthic samples in 1986 were the only ones collected during spring. To determine whether the season of sampling in predreissenid years influenced our results, we used multivariate analysis to assess whether spring-sampled benthic communities in 1986 were similar to autumn-sampled communities in 1982 and 1983. We used principal coordinates analysis of chord distance measures among benthic invertebrate communities at each site (log[x]-transformed biomass values). Chord distance (Orlóci 1967) emphasizes changes in the proportional composition of taxa, and de-emphasizes the effects of large differences in overall quantity among sites (Legendre and Legendre 1998). We examined year groups visually on biplots to determine if the 1986 data were similar enough to samples collected in late summer to be included in the study.

Detailed taxonomic changes in Chironomidae

We assessed the degree to which temporal increases in biomass and size distributions of chironomids in our study and in the study by Jimenez et al. (2011) might be linked to changes in the chironomid community. We also assessed the potential effect of improved water quality (hypolimnetic O_2 concentrations) on the chironomid community. We obtained data on length distributions (Wiederholm 1983) and O_2 tolerances (Quinlan and Smol 2001) of chironomid taxa where they were available. We used proportional changes in the most common chironomid taxa over time to estimate mean weighted chironomid length and infer dissolved O_2 condition of the hypolimnion pre- and postdreissenid invasion. We used the midpoint as an estimate of mean chironomid length for weighted-average estimates among species where size ranges were reported for chironomid taxa. We evaluated differences among weighted means with linear models so the weighting factor could be accounted for appropriately. We estimated standard errors of weighted means with common methods (Cochran 1977, Rennie et al. 2009b).

Results

Length distributions

Scatterplots of mean lengths with depth were created for those taxa with sufficient data (Fig. 2A–I). Length data for Ephemeroptera (Fig. 2A), Dreissenidae (Fig. 2B) and Isopoda (Fig. 2G) were available for a single time period only. Lengths of chironomids (Fig. 2C), amphipods (Fig. 2D) at greater depths, and gastropods (Fig. 2F) at shallow depths tended to be larger post- than preinvasion, whereas no consistent changes were observed in the length distributions of oligochaetes (Fig. 2E), ostracods (Fig. 2H), and nondreissenid bivalves (Fig. 2I).

For Chironomidae, Oligochaeta and nondreissenid Bivalvia, either slopes or intercepts of length–mass relationships differed significantly among time periods ($p < 0.05$; Table 2). Slopes of regressions for chironomids (Fig. 3A) and oligochaetes (Fig. 3B) were lower post- than preinvasion. Slopes were similar but intercepts of regressions for nondreissenid bivalves were lower pre- than postinvasion (Fig. 3C). Therefore, we used period-specific regressions to estimate biomass of these taxa.

Total invertebrate density and biomass

Statistical models including the depth × invasion interaction explained significantly more variation in total invertebrate density than did reduced models, regardless of whether dreissenids were included in the totals (Table 3). This interaction was reflected by a general decrease in invertebrate density at all but the deepest sites postinvasion. Total invertebrate densities did not differ among depths preinvasion, whereas total densities were lower overall and generally increased with depth postinvasion (Fig. 4A). When dreissenids were excluded from the totals, the postinvasion increase in invertebrate densities with depth was more pronounced (Fig. 4A). In contrast, postinvasion total shelled invertebrate biomass (corrected for preservation effects) increased at 10 and 15 m, but did not change at deeper depths (Fig. 4B) as indicated by the significant additional variance explained by the inclusion of depth × invasion interaction terms (Table 3). This pattern was not evident when dreissenids were excluded from the analysis. No means for total biomass excluding dreissenids differed significantly in post hoc comparisons of pre- and postinvasion periods. This suggests that the increase in total invertebrate biomass at 10 and 15 m was primarily dreissenid biomass.

Temporal changes in benthic invertebrate communities

Benthic invertebrate communities in Lake Simcoe changed following dreissenid establishment. The first 2 axes of the principal coordinates analysis of chord distances among sites explained 57% of the total variation in invertebrate biomass. The major separation among years was between pre- (1982–1986) and post- (2008–2009) invasion periods (Fig. 5A). During the 1980s, benthic invertebrate communities were dominated by chironomids, nondreissenid bivalves, oligochaetes, and ostracods. In contrast, taxa typical of nearshore habitats dominated invertebrate communities in 2008 and 2009 (dreissenids, amphipods, isopods, and gastropods; Fig. 5B). Species scores for dreissenids were most similar to site scores for 2008 and 2009 at 5 to 15 m (Fig. 5B).

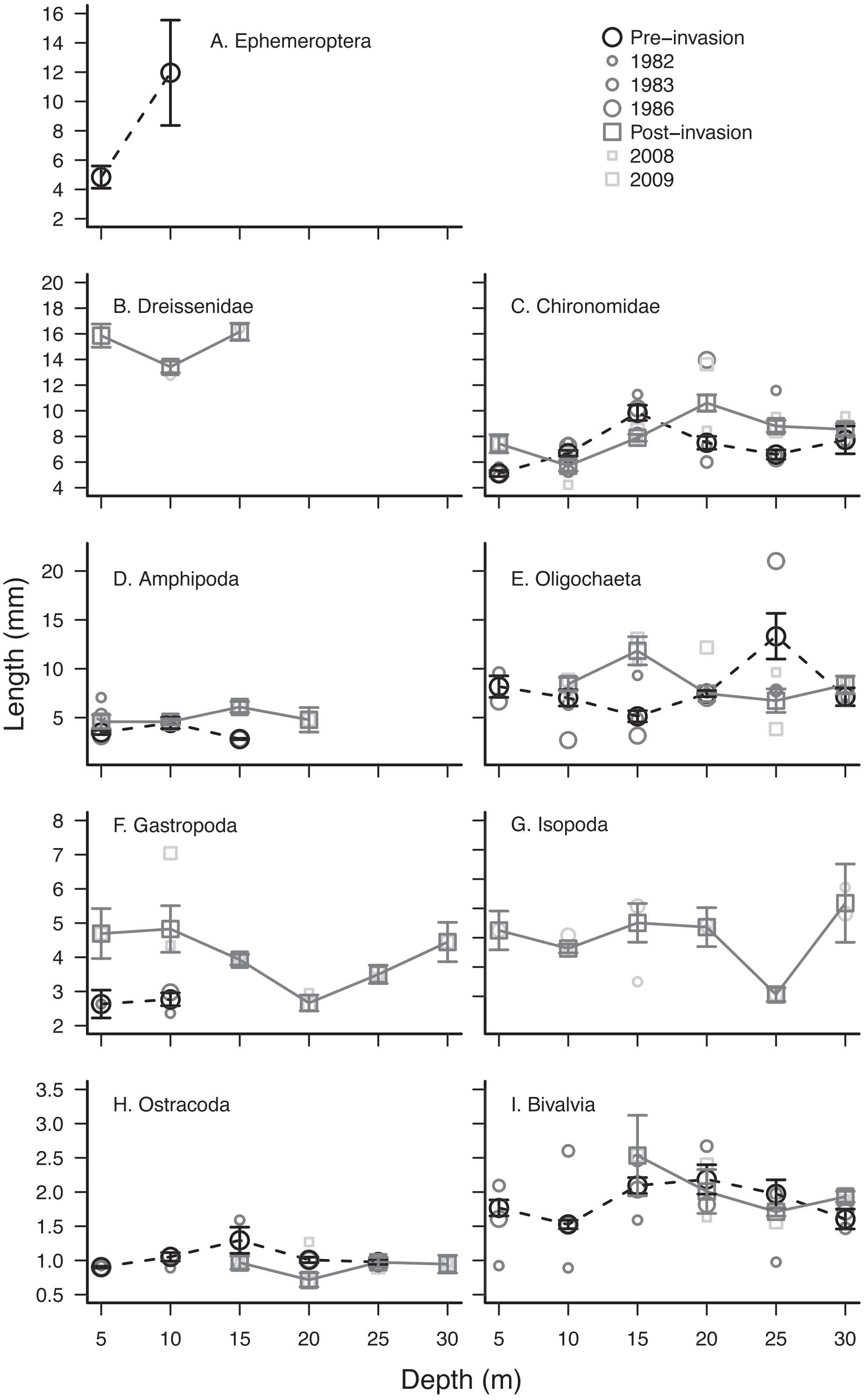

FIG. 2. Trends in body length of preserved Ephemeroptera (A), Dreissenidae (B), Chironomidae (C), Amphipoda (D), Oligochaeta (E), Gastropoda (F), Isopoda (G), Ostracoda (H), and nondreissenid Bivalvia (I) over years pre- (1982, 1983, 1986) and post- (2008, 2009) dreissenid invasion in Lake Simcoe, Ontario.

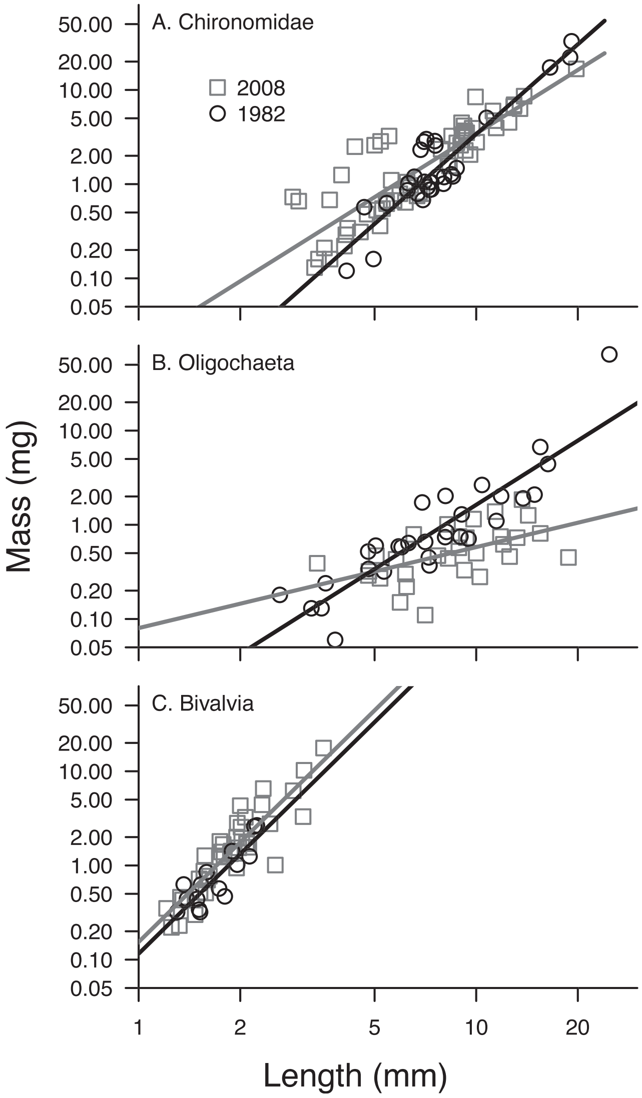

FIG. 3. Relationships between length (mm) and preserved mass (mg) for Chironomidae (A), Oligochaeta (B), and Bivalvia (C) in Lake Simcoe. Only taxa for which time periods (pre- or postinvasion) or the interaction between time period and mass were significant are shown. Mass is shelled mass for nondreissenid Bivalvia. Note log scale in panels.

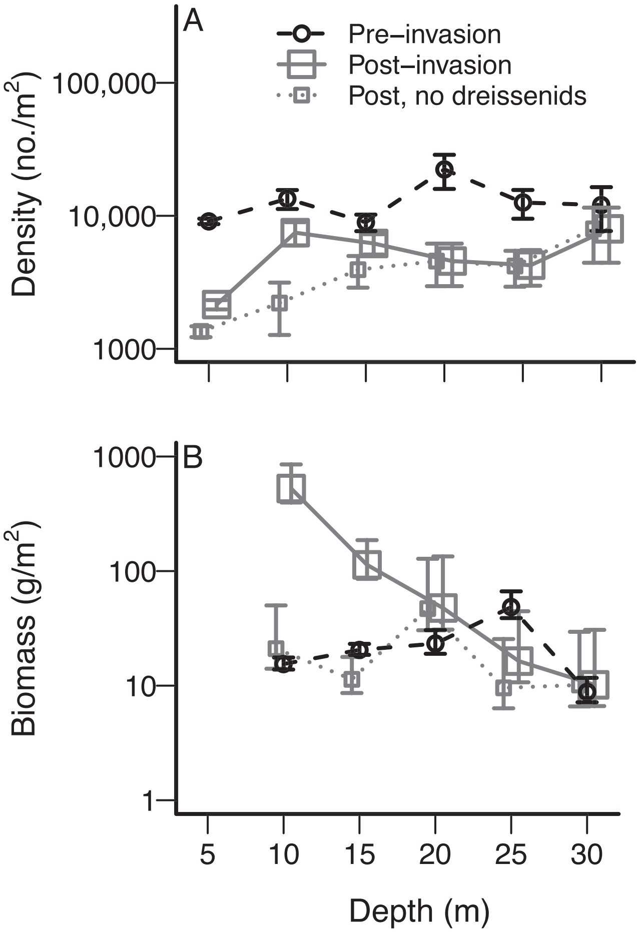

FIG. 4. Changes in total invertebrate density (A) and total biomass (fresh mass, unshelled) (B) pre- and postdreissenid invasion in Lake Simcoe, Ontario, 1982–2009. Note log scale in panels.

Taxon-specific trends

Depth-specific patterns of invertebrate density differed pre- and postinvasion for most taxa (Table 3; Fig. 6A–I). Depth × invasion interaction terms increased the explanatory power of density models (when compared with simpler models) for all but 1 taxon (Ephemeroptera; Fig. 6A). Preinvasion densities of most taxa (except oligochaetes and ostracods, Fig. 6E, H) decreased with depth. Postinvasion densities tended to be more evenly distributed across depths (Chironomidae, Amphipoda, Gastropoda, Isopoda; Fig. 6C, D, F, G) or increase with depth (e.g., nondreissenid Bivalvia; Fig. 6I). Organisms typically regarded as occupying nearshore habitats tended to be detected offshore more frequently post- than preinvasion (e.g., Amphipoda, Gastropoda, Isopoda; Fig. 6D, F, G). Postinvasion densities of ostracods (Fig. 6H) and ephemeropterans (Fig. 6A) appeared to decrease at shallower depths, where dreissenids were most abundant (Fig. 6B).

For the most part, taxon-specific trends in biomass with depth and invasion status reflected those observed for density. However, depth × invasion interactions and invasion status contributed less frequently to variance explained in the models (i.e., were nonsignificant) even though biomass appeared to differ more than density between pre- and postinvasion periods for some taxa (Fig. 7A–I). Most dreissenid biomass was found between 5 and 15 m depth (Fig. 7B). Biomass of chironomids appeared to

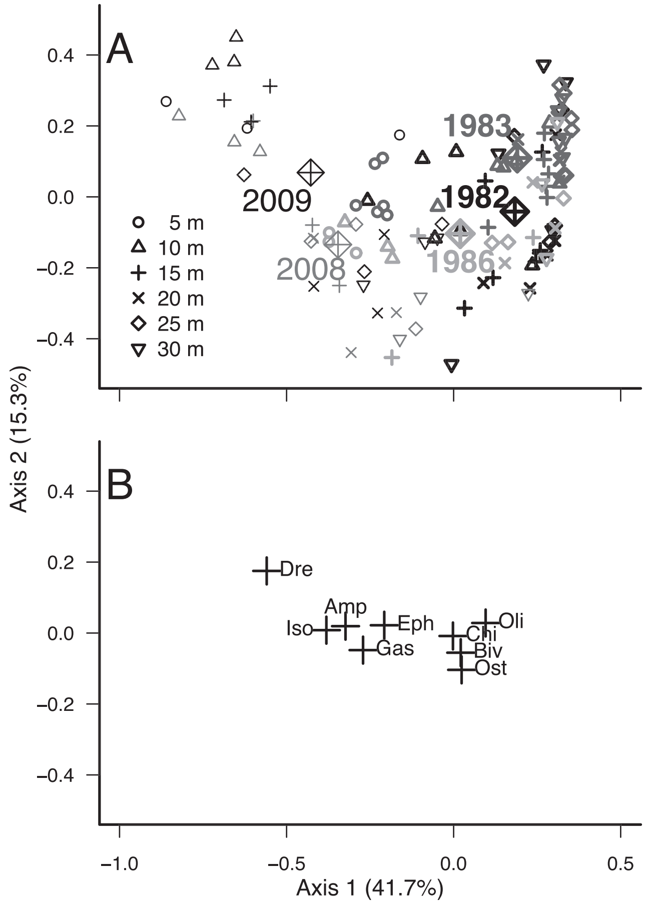

FIG. 5. Principal Coordinates Analysis of benthic invertebrate communities (based on biomass) collected at sites in years pre- (1982, 1983, 1986) and post- (2008, 2009) dreissenid invasion in Lake Simcoe showing site scores of benthic communities at various depths in all years (A) and taxon scores (B). Crossed diamonds in panel A are centroids for each year. Site scores prior to dreissenid invasion are heavy symbols. Amp = Amphipoda, Chi = Chironomidae, Dre = *Dreissena*, Eph = Ephemeroptera, Gas = Gastropoda, Iso = Isopoda, Oli = Oligochaeta, Ost = Ostracoda, Biv = nondreissenid Bivalvia.

be lower at shallow sites and higher at deeper sites post- than preinvasion (Fig. 7C), but only means at 15-m differed significantly pre- and postinvasion. Inclusion of the invasion status × site depth term did not increase the variation explained compared with additive chironomid models. Oligochaete biomass was 1 to 2 orders of magnitude lower post- than preinvasion (Fig. 7E). Paired pre- and postinvasion differences were significant at each depth, but neither the depth × invasion status nor invasion alone contributed significantly to the explanatory power of the model compared to simpler models. Postinvasion biomass of nondreissenid bivalves was lower at shallow sites and higher at deeper sites than preinvasion biomass (Fig. 7I). Post hoc tests revealed significant differences at the 10-, 20-, and 30-m sites. Inclusion of the site depth × invasion interaction increased the variation explained by the model compared with simpler additive models (Table 3). Biomasses of amphipods (Fig. 7D), gastropods (Fig. 7F), and isopods (Fig. 7G) were significantly higher post- than preinvasion. Biomass of ostracods (Fig. 7H) and ephemeropterans (Fig. 7A) did not change significantly between pre- and postinvasion periods.

Changes in chironomid community composition

Six chironomid taxa made up 78% of all chironomids identified (Table 4). Of these 6 taxa, all but *Tanytarsus* spp. are typically identified as profundal (Quinlan and Smol 2001). The relative abundance of 2 of these common taxa increased postinvasion, whereas relative abundance of 4 decreased (Table 4). The mean length of common chironomid taxa (weighted by relative abundance) increased from 11.0 ± 3.0 mm preinvasion to 12.1 ± 4.4 mm postinvasion, but the increase was not significant ($p > 0.05$). Mean length for all chironomid taxa was significantly higher (0.96 mm) post- than preinvasion over all depths and was 2.3 mm higher post- than preinvasion at profundal (20–30 m) depths only (both $p < 0.05$, Fig. 2C). Mean hypolimnetic dissolved O_2 conditions inferred from the 6 common taxa (O_2 preferences weighted by relative abundance) increased from 4.0 ± 0.26 mg O_2/L preinvasion to 4.7 ± 0.7 mg O_2/L postinvasion (Table 4), but the increase was not significant ($p > 0.05$).

Seven rare chironomid taxa occurred only pre- or only postinvasion. The mean length and inferred hypolimnetic O_2 concentration based on preinvasion rare species were 10.4 mm and 4.03 mg/L, respectively. Mean length and inferred hypolimnetic O_2 concentrations based on postinvasion rare species were 9.8 mm and 5.43 mg/L, respectively (Table 4).

Discussion

Effects of dreissenids on benthic invertebrate biomass

A 17-fold increase in the biomass of benthic invertebrates at 10 to 15 m offshore sites in Lake Simcoe between 1982 and 2009 was caused primarily by dreissenid biomass. In contemporary samples taken at 5 to 15 m, 72% of the postinvasion wet, shell-free invertebrate biomass consisted of dreissenids (mean shell-free dreissenid biomass at these sites = 0.3 kg/m^2 in 2008–2009), whereas total nondreissenid biomass did not differ pre- and postinvasion. In both Lake Simcoe and elsewhere, dreissenids seem to

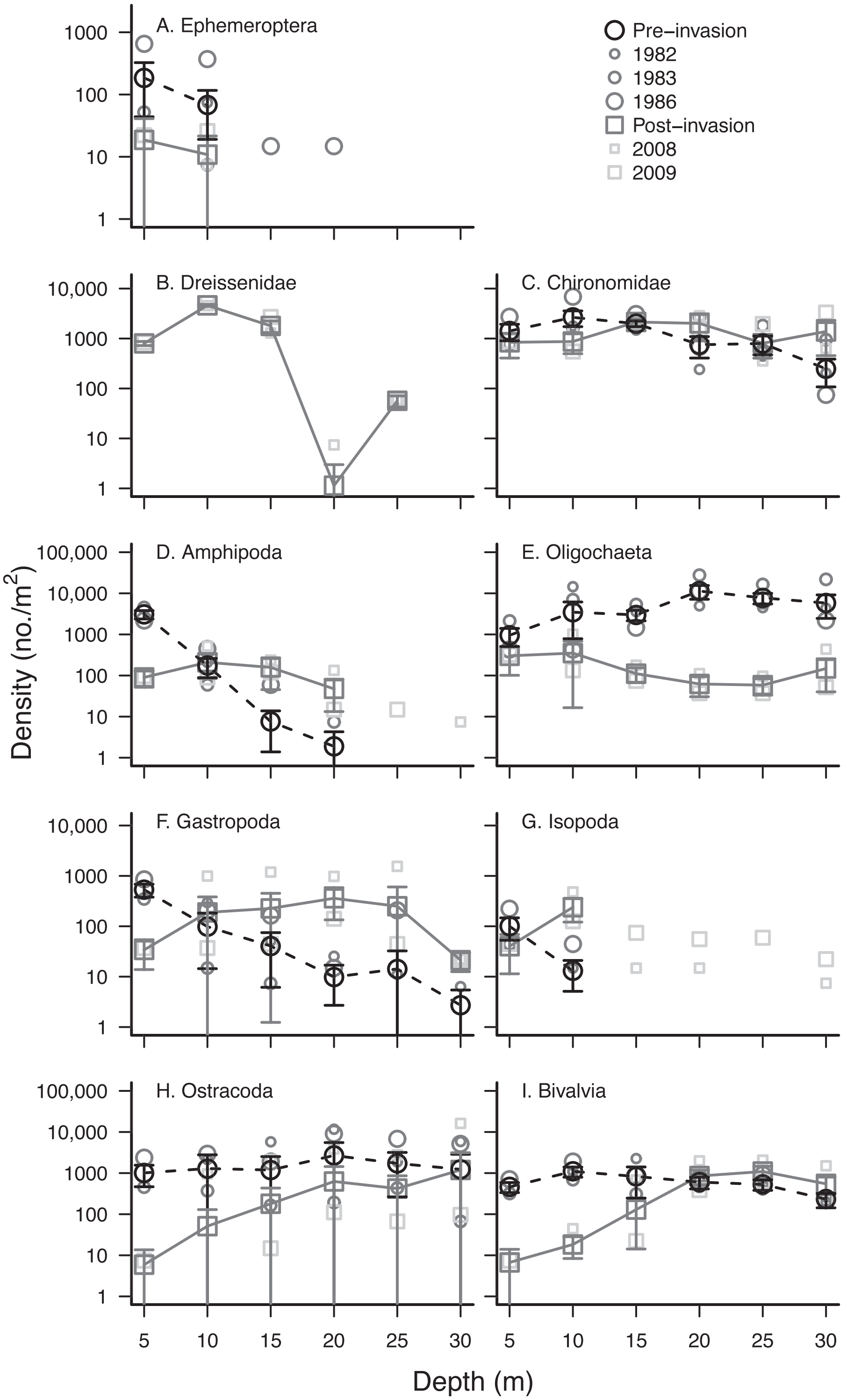

FIG. 6. Density of Ephemeroptera (A), Dreissenidae (B), Chironomidae (C), Amphipoda (D), Oligochaeta (E), Gastropoda (F), Isopoda (G), Ostracoda (H), and nondreissenid Bivalvia (I) pre- and postdreissenid invasion in Lake Simcoe, Ontario (1982–2009). Note log scale in panels.

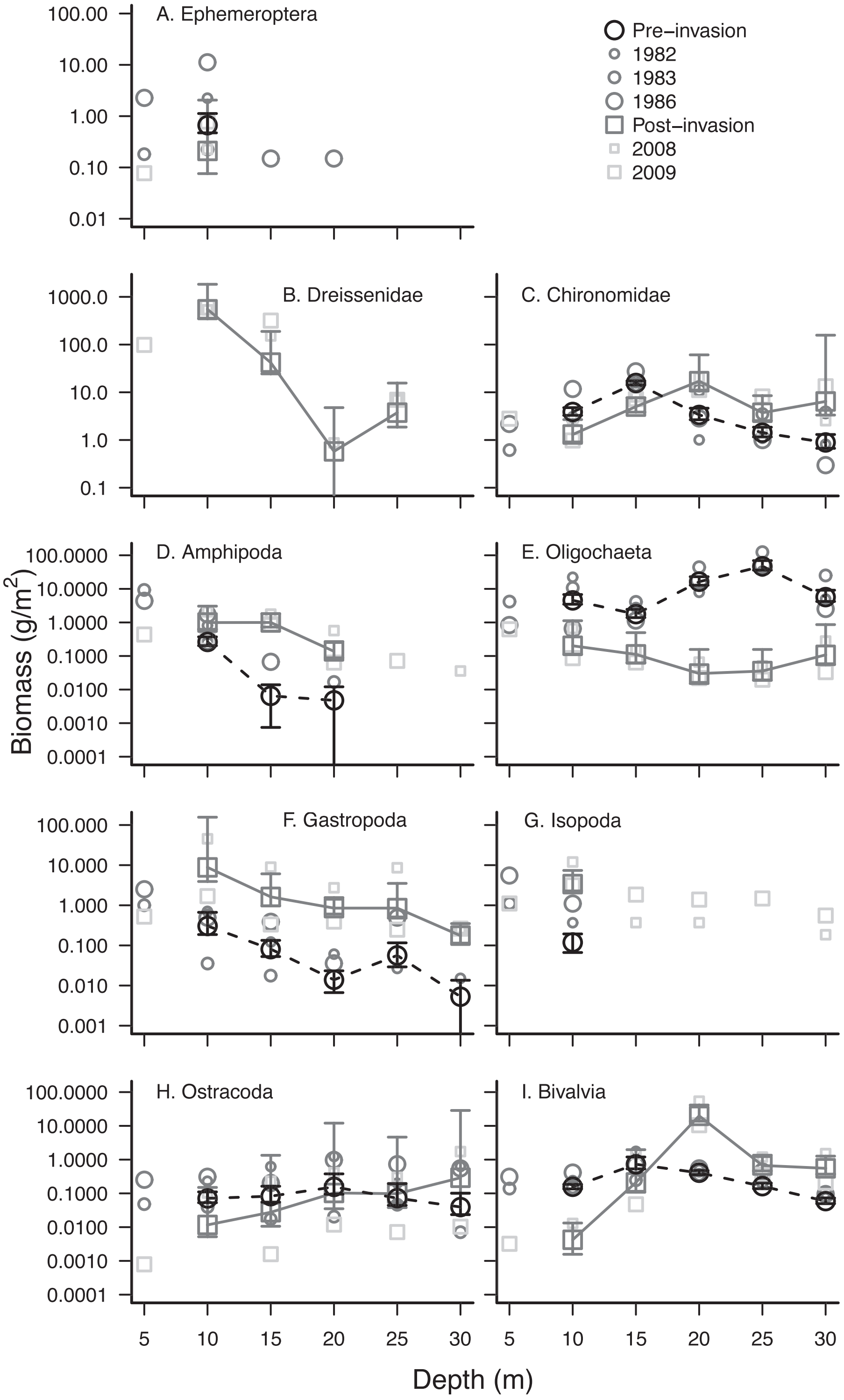

FIG. 7. Biomass (fresh mass, unshelled) of Ephemeroptera (A), Dreissenidae (B), Chironomidae (C), Amphipoda (D), Oligochaeta (E), Gastropoda (F), Isopoda (G), Ostracoda (H), and nondreissenid Bivalvia (I) pre- and postdreissenid invasion in Lake Simcoe, Ontario (1982–2009). Note log scale in panels.

TABLE 4. Size range and O_2 preferences (volume-weighted hypolimnetic O_2 [VWHO]) for common chironomid taxa and rare taxa found only pre- or postdreissenid invasion in Lake Simcoe, Ontario, Canada. VWHO estimates are from Quinlan and Smol (2001) unless otherwise indicated.

Taxa		Mean relative abundance (%)		Mean length or length range (mm)	O_2 preference (mg O_2/L)
		Pre	Post		
Common taxa	*Chironomus major*	8.79	19.4	25–30	3.3[a]
	Chironomus riparius	7.95	3.49	20	3.3[a]
	Micropsectra gr.	4.27	36.6	6–8	6.1
	Procladius spp.	27.2	17.3	6–11	3.7
	Tanytarsus spp.	30.7	13.5	5–8	4.1–4.7
	Cryptochironomus spp.	2.65	<1.0	10–15	4.7
Rare taxa	*Thienemannimyia* sp.	<1.0	–	10	4.2
	Monodiamesa bathyphila	<1.0	–	13–16	–
	Paracladopelma sp.	<1.0	–	10	4.1[b]
	Paratendipes sp.	<1.0	–	6–8	3.8
	Heterotrissocladius spp.	–	<1.0	7	7.0
	Dicrotendipes spp.	–	<1.0	8–11	4.1
	Sergentia sp.	–	<1.0	8–18	5.2

[a] Single value for *Chironomus* spp. applied to both *C. major* and *C. riparius*

[b] *Paracladopelma* sp. estimated from Brodersen et al. (2004); converted to VWHO using relationship reported in Brodersen and Quinlan (2006)

be the dominant contributor to postinvasion increases in total invertebrate biomass on sublittoral, mud substrates. At 1 m depth in Rice Lake, Ontario, total benthic invertebrate biomass increased 1 order of magnitude from pre- to postinvasion, and ~85% of total biomass postinvasion was zebra mussels (Mercer et al. 1999). Total invertebrate biomass increased by an order of magnitude at matched sites 29 to 48 m deep in Lake Erie between 1979 (pre-) and 1993 (postinvasion) (Dermott and Kerec 1997). Most of the postinvasion biomass (92%) was dreissenids, and total nondreissenid biomass declined during the same period. Higgins and Vander Zanden (2010) described responses of total nondreissenid invertebrate biomass as neutral or positive, consistent with our results.

Despite a major increase in total benthic invertebrate biomass, total invertebrate density at the same sites declined following dreissenid establishment (Jimenez et al. 2011, our study). Nondreissenid invertebrate density typically increases postinvasion (Higgins and Vander Zanden 2010). Measured effects of dreissenids may be overestimated in evaluations of nearshore benthic communities, which are often sampled in close proximity to dreissenid colonies (Strayer and Smith 2001). Depending on the taxon under consideration, habitat type and dreissenid density at a sampling location can significantly affect the measured response of benthic taxa to dreissenids (Strayer and Smith 2001). We sampled a wide range of depths and habitats and obtained results very similar to those of Jimenez et al. (2011) who conducted a geographically broader survey of Lake Simcoe. Thus, the patterns we observed probably are independent of local effects of dreissenid density. Instead, we suggest that they reflect real ecosystem-level effects of dreissenids on the benthic invertebrate community in the main basin of Lake Simcoe.

Our results are generally consistent with other community-level assessments of dreissenid effects on invertebrate biomass and density. Jimenez et al. (2011) used an expanded version of our 2008 data set and independent data collected in 1983 from sites throughout the main basin of Lake Simcoe and reported similar changes among taxa to those observed in our study. Our characterization of the chironomid community suggests (though not conclusively) that the postinvasion increase in chironomid length and biomass at profundal sites in Lake Simcoe (Jimenez et al. 2011, our study) might be a consequence of shifts in community composition. Mercer et al. (1999) reported a postinvasion increase in amphipod, chironomid, and oligochaete biomass, and a decline in isopod biomass, but their data were highly variable among postinvasion years. In the Bay of Quinte and Lake Oneida, amphipod and isopod biomass responded positively to dreissenids, whereas chironomid and nondreissenid bivalve biomass responded negatively (Miehls et al. 2009a, b). Oligochaetes responded negatively to dreissenid invasion in Lake Oneida and positively in the Bay of Quinte. Nearshore amphipod (*Gammarus*) and gastropod biomass increased postinvasion in Lake Erie, but isopod biomass decreased. Chironomid and oligochaete biomass also decreased postinvasion in Lake Erie, though not significantly (Dermott and Kerec 1997).

In Lake Simcoe, total invertebrate density decreased on nearshore (5 m) soft substrates (our study), but increased dramatically on hard substrates at similar depths (Ozersky et al. 2011). Responses of benthos to dreissenids differ between soft and hard nearshore sediments (Ward and Ricciardi 2007). Preinvasion hard substrates would have represented relatively poor habitat for benthic invertebrates compared with softer nearshore substrates. The postinvasion addition of structure and nutrients via shells and pseudofeces might have improved suitability of hard substrates as habitat for benthic invertebrates, whereas similar deposition on softer nearshore substrates may have inhibited a region already supporting an abundant invertebrate community. A comparison of preinvasion invertebrate densities between hard and soft nearshore substrates supports this hypothesis. Preinvasion invertebrate densities on rocky substrates 4 to 6 m deep at Sibbald Point in 1993 were ~400 organisms/m^2 (Ozersky et al. 2011). This value is 1 to 2% of preinvasion densities at 5-m sites on softer substrates in our study (predreissenid average, 9141 ± 1027 organisms/m^2). In contrast, postinvasion densities were much greater on rocky (~22,000 organisms/m^2) than on soft (2252 ± 727, our study) substrates at the same sites.

Negative effects of dreissenids on burrowing organisms adapted to soft sediments may be the result of changes in sediment chemistry caused by dreissenid invasion. Deposition of dreissenid shells on soft sediments affects nutrient and gas exchange at the sediment–water interface, which ultimately affects sediment and porewater chemistry (Bruesewitz et al. 2006, Turner 2010). Sediments under dreissenid beds and shell deposits are O_2-deficient relative to sediments without dreissenids (Turner 2010, Zaiko et al. 2010). Mussels also release more nutrients when in direct contact with sediments (Turner 2010). The observed decline of burrowing taxa (chironomids, nondreissenid bivalves) at shallow (5–15-m) sites where dreissenids are most abundant is consistent with deteriorating sediment conditions. Density and biomass of oligochaetes also decreased at these depths, but their postinvasion decline was ubiquitous, a result suggesting that additional or alternative mechanisms may be contributing factors. Taxa that were likely to respond positively to increased structure and habitat complexity (e.g., amphipods, isopods, and gastropods) increased postinvasion and appeared to expand their range to deeper depths, as reported in other studies (Ricciardi et al. 1997, Higgins and Vander Zanden 2010, Jimenez et al. 2011).

While dreissenids now occupy most available depths in the main basin of Lake Simcoe (Jimenez et al. 2011, our study), they are sparsely distributed at depths >20 m. Quagga mussels make up only a small fraction of the total dreissenid assemblage in Lake Simcoe (<10% numerically) and this fraction does not increase with depth sampled (MDR and DEO, unpublished data; MDR and W. G. Sprules [University of Toronto], unpublished data).

Effects of changes in water quality

Changes in water quality may also explain some of the changes we observed in the Lake Simcoe benthic communities. Improvements in hypolimnetic water quality in Lake Simcoe have been attributed to implementation of P control strategies in the early 1980s. In the profundal zone (>15 m deep), shifts in taxonomic composition of chironomids (e.g., an increase in *Microspectra* and a decrease in *Procladius*; our study) and chironomid head capsules in profundal sediment cores (Rodé 2009) are consistent with improved hypolimnetic O_2 concentrations (Young et al. 2011). Furthermore, decreases in oligochaete density and biomass have been greatest (at 20–30 m) where O_2 concentrations have increased (Jimenez et al. 2011, our study). Similar patterns have been observed at comparable depths at Great Lakes sites where dreissenid invasion has coincided with nutrient abatement. In Lake Michigan, significant decreases in oligochaete density (at 16–30 m) were accompanied by an increased proportion of oligochaete taxa associated with oligotrophic conditions (Nalepa et al. 1998). In Lake Erie (at 29–48 m), biomass of tubificid oligochaetes (a family dominated by taxa tolerant of meso- to eutrophic conditions in the Great Lakes; Nalepa et al. 1998) decreased significantly between 1979 and 1993 (Dermott and Kerec 1997).

Young et al. (2011) evaluated models linking estimated P loading on the lake to hypolimnetic O_2 concentrations via relationships with ice-free (May–October) in-lake total P (TP) and chlorophyll *a* (Chl *a*) in Lake Simcoe and found that preinvasion models successfully predicted postinvasion hypolimnetic O_2 concentrations. After initial steep declines in TP and PO_4^{3-} during the early to mid 1980s, ice-free TP, PO_4^{3-}, and Chl *a* have been variable but relatively stable for 20 y (Young et al. 2011). Major improvements in hypolimnetic O_2 concentrations occurred postinvasion (fig. 3F by Young et al. 2011), but we cannot rule out the possibility that some component of changes in profundal benthos (>15 m depth) since the 1980s might also reflect earlier reductions in TP load.

The dreissenid invasion of Lake Simcoe could possibly have influenced water quality, and thus, could have had indirect effects on the profundal benthos via water-quality changes (Watkins et al. 2007). Secchi depth typically increases in response to dreissenid invasion, whereas TP and Chl *a* typically decline (Higgins and Vander Zanden 2010). Furthermore, estimates of spring phytoplankton production and biomass were significantly lower after invasion of Lake Michigan by quagga mussels (Fahnenstiel et al. 2010). Ice-free TP and Chl *a* do not appear to have been affected by the invasion of dreissenids in Lake Simcoe (Young et al. 2011), but mean ice-free Secchi depth increased markedly between 1995 and 1997 (Eimers et al. 2005). Decreases in mean annual algal biovolume and shifts in phytoplankton community composition at some monitoring sites were also coincident with dreissenid invasion (Winter et al. 2011). Young et al. (2011) found significant breakpoints (sudden declines) in temporal trends of spring TP that were coincident with dreissenid invasion at 2 shallow lake sampling stations. However, patterns were not consistent among all stations evaluated. The abrupt nature of these changes strongly suggests the influence of a sudden change in the ecosystem (i.e., dreissenid invasion) rather than more gradual changes like reductions in TP loads to the lake over the past 30 y (Winter et al. 2002, Young et al. 2011).

Increased postinvasion water clarity probably has increased benthic algal production and the maximum depth at which it can occur. This change could lead to increased shallow-water benthic invertebrate density, biomass, and their occupation of deeper sites. In Lake Simcoe, biomass and density of scraper species like gastropods have increased, and amphipods and isopods have appeared at greater densities in deeper water postinvasion (Jimenez et al. 2011, our study).

Changes in the nearshore benthic invertebrate community (<20 m deep) probably were caused by dreissenids rather than nutrient abatement. In shallow areas of Rice Lake, Ontario, postinvasion changes in benthic invertebrate biomass similar to our study could not be attributed to reduced P loading (Mercer et al. 1999). Furthermore, some changes in Lake Simcoe benthos are inconsistent with reductions in TP. For example, isopods tend to increase with TP (Donohue et al. 2009) and would therefore be expected to decrease as TP loads decreased in Lake Simcoe (Young et al. 2011). Instead, density and biomass of isopods increased and their distribution shifted to deeper habitats, a result suggesting nutrient enrichment of sediments inhabited by dreissenids, consistent with the nearshore P shunt model (Hecky et al. 2004).

Our findings also highlight how the metric used (biomass vs density) can influence our perception of changes in the Lake Simcoe benthos since dreissenid invasion. Postinvasion, total benthic invertebrate biomass increased on nearshore soft substrates ($\leq$15 m deep) and changed little in the offshore ($\geq$20 m) region. In contrast, total density of benthic organisms decreased significantly over all depths. Interpreting benthic density data without reference to biomass would lead to a very different conclusion about energy flow between nearshore and offshore regions of Lake Simcoe. For instance, the increase in invertebrate biomass at shallow depths is consistent with the nearshore P shunt model (Hecky et al. 2004), which predicts an overall increase and concentration of benthic production associated with dreissenid invasion of the nearshore region. We did not measure benthic production, but the dramatic increase in standing shelled biomass at 10 to 15 m indicates increased nearshore benthic production. In the absence of biomass data, the observed decline in total invertebrate density (Jimenez et al. 2011, our study) might be misinterpreted as inconsistent with model predictions. Moreover, biomass can be related more directly than density to the distribution and movement of energy through the ecosystem and provides a clearer picture of how dreissenids have altered the benthos in the lake.

Potential consequences of changes in biomass distribution

The combination of increased nearshore benthic biomass and slightly reduced offshore biomass indicates that benthivorous fish may focus a greater proportion of their resource acquisition in nearshore regions postinvasion. Rennie et al. (2009b) demonstrated a significant and marked postinvasion shift in fish distributions and increased reliance on the nearshore region as an energy source in South Bay, Lake Huron. Two benthivorous fishes, yellow perch (*Perca flavescens*) and lake whitefish (*Coregonus clupeaformis*), are economic cornerstones of the multimillion-dollar recreational fishery on Lake Simcoe. Yellow perch now occur at all depths (0–30 m) in the main basin of the lake, whereas lake whitefish (a cold-water species) is restricted to offshore areas during summer stratification. Both lake whitefish and yellow perch can consume dreissenids (Owens and Dittman 2003, Watzin et al. 2008, Madenjian et al. 2010, Rennie et al. 2012).

In summary, significant postinvasion changes have occurred in biomass and composition of the Lake Simcoe benthos. The dramatic increase in shallow-water benthic biomass on soft substrates consists almost entirely of dreissenid biomass. Thus, rather than augmenting this habitat for native benthos, dreissenids appear to have preempted their own space. The total biomass of native benthos did not change at shallow sites, but the composition of that biomass was altered (e.g., decreased biomass and density of oligochaetes, ostracods, and nondreissenid bivalves, and increased biomass and density of amphipods and gastropods). Our assessment of the effects of dreissenids on benthic invertebrate biomass is largely consistent with the limited information available from other inland lakes (Mercer et al. 1999, Miehls et al. 2009a) and the Laurentian Great Lakes (Dermott and Kerec 1997, Miehls et al. 2009b). Chironomid communities appear to reflect improvements in deepwater O_2 concentrations coincident with invasion of dreissenids. Changes in spring TP, Secchi depths, and algal community composition/biovolume in Lake Simcoe (all of which are linked to deepwater O^2 levels; Nicholls 1997) also occurred with the invasion of dreissenids. Additional study is warranted to determine whether dreissenid effects on the offshore benthic community are direct or indirect via effects on water quality.

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