Changes in Benthic Invertebrate Communities of South Bay, Lake Huron Following Invasion by Zebra Mussels (*Dreissena polymorpha*), and Potential Effects on Lake Whitefish (*Coregonus clupeaformis*) Diet and Growth

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ABSTRACT. *In this study we evaluated changes in benthic invertebrate communities of South Bay, Lake Huron following the invasion of zebra mussels* (Dreissena polymorpha) *and considered the implications for diets and growth of whitefish* (Coregonus clupeaformis), *a commercially important fish in the Great Lakes. Of the ten benthic invertebrate groups identified prior to invasion (1980–81), only densities of* Diporeia *and Oligochaeta have changed since the appearance of the zebra mussel, and only* Diporeia *and Chironomidae changed in relative abundance. These changes are similar to those observed in other areas of the Great Lakes, with the exception of an increase in Oligochaeta density. Post-invasion (2002–03) shallow-water communities appear to be more homogeneous, dominated by zebra mussels and Isopoda, whereas deep-water sites are more heterogeneous due to the loss of* Diporeia. *Additional data on* Diporeia *density for several years between 1959 and 2004 indicated that current low densities are not typical of South Bay. Based on changes in the benthic communities and published literature on whitefish diets, we predict that unless whitefish are able to switch to* Mysis *as an alternative to* Diporeia, *post-invasion whitefish diets will only contain a maximum of 57 to 84% of their former energy content. These predictions are likely underestimates, as they do not take into account increased energy costs associated with reductions in total invertebrate density at historical foraging depths.*

INDEX WORDS: *Dreissenid, Lake Huron,* Diporeia, *lake whitefish, South Bay, benthos.*

INTRODUCTION

Biological invasions have become an increasing concern in recent decades for stakeholders in both terrestrial and aquatic ecosystems, with global trade opening artificial migration corridors among areas that are geographically separated. The Laurentian Great Lakes of North America have received a large number of exotic species since the construction of the St. Lawrence Seaway. As of 2001, 162 exotic species had been documented in the Great Lakes system, 77% of which were likely delivered via ship ballast water (Ricciardi 2001). This implies that since 1970 there has been, on average, one suc-cessful invader introduced to the Great Lakes every 8 months (Ricciardi 2001). These invasions represent a serious and significant change to the function and biodiversity of the Great Lakes (Bronte *et al.* 2003, Madenjian *et al.* 2002, Mills *et al.* 2003).

The zebra mussel (*Dreissena polymorpha*) is a particularly troublesome invader, which has been implicated as the cause of many changes in invertebrate communities in the Great Lakes, and has been blamed for causing shifts in diets and growth patterns of fish populations throughout the Great Lakes region (Pothoven *et al.* 2001, Owens and Dittman 2003). Changes that have been attributed to the presence of the zebra mussel include reduced algal densities, increases in water clarity, loss of native bivalve diversity, and an overall shift of productivity from pelagic to benthic communities

(Dermott and Kerec 1997, Gonzalez and Downing 1999, Ricciardi 2003). However, not all zebra mussel effects have been detrimental to native species. Through the addition of nutrients from feces and pseudofeces and increased spatial complexity of lake bottoms, *Dreissena* can have positive effects on the density of some benthic invertebrates (Gonzalez and Downing 1999). The zebra mussel was first documented in South Bay, Lake Huron in 1997 (D. Anderson, Ontario Ministry of Natural Resources, Lake Huron Research Unit, Owen Sound, ON, pers. comm.).

The lake whitefish (*Coregonus clupeaformis*), a prominent benthivore in the Great Lakes, may be highly sensitive to changes in the composition of benthic communities (Pothoven *et al.* 2001, Owens and Dittman 2003). The lake whitefish has supported a fishery since the 1800s and is by far the most commercially important fish in the Great Lakes region (Madenjian *et al.* 2002, Bronte *et al.* 2003). Recent population instability and declines in whitefish growth and condition observed throughout the Great Lakes have been attributed, at least in part, to the effects of zebra mussel invasion (Madenjian *et al.* 2002). Preliminary data show that the growth rate of South Bay whitefish between their second and third year is 47% lower, individual mass for the entire stock is 9% lower, and the median age of the whitefish stock is higher in post-invasion fish (after 1997) than in pre-invasion fish (Michael D. Rennie, University of Toronto at Mississauga, unpubl.).

Historically one of the most important prey species of lake whitefish was the benthic amphipod, *Diporeia hoyi* (Hart 1931, Reckahn 1970). *Diporeia* has high nutritional value because of its high lipid content (Cavaletto *et al.* 1996, Johnson 1988). Prior to dreissenid invasion, *Diporeia* made up an average of 82% by volume of the stomach contents of South Bay whitefish and furthermore was one of the most abundant benthic invertebrates in the Great Lakes (Ihssen *et al.* 1981, Reckahn 1970). In general, increases in zebra mussel density have been correlated with decreases in *Diporeia* density (Dermott and Kerec 1997, Nalepa *et al.* 1998).

South Bay, Lake Huron, offers a unique opportunity to assess the effects of zebra mussel invasion on aquatic communities in a relatively undisturbed habitat. Data on invertebrate communities and fish stocks in South Bay have been recorded intermittently between 1947 and the present which allows comparisons of present and historical communities. In the main basin of Lake Huron, phosphorus lev-

els have remained below target levels of 5 μg/L since 1980 (Governments of Canada and the United States 2003). South Bay has received relatively little anthropogenic stress relative to other regions of the Great Lakes because of its geographic location and lack of commercial fishing pressure (Gordon G. McNickle, University of Toronto at Mississauga, pers. obs.). The relatively small size of South Bay (89 km^2) means the entire benthic community can be sampled on a scale that would be difficult to attain in the main basin of Lake Huron. Mark-recapture and genetic investigations (Ihssen *et al.* 1981) have shown that the whitefish population of the inner basin of South Bay is isolated from the rest of Lake Huron, and hence changes in the benthic community of this embayment may directly affect the resident whitefish that prey on these organisms. This isolation is likely due in part to the shallow narrows between the inner and outer basin (see Fig. 1 below) that would limit the movement of cold-water fish species during the summer. Information about interactions between whitefish and the benthic community in South Bay will add to a growing body of literature concerning the effects of zebra mussels in the Great Lakes (Ricciardi 2003).

The purpose of this study was to document changes in the overall density and composition of benthic invertebrate communities in South Bay associated with the invasion of zebra mussels (the quagga mussel, *D. bugensis*, had not invaded South Bay at the time of this study). We also present additional long-term population data for *Diporeia* in South Bay to determine whether current low *Diporeia* densities are typical of historical values. Finally, using data from the literature and data on benthic invertebrate populations in South Bay, we assess the extent to which changes in the benthos will influence the energy content of whitefish diets.

METHODS

Data on the benthic invertebrate community of the inner basin of South Bay, Lake Huron (Fig. 1) for the years 1980 and 1981 were obtained from the Ontario Ministry of Natural Resources (D. Anderson, Ontario Ministry of Natural Resources, Lake Huron Research Unit, Owen Sound, ON, unpubl.). The original sampling procedures from these surveys were replicated in the summers of 2002 and 2003 and we analyzed these samples to allow comparisons of benthic communities before and after invasion of dreissenid mussels.
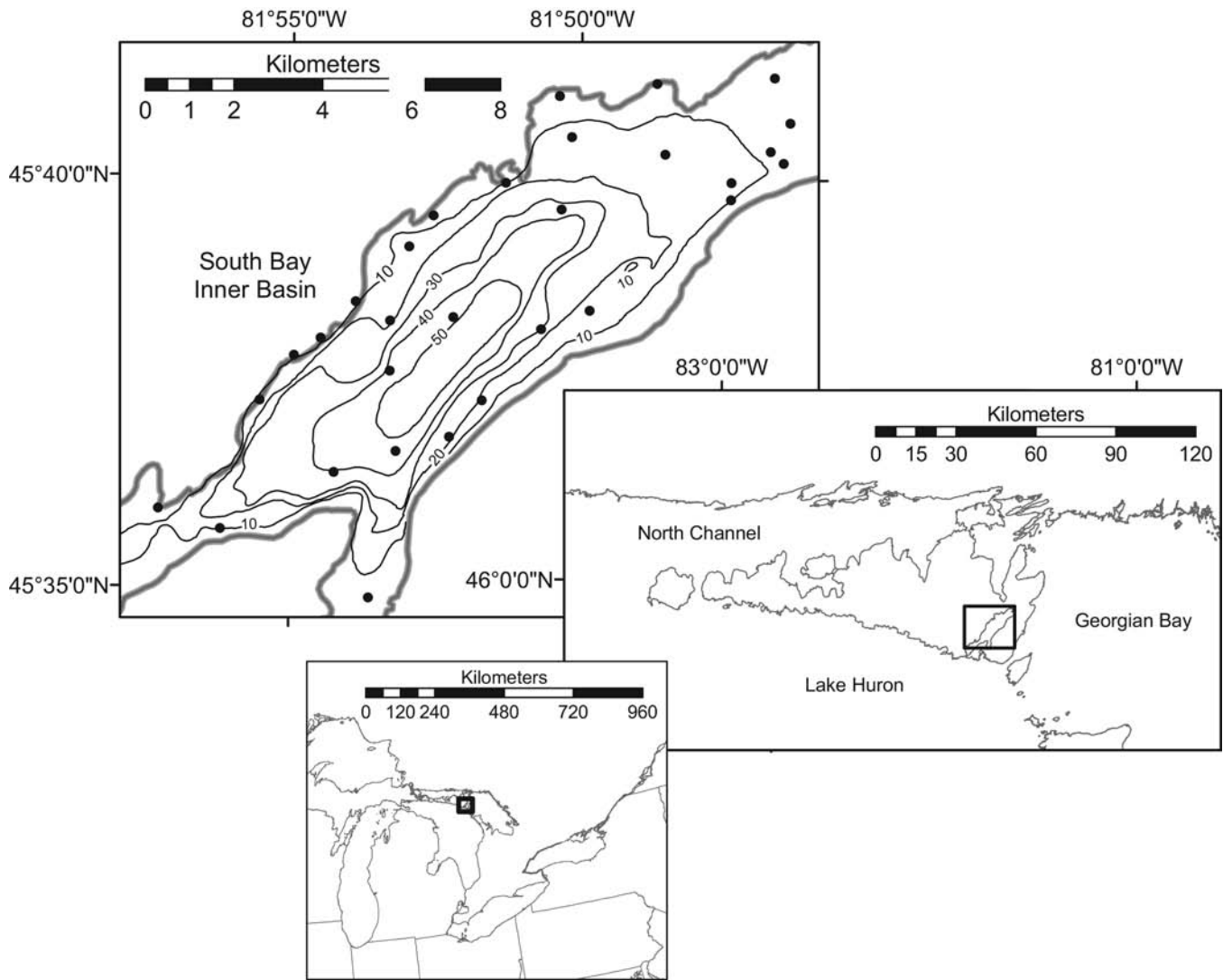
FIG. 1. *Location of the inner basin of South Bay, Lake Huron. The closed circles indicate locations at which benthic samples were taken. Contour intervals are in meters. Data for the maps are from Great Lakes Bathymetry (2005) and United States Boundary Layer (2005).*

Benthic samples were collected from three depth zones. Zone 1 included depths from 0–10 meters, zone 2 from 11–30 meters, and zone 3 from 31 meters to the deepest point at 57 meters. In 1980, sites were randomly selected from each depth zone and these same sites were revisited in subsequent years. Fifteen sites were selected in zone 1, ten in zone 2 and five in zone 3. More emphasis was placed on sampling zone 1 because greater variability among samples in shallower sites was expected from preliminary sampling (D. Anderson, Ontario Ministry of Natural Resources, Lake Huron Research Unit, Owen Sound, ON, unpubl.). Benthic samples were

collected with a 15.2×15.2 cm Ekman grab during the last week of August and the first week of September in all sampling years. Two grabs were collected from each site in all years and combined into a single sample.

Samples were sieved through a 0.5 mm screen, and sorted into broad taxonomic groups; Sphaeriidae, Gastropoda, Oligochaeta, Ephemeroptera, Trichoptera, Chironomidae, Acari, *Diporeia*, other Amphipoda, Isopoda, and Dreissenidae (zebra mussels). Every organism was counted except in a few very large samples for which a subsample of one quarter of the original sample was enumerated. Size

distributions of organisms were unavailable for 1980 and 1981, thus comparisons of biomass were not possible.

Additional data on *Diporeia* densities from depths greater than 25 m (roughly our zone 3) in South Bay were available for many of the years between 1959 and 2004 from various sources. 1959–62 data were taken from Cooper (1964) and unpublished data from 1972–73 and 1976–79 were provided by J. Reckahn (Ontario Ministry of Natural Resources, Elliot Lake, ON), and from 2001 by R. Dermott (Department of Fisheries and Oceans Canada, Canada Centre for Inland Waters, Burlington ON). Benthic sampling was repeated in 2004, but only *Diporeia* densities at the deepest sites were available at the time this manuscript was being prepared. These represent all data currently available on *Diporeia* populations of South Bay.

Statistical analyses of benthic community data were performed on log(x+1) numerical density and arcsine-square root relative abundance data. Changes in the density and relative abundances of benthic communities before and after dreissenid invasion were compared using Correspondence Analysis (CA) in NTSYS Version 2.02h. Furthermore, to contrast differences in invertebrate community structure before and after dreissenid invasion with differences due to interannual variability, we performed the following test. For each sampling site we calculated the Euclidean distance (from the CA) between 1980 and 1981 as well as between 2002 and 2003. We then determined the mean of these two distances as a measure of annual difference in community structure at each site. We also calculated Euclidean distances for all sites across the dreissenid invasion (i.e., between 1980 and 2002, 1980 and 2003, 1981 and 2002, 1981 and 2003), and determined the mean of these as a measure of difference in community structure due to dreissenid invasion. We then contrasted annual difference in community structure with dreissenid effects on community structure across sampling sites using a paired t-test. We hypothesized that differences due to dreissenid invasion would be larger than those due to annual change and therefore used one-tailed tests to make comparisons. We examined differences for each depth zone as well as across the entire bay. Sequential Bonferroni corrections to critical p-values were made to control for multiple tests (Zar 1999).

In addition, separate two-factor Analyses of Variance (ANOVA) were performed to test the effects of year and depth zone on density and relative abundance of each individual taxonomic group. ANOVAs were performed using Minitab (Version 13), which accounts for proportional differences in samples sizes among factors (Sokal and Rolf 1995). The critical probability in each two factor ANOVA was Bonferroni corrected to 0.00625 to allow for comparisons among multiple taxonomic groups (Zar 1999). Although the data from several invertebrate groups did not meet one or more of the parametric assumptions of ANOVA (either normal distribution of residuals or homogeneity of treatment group variances), no clear non-parametric or computer intensive alternative was available. It has been shown that ANOVA is a robust statistical test on which even large departures from the parametric assumptions have little effect (Zolman 1993, Zar 1999). Results of ANOVAs on invertebrate groups that did not meet the parametric assumptions are identified (see below). Trichoptera and Acari were present in such low numbers that they were excluded from these analyses.

To test the hypothesis that changes in benthic communities will lead to reduced energy content in adult whitefish, we estimated the energy available to whitefish over 100 mm long (that forage principally in deeper water—our depth zones 2 and 3) before and after dreissenid invasion through simple diet calculations. We first determined the typical wet mass of whitefish stomach contents from a size-stratified subsample of 65 fish taken from 16 multi-mesh gillnets set overnight by OMNR in 2003. This gear typically selects adult lake whitefish 2 years of age and older in the range of 120–509 mm (15–1,725 g). Stomach contents were weighed and the average mass of stomach contents determined to be 4.4 fresh g. Diets of whitefish across these size classes appear to be consistent (Hart 1931) and there was no clear relationship between fish size and stomach content weight. We also assumed that the fish did not change their consumption rate over the pre- to post-mussel time period and hence that stomach content mass is the same for the two periods. This assumption is reasonable given that whitefish round weight in South Bay was only slightly greater before dreissenid invasion (557 ± 393 g, mean ± standard deviation) than after (502 ± 362 g, M.D. Rennie, unpubl.).

The average weight of the stomach contents was then used to calculate energy values from percent composition of diet for the pre- and post-invasion period. For the pre-invasion period we applied proportional whitefish diet composition (Ihssen *et al.* 1981) to the average total wet mass of whitefish

stomach contents to estimate the mass of each prey group in a typical whitefish stomach. The mass of each prey item was multiplied by species-specific energy densities from the literature (Hanson *et al.* 1997, Eggleton and Schramm 2004) and summed to give the total energy content of a typical whitefish diet. We are aware of no published data on whitefish electivity for the post-invasion period and thus we constructed hypothetical post-invasion diets designed to be as conservative as possible and to include the range of all possible foraging behaviors. Our reasoning was that if extremes of post-invasion foraging behavior resulted in lower energy intake than during the pre-invasion period, actual post-invasion diets would certainly be lacking in energy. To represent random foraging, we assumed whitefish fed on zebra mussels, oligochaetes, chironomids, and sphaeriids in proportion to their relative abundances in the field. These species are common in the diets of more than 25% of whitefish sampled from Lakes Michigan and Ontario after the dreissenid invasion (Pothoven *et al.* 2001, Owens and Dittman 2003). We applied our field estimates of the relative abundance of these benthic groups, scaled to sum to unity, to the mean stomach content mass and computed total energy content in the same way as pre-invasion diets.

To represent non-random foraging we assumed that whitefish fed on only the most energy rich prey items remaining in South Bay after the major post-invasion reduction in *Diporeia* abundance. After *Diporeia*, *Mysis* is the most energy rich whitefish prey in the Great Lakes, although in the past South Bay whitefish did not eat *Mysis* nor do they consume many *Mysis* in some areas of Lake Michigan (Ihssen *et al.* 1981, Pothoven *et al.* 2001). Next to *Mysis*, oligochaetes are the most energy rich prey eaten by whitefish and are a common prey item of whitefish throughout the Great Lakes (Pothoven *et al.* 2001, Owens and Dittman 2003). We therefore present the energy content of diets of 100% *Mysis* as well as 100% oligochaetes to represent the maximum energy intake theoretically possible from non-random foraging on high-energy prey.

RESULTS

Multivariate Description of Benthic Invertebrate Community Change

Correspondence analyses (CA) demonstrated clear differences between invertebrate communities before and after the dreissenid invasion of South Bay (Fig. 2). The first two axes explained almost 65% of the variation in density ($X^2 = 659.697$; $df = 1190$, p << 0.001), and 59% of the variation in relative abundance ($X^2 = 307.852$; $df = 1190$, p << 0.001). *Diporeia* was always the most important taxon on axis 1, explaining 83% and 78% of the variation in the first axis due to density and relative abundance respectively. Sphaeriids were the second most important taxon on axis 1 for density (45%), and dreissenids for relative abundance (30%). Dreissenids were the most important taxon in explaining variation along the second axis (49% and 54% for density and relative abundance plots, respectively), followed by chironomids (31% and 37%).

The proximity of a site to organism scores indicates the relative importance of those organisms to a particular site (Fig. 2). Thus, sites occurring in the upper left-hand quadrant of the biplots, where eight of 11 organisms also appear, support the greatest diversity, whereas communities near the ends of the curve are dominated more by particular species (Fig. 2). Generally, shallower pre-invasion sites (zones 1 and 2) were located on the upper left-hand quadrant of the biplots, whereas deeper pre-invasion sites (zone 3) were found in the bottom right-hand quadrant (Fig. 2). After invasion of zebra mussels, sites less than 10 m (zone 1) shifted down along the second axis away from more heterogeneous communities toward those dominated by zebra mussels and isopods. Similarly, deepwater sites (zone 3) are less dominated by *Diporeia*, and are approaching more heterogeneous communities. Mid-water sites (zone 2) show no clear directional trend post-invasion, other than perhaps a greater heterogeneity amongst sites after the arrival of zebra mussels.

A comparison of Euclidian distances among sites demonstrated that in general differences due to annual variation were significantly smaller than differences associated with the arrival of *D. polymorpha* (Table 1).

Changes to Particular South Bay benthic invertebrate taxa

Univariate two-factor ANOVAs of invertebrate density showed a significant interaction between year and depth zone for both oligochaete and *Diporeia* density (Table 2). *Diporeia* density declined dramatically in the deepest zone following invasion but remained negligible in the shallow zones (Figs. 3 and 4). Oligochaete density increased in zone 1 after dreissenid invasion, but did not change in zones 2 and 3 (Figs. 3 and 4). Gastropods, Ephemeroptera, other amphipods, and isopods dif-
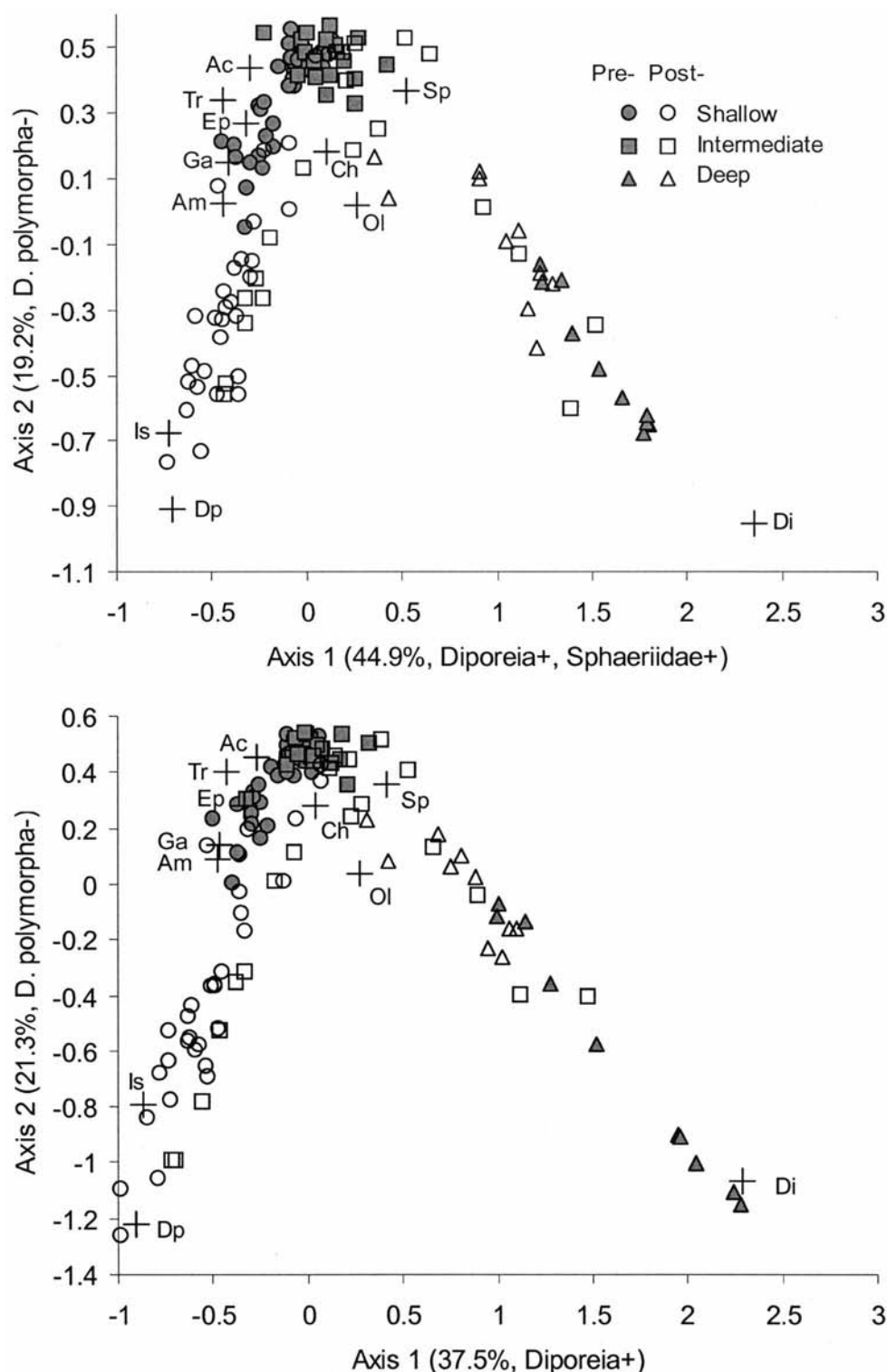
FIG. 2.   *First two axes of Correspondence Analysis of numeric density and relative abundance on invertebrates in South Bay, 1980–2003. Site scores for the depth zones before and after invasion are indicated with circles, triangles, and squares, and taxa scores are plotted as plus signs. Proportion of variation explained by each axis and the taxa accounting for more than 40% of this variation along with sign of the correlation are shown in parentheses. Abbreviations for taxa are: Ac = Acari, Am = Amphipoda (non-Diporeia), Ch = Chironomidae, Di = Diporeia, Dp = **Dreissena polymorpha**, Ep = Ephemeroptera, Ga = Gastropoda, Is = Isopoda, Ol = Oligochaeta, Sp = Sphaeriidae, and Tr = Trichoptera.*

TABLE 1. *Paired t-tests of mean Euclidean distances between benthic sampling sites based on annual change versus change due to the invasion of dreissenids. Degrees of freedom (df), t-values (annual minus invasion), and one-tailed probabilities of no difference (p) are shown. p_{crit} is the critical probability based on sequential Bonferroni correction. * indicates statistical significance at the corrected p-value.*

	Depth zone	df	t	p (one-tailed)	p_{crit}
Density	Zone 3	4	−3.31	0.023*	0.025
	Zone 2	9	−2.52	0.018	0.0125
	Zone 1	14	−6.95	< 0.0001*	0.006
	All zones	29	−6.91	< 0.0001*	0.003
Relative abundance	Zone 3	4	−2.3	0.042	0.025
	Zone 2	9	−2.62	0.014	0.0125
	Zone 1	14	−8.56	< 0.0001*	0.006
	All zones	29	−7.18	< 0.0001*	0.003

fered significantly among depth zones, but not among years, indicating that there has been no detectable change in the average density of these groups since the invasion of zebra mussels (Table 2). Sphaeriid and chironomid density significantly differed across both zones and years (Table 2). Chironomids, however, do not show any yearly trends consistent with an invasion effect (Figs. 3 and 4). Sphaeriids decreased in density in shallow waters, and did not change in the deeper zones (Figs. 3 and 4).

Analyses of relative abundance indicated a significant interaction between depth zone and year for *Diporeia* and chironomids (Table 3). *Diporeia* was absent from intermediate zone 2 in pre-invasion years but increased in relative abundance in post-invasion years; in the deep zone 3 it declined in relative abundance from pre- to post-invasion years (Figs. 5 and 6). Oligochaetes showed an increase in relative abundance in zone 2, but no obvious effect of invasion at other depths (Figs. 5 and 6). Chironomids decreased in relative abundance from pre- to post-invasion years in shallow zone 1, but did not change significantly at other depths (Figs. 5 and 6). Sphaeriids, Ephemeroptera, non-*Diporeia* amphipods, and isopods differed in relative abundance only among depth zones, but did not differ among years (Table 3). Gastropods differed significantly in both depth zone and year, however this was due to year-to-year variation in each of the depth zones (Figs. 5 and 6).

Long-term *Diporeia* density data from South Bay show that post-invasion densities are much lower than typical pre-invasion densities (Fig. 7). The pre-invasion mean density between 1959 and 1981 was 1,615±354 m^{-2}, whereas the post-invasion mean between 2001 and 2004 was only 180±42 m^{-2}, a decline of almost an order of magnitude. *Diporeia* density was low in pre-invasion years 1959 (315 m^{-2}) and 1960 (43 m^{-2}), but these appear to be anomalous. By contrast, post-invasion densities have been consistently low for all recorded years (Fig. 7).

Effects on Whitefish Diet

Our whitefish diet calculations showed that the typical pre-invasion whitefish stomach contained 17,512 J of invertebrate tissue (Table 4). The random feeding model for the post-invasion period indicated a typical whitefish stomach contained 10,037 J, only 57% of the pre-invasion energy. Feeding on oligochaetes alone would provide 14,728 J or 84% of pre-invasion energy intake, whereas a diet of pure *Mysis* could yield as much as 18,972 J or 108% of pre-invasion energy intake.

DISCUSSION

Changes in Benthic Communities

Following the dreissenid invasion of South Bay, benthic invertebrate communities changed across all depth zones even though dreissenids were generally found only at sites less than 10 m deep. These changes are broadly similar to changes seen in the other Great Lakes. The lack of changes for some groups is also generally consistent with findings across the Great Lakes where some groups do not seem to be affected by presence of zebra mussels in all habitats (Nalepa *et al.* 1998, Nalepa *et al.* 2003,

TABLE 2. *Results of two-factor ANOVAs of densities of benthic invertebrate groups. F-values and probabilities of no treatment effect (p) are shown. † represents a group that did not meet one or more of the parametric assumptions of ANOVA. There were three degrees of freedom associated with the year effect and two degrees of freedom associated with the depth effect. Results are based on a total of 120 observations. * indicates statistical significance at the Bonferroni-corrected probability of 0.00625.*

Group	Factor	F	P
Sphaeriids	Year	4.78	0.004*
	Zone	11.21	< 0.001*
	Year×zone	2.19	0.049
Gastropods	Year	1.51	0.215
	Zone	72.95	< 0.001*
	Year×zone	1.76	0.114
Trichopterans	Year	0.76	0.521
	Zone	30.17	< 0.001*
	Year×zone	0.54	0.775
Oligochaetes	Year	5.53	0.001*
	Zone	0.93	0.339
	Year×zone	4.62	< 0.001*
Diporeia†	Year	17.03	< 0.001*
	Zone	189.24	< 0.001*
	Year×zone	19.3	< 0.001*
Other amphipods	Year	0.07	0.975
	Zone	23.68	< 0.001*
	Year×zone	1.11	0.363
Chironomids†	Year	7.76	< 0.001*
	Zone	10.5	< 0.001*
	Year×zone	1.02	0.415
Isopods†	Year	1.44	0.236
	Zone	19.27	< 0.001*
	Year×zone	1.31	0.257

Owens and Dittman 2003, Dermott and Kerec 1997).

Our study is the first to detect a consistent and significant increase in oligochaete density associated with dreissenid invasion. This contrasts with results for Lakes Michigan and Ontario, where lake-wide declines in oligochaete density were recorded following dreissenid invasion (Nalepa *et al.* 1998, Owens and Dittman 2003). Nalepa *et al.*

(2003) report variable changes in oligochaete density in some locations of southern Lake Huron, but argued that it was a product of natural variation. We believe that our results may be partially due to the differences in anthropogenic stress in South Bay relative to the other Great Lakes. Throughout the Great Lakes the general decline of some benthic groups such as oligochaetes has been correlated with the planned decrease in phosphorus due to control programs of the mid 1980s (Madenjian *et al.* 2002, Nalepa *et al.* 1998). Nalepa *et al.* (1998) argued that zebra mussel effects on oligochaetes were negligible compared to the effects of phosphorous. Phosphorus levels in Lake Huron have remained below target levels since 1980 and South Bay may have experienced much less nutrient change since phosphorous control was initiated (SOLEC 2003). Gonzalez and Downing (1999) demonstrated that some invertebrate groups increase in density in the presence of dreissenids due to increased nutrients from pseudofeces. This may explain our results, and suggests that changes in oligochaete density associated with zebra mussel invasion can only be detected in the absence of anthropogenic influences on nutrient levels.

The significant decline of *Diporeia* in South Bay following the invasion of dreissenids is consistent with other benthic surveys in the Great Lakes. Declines in *Diporeia* density have been well documented in Lake Erie (Dermott and Kerec 1997), Lake Michigan (Nalepa *et al.* 1998), and Lake Ontario (Owens and Dittman 2003). It should be noted that though our data suggest an increase in *Diporeia* abundance at mid-water depths (11–30 m), this increase is inconsistent with other findings where *Diporeia* consistently decrease with increases in zebra mussels, or retreat into deeper waters (Nalepa *et al.* 1998, Nalepa *et al.* 2003, Dermott and Kerec 1997). This is probably not a real effect but rather an artefact of historical sampling practice. In 1980, only five out of 30 samples were examined specifically for the taxon *Diporeia*, one in shallow zone 1, two in intermediate zone 2, and two in deep zone 3, and the proportions of each species found in these samples were applied to the rest of the data. However, all post invasion samples were examined for the presence of *Diporeia*. Thus, the apparent increase in intermediate zone 2 may be a result of a more rigorous identification of Amphipoda in the recent samples. Despite this, we are confident that the data can be analyzed with *Diporeia* as a separate category from other amphipods. The benthic surveys performed between 1959 and 1962 in South Bay
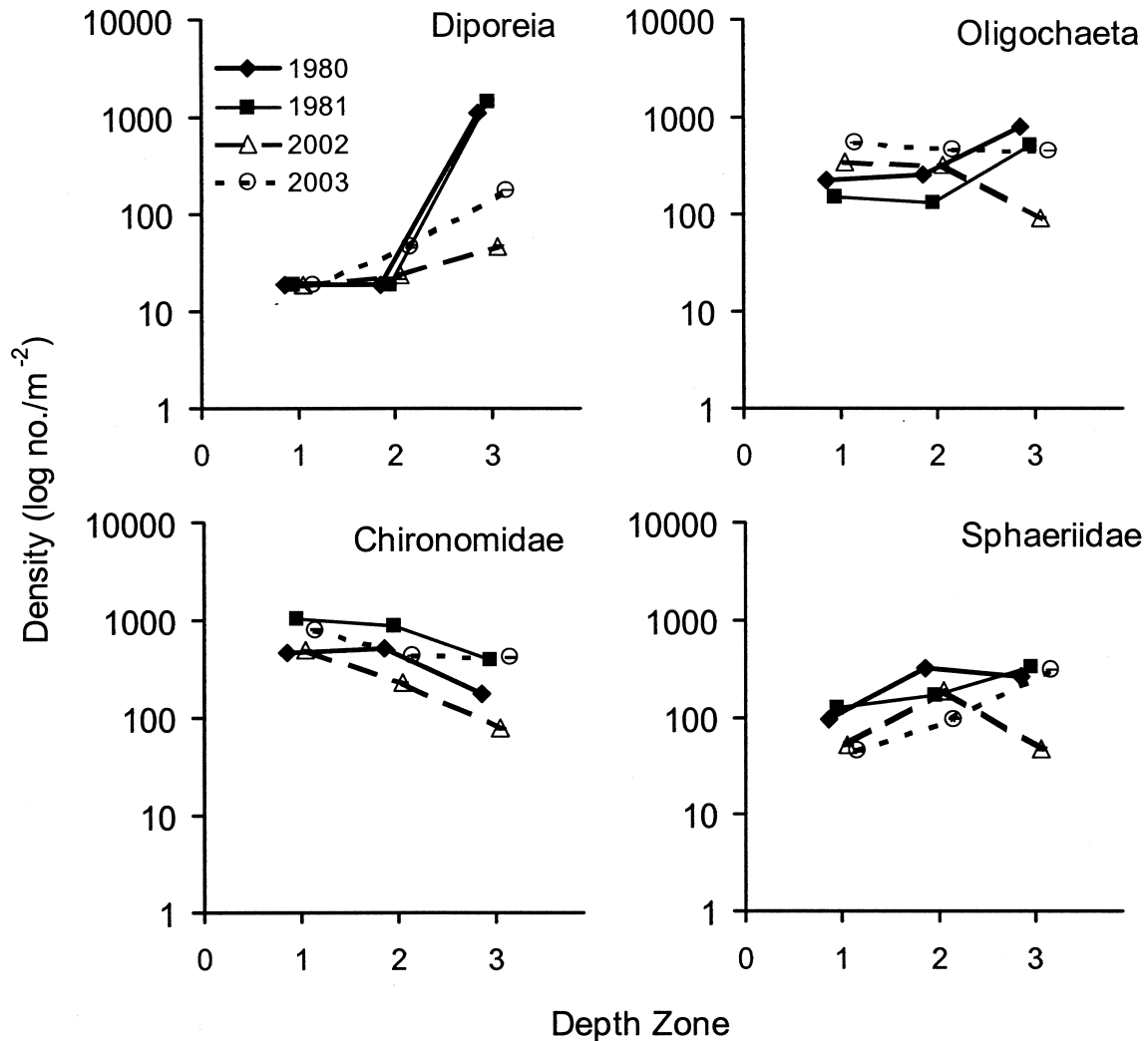
FIG. 3.   *Interaction of year and depth zone on log(x+1) mean density of organisms (one standard error is shown but is not visible on the log scale) for various taxonomic groups. Depth zones 1, 2, and 3 correspond to shallow, intermediate, and deep, respectively. For clarity depth zone values are offset for each group.*

showed that *Diporeia* was never found at depths that corresponded to our shallow zone 1, nor at most of the sites in intermediate zone 2 (Cooper 1964). These data also show that other amphipods were restricted to the shallow waters of our zones 1 and 2. Data from Lakes Ontario, Michigan, and Erie also show similar distributions of *Diporeia* relative to other amphipod species and support the separation of *Diporeia* from other amphipods by depth (Owens and Dittman 2003, Nalepa *et al.* 1998, Dermott and Kerec 1997). Furthermore, in the post-invasion period (2002–2003) *Diporeia* made up 100% of amphipods found in deep zone 3,

and only 5% of amphipods found in shallower zones 1 and 2, suggesting any overlap in shallow water is likely insignificant.

Though our univariate analyses show patterns for single groups of invertebrates, the multivariate approaches we present offer insights into community-wide changes in benthic communities. We have detected significant shifts in community composition due to dreissenid invasion that show a trend toward more homogeneous shallow water communities dominated by dreissenids, and a shift in deep-water communities away from dominance by *Diporeia.*
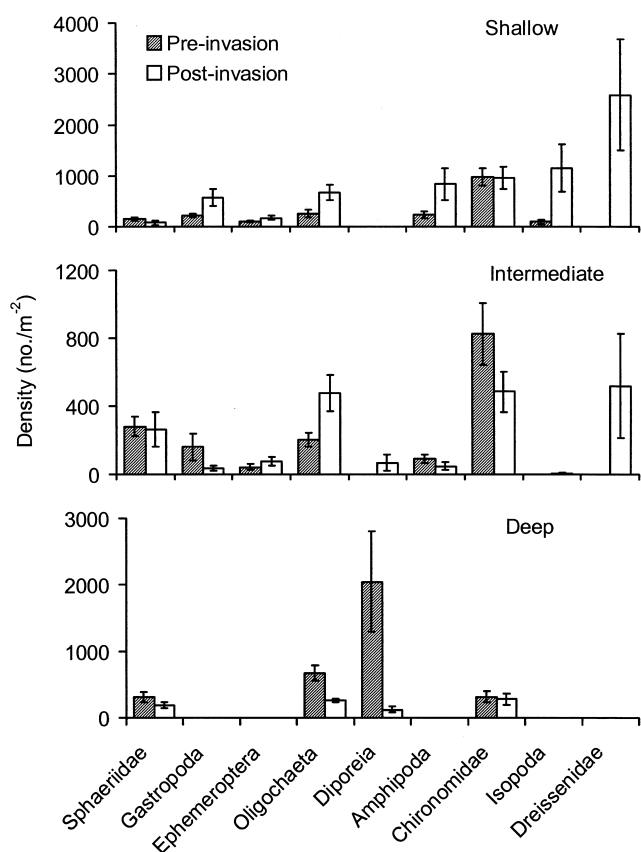
FIG. 4. Mean density (no.m⁻²) of each benthic invertebrate group by depth zone and invasion status. One standard error on either side of the mean is shown. Acari and Trichoptera were rare in all years and are excluded.

TABLE 3. Results of two-factor ANOVAs of the relative abundance of benthic invertebrate groups. Details as in Table 2.

Group	Factor	F	P
Sphaeriids	Year	1.41	0.243
	Zone	19.33	< 0.001*
	Year×zone	2.58	0.022
Gastropods†	Year	4.33	0.006*
	Zone	53.99	0.006*
	Year×zone	1.94	0.081
Trichopterans†	Year	0.2	0.897
	Zone	19.81	< 0.001*
	Year×zone	0.74	0.621
Oligochaetes†	Year	8.83	< 0.001*
	Zone	14.79	< 0.001*
	Year×zone	1.85	0.096
Diporeia†	Year	10.1	< 0.001*
	Zone	148.55	< 0.001*
	Year×zone	13.23	< 0.001*
Other amphipods	Year	0.9	0.443
	Zone	19.5	< 0.001*
	Year×zone	0.55	0.767
Chironomids	Year	10.39	< 0.001*
	Zone	6.89	0.002*
	Year×zone	4.5	< 0.001*
Isopods†	Year	0.84	0.475
	Zone	17.64	< 0.001*
	Year×zone	0.6	0.733

Potential Effects of Changes in Benthos on Whitefish

We have shown that changes to benthic invertebrate communities could potentially explain at least some of the declines in whitefish growth rate that have been observed in South Bay and the rest of the Great Lakes. Whitefish diets changed dramatically in Lakes Ontario and Michigan following the invasion of zebra mussels and the subsequent collapse of *Diporeia*. Following the collapse of *Diporeia* in these lakes, whitefish diets included greater quantities of oligochaetes, chironomids, sphaeriids, and zebra mussels (Owens and Dittman 2003, Pothoven et al. 2001). Increased reliance on *Mysis* in whitefish diets was observed in Lake Ontario following the collapse of *Diporeia* (Owens and Dittman 2003). Whitefish in Lake Michigan showed more variable reliance on *Mysis* following the loss of *Diporeia*. In some regions of the lake *Mysis* effectively made up for any missing *Diporeia* in whitefish diets (percent weight), and in other areas no increase in *Mysis* consumption was observed (Pothoven et al. 2001). Historically, whitefish in South Bay did not eat *Mysis*, even though it was available, whereas *Mysis* was a historical food item in both Lakes Michigan and Ontario (Ihssen et al. 1981, Owens and Dittman 2003, Pothoven et al. 2001).

Our calculations show that *Mysis* could replace *Diporeia* as the principal source of energy in whitefish diets. However, energy densities for *Mysis* are known to vary from 2,972–4,312 J/g (Hanson et al. 1997). Our estimates use the highest value from the literature to make our predictions about detrimental effects on whitefish as conservative as possible. Whitefish diets would contain only 75% of pre-
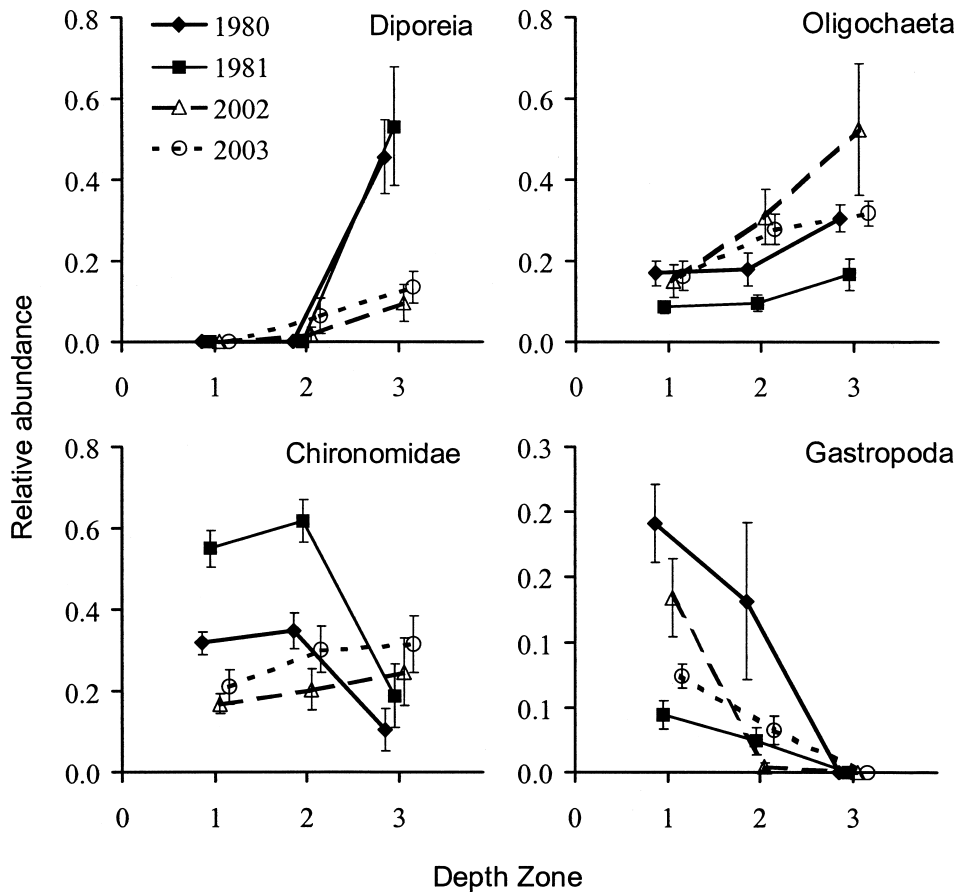
FIG. 5.   *Interaction of year and depth zone on mean relative abundance of organisms (one standard error on either side of the mean is shown) for various taxonomic groups. Depth zones 1, 2, and 3 correspond to shallow, intermediate, and deep, respectively.*

invasion energy if the lowest value from the literature is used in our calculations. Thus, *Mysis* may not always be able to replace *Diporeia* because of variability in caloric density, nor do all whitefish stocks take advantage of *Mysis* as prey for reasons that are unclear.

The next most energy rich prey item after *Mysis* is oligochaetes. However, our calculations show an exclusive diet of oligochaetes would provide only 84% of historical energy intake on average, and thus oligochaetes may not be a viable alternative prey to *Diporeia*. Also, our calculations do not take into account the energetic cost associated with foraging on a single prey and ignoring others. In reality whitefish will eat more than one prey. Adding any other prey to this hypothesized high-energy diet would further reduce total energy intake. If whitefish are not selective in their feeding habits, then they will only achieve 57% of historical en-

ergy intake. None of these calculations takes account of the effects of increased foraging time associated with average declines in total invertebrate density in deep water associated with zebra mussel invasion throughout the Great Lakes (from 3,788 to 1,104 m^{-2} in South Bay). Furthermore, few data are available on differences in caloric content of invertebrates among populations, and at different times of the season many invertebrates likely show considerable variation. Thus, our predictions about reductions in energy availability to whitefish after mussel invasion are very likely underestimates. We believe these results can be generalized to other regions of the Great Lakes where, even though there will be variability in the benthos available, the consistent loss of *Diporeia* as the principal source of energy means that unless whitefish eat only *Mysis* they will have lower energy intake than in the past.
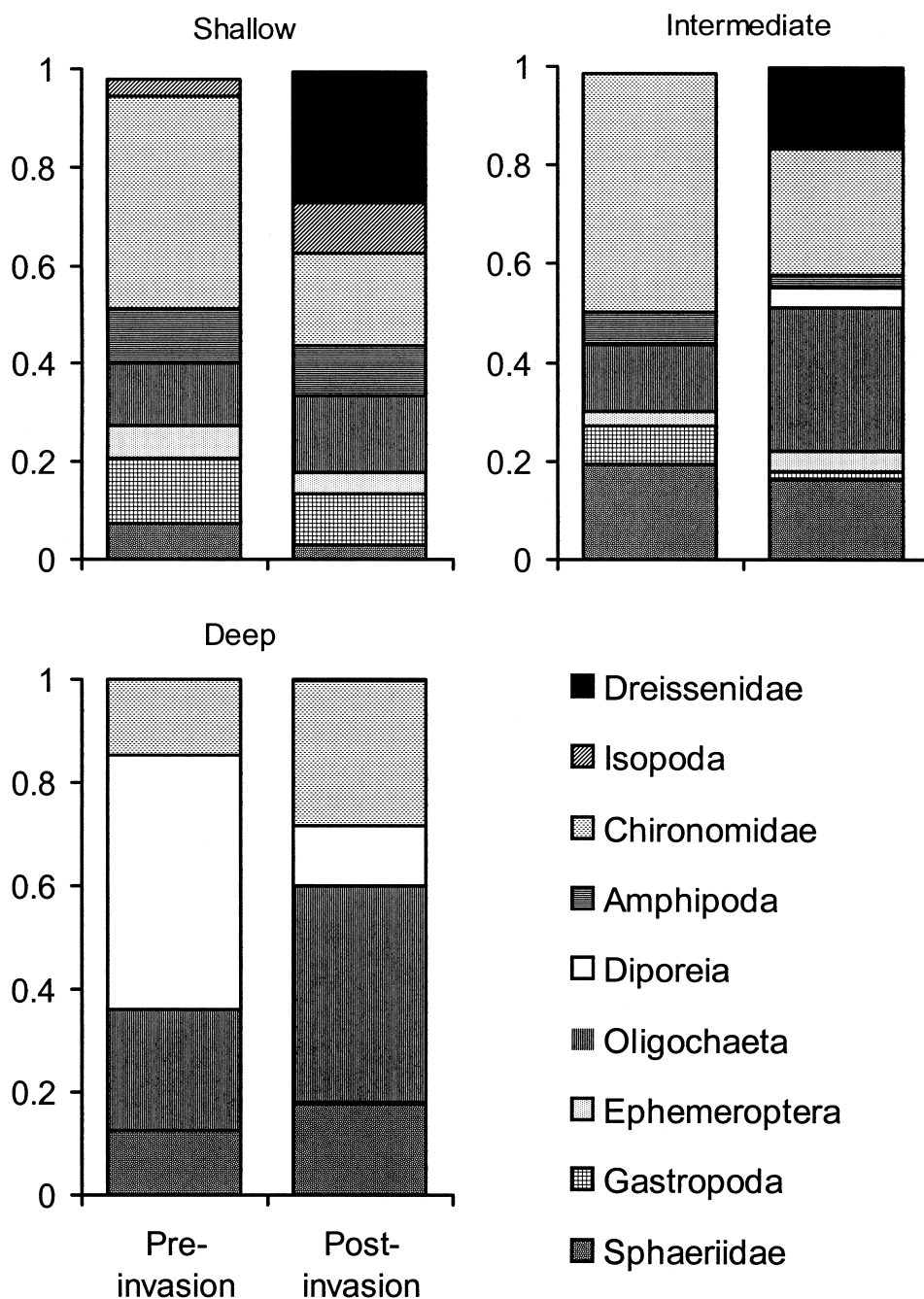
In summary, our study indicates there has been a

FIG. 6. *Mean relative abundance of benthic invertebrates in South Bay by depth zone and invasion status. Acari and Trichoptera were rare in all years and are excluded.*

shift in some components of the benthic community of South Bay that broadly complement observations elsewhere in the Great Lakes. The fact that changes in oligochaete populations due to zebra mussel invasion may be confounded with changes in phosphorus suggests that more research is needed to separate the effects of environment and invasive species so that management strategies can be effectively implemented. We also show that the changes in benthic communities in South Bay alter the prey available to adult lake whitefish in a manner that potentially explains at least part of the reduced
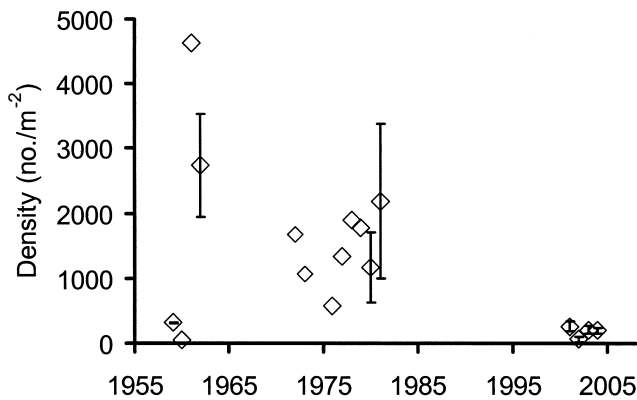
FIG. 7.   Mean density of Diporeia in the deep waters of South Bay between 1959 and 2003 from depths that roughly correspond to our deep zone 3. (±1 standard error is shown for time periods when raw data were available.)

growth rate of this important commercial species. These results can be generalized to other regions of the Great Lakes and we predict the response will vary from stock to stock, depending upon *Mysis* consumption, but that whitefish throughout the

Great Lakes will experience a decline in growth and condition. More research is needed to determine how these differences will affect whitefish in different regions and life stages.

TABLE 4.   Estimated energy content of the diet of a typical adult whitefish in South Bay before and after zebra mussel invasion (see text for details).

	Taxon	Energy density (J/g) (wet mass)	Proportion of stomach contents	Mass (g)[d]	Energy (J)
Pre-invasion	*Diporeia*	4,429[a]	0.82[c]	3.61	15,980
	Chironomids	2,428[a]	0.14	0.62	1,496
	Sphaeriids	209[b]	0.04	0.18	37
			Total	4.41	17,512
Post-invasion, random feeding	*Diporeia*	4,429[a]	0.05[e]	0.22	974
	Chironomids	2,428[a]	0.28	1.21	2,939
	Sphaeriids	209[b]	0.13	0.59	123
	Oligochaetes	3,347[b]	0.39	1.73	5,800
	Dreissena	318[b]	0.14	0.63	200
			Total	4.38	10,037
Post-invasion, non-random feeding	*Mysis*	4,312[a]	1.0	4.4	18,972
	Oligochaetes	3,347[b]	1.0	4.4	14,728

[a] Hanson *et al.* 1997 (Estimates of caloric content for *Mysis* vary from 2,972–4,312 J/g. We used the highest value to make our estimates more conservative)

[b] Eggleton and Schramm 2004

[c] Ihssen *et al.* 1981

[d] mean fresh mass of whitefish stomach contents (OMNR, unpubl.).

[e] mean proportions in habitat from our 2002 and 2003 depth zones 2 and 3 scaled to sum to 1 for listed taxa.

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