The distribution of *Dreissena* and other benthic invertebrates in Lake Erie, 2002.

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

A lake-wide benthic survey of Lake Erie during summer 2002 indicated that *Dreissena bugensis* is the dominant dreissenid in Lake Erie, especially in the east basin where this species was found at every station but no *Dreissena polymorpha* were collected. Mean (±SD) densities of dreissenid mussels were comparable between the west (601±2,110/m^2,n=49) and central (635±1,293/m^2; n=41) basins, but were much greater in the east basin (9,480±11,173/m^2;n=17). The greater variability in mussel density among stations and replicate samples in the central and west basins than in the east basin is attributable to the preponderance of fine-grained substrata in the nearshore, higher episodic rates of sediment deposition and periodic hypoxia in bottom waters. Although there was little change in lake-wide mean dreissenid densities between 1992 and 2002 (declining from ca. 2,636 individuals/m^2 to 2,025 individuals/m^2), basin-averaged shell-free dry tissue mass increased by almost four-fold from ca. 6.8±15.6 g /m2 to 24.7±71.3 g/m^2 in the same interval. Up to 90% of this biomass is in the eastern basin. Other changes in 2002 include the virtual absence of mussels in the 3 to 12 mm size range, probably because of predation by round gobies, and an increase in the average size of mature mussels. The substantial changes observed between 1992 and 2002 suggest that dreissenid populations in Lake Erie were still changing rapidly in abundance and biomass, as well as species composition. The results of this survey suggest that a direct link between *Dreissena* spp. and hypolimnetic hypoxia in the central basin is unlikely.

The dominant organisms of Lake Erie in 2002 were *D. rostriformis bugensis* (38%), Oligochaeta (33%), Chironomidae (18%), Sphaeriidae (2.7%), Amphipoda (2.3%) and Hydrozoa (2.2%). Mean invertebrate density was greater in the east basin, especially on hard substrates, than either the west or central basin. In the central basin, sites ≥5m supported greater numbers of organisms, than shallow (≤2m) sites in the nearshore wave zone. The greatest number of taxa were observed in the central basin, likely a resutlt of greater sampling effort there. *Gammarus fasciatus* comprised 80% of all amphipods, being most abundant on *Dreissena*-dominated hard substrates in the east basin. The introduced species, *Echinogammarus ischnus* occured at only 11 of 69 sites, and was the only amphipod found at 4 east basin sites, but at relatively low densities. *Diporeia* were not found in our survey. *Hexagenia* was collected at only 4 stations, all in the west basin.

Chironomids were dominated by *Tanytarsus* and *Chironomus*, with *Procladius*, *Dicrotendipes* and *Polypedilum* also being relatively common. Oligochaete Trophic Index for 2002 indicates a similarly mesotrophic condition throughout the lake and marginal nutrient enrichment of sediments between years 1979-2002. Multivariate ordination of community data indicates clear separation of sites by year and basin as expected given the extirpation of *Diporeia* and the introduction of *Dreissena* and *E. ischnus*, but also reveals subtle changes in benthic structure over the last 2 decades. The benthic community of Lake Erie in 2002 does not likely represent an equilibrium condition.

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Dedication

Michael H. Spironello
Dipterist and Friend
October 21, 1977 – May 24, 2006.

Long may you run.

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"…an investigation of any biological system without defining species precisely is as fruitless as studying a chemical reaction without knowledge of the elements."

Cook and Johnson (1974)

"Chemical measurements are like taking snapshots of the ecosystem, whereas biological measurements are like making a videotape."

Rosenberg (1998)

"Not everything that can be counted counts, and not everything that counts can be counted."

Albert Einstein

Chapter 1 - General Introduction

1.1 A brief history of synoptic zoobenthic surveys of Lake Erie

Benthic invertebrate assemblages throughout Lake Erie are diverse and often naturally patchy. However, among Lake Erie's basins, readily identifiable communities can exist within similar depth strata, substrate and habitats indicative of the lake's morphology, east to west gradient of increasing nutrient concentration and episodic occurrence of low hypolimnetic dissolved oxygen (Brinkhurst et al. 1968, Brinkhurst 1969a, Cook and Johnson 1974, Barton 1988a, Dermott 1994). Attention has often focused on the west (Krecker and Lancaster 1933, Shelford and Boesel 1942, Wright 1955, Wood 1963, Carr and Hiltunen 1965, Veal and Osmond 1968, Hiltunen 1969, Britt et al. 1980, Keeler 1981, Steane and Cooper 1981) or central basin (Britt et al. 1980, Barton 1988b), with only one published study from 1973-1976 focusing entirely on the east basin (Flint and Merckel 1978). The formative work by Veal and Osmond (1968) in the 1960s and Barton and Hynes in the 1970s (Barton and Hynes 1978a, Barton and Hynes 1978b, Barton and Hynes 1978c, Barton 1988b) characterized the effects of nearshore wave dynamics, substrate and seasonal changes on macroinvertebrate distributions along Lake Erie's northern shoreline. One study in 1978-1979 focused on the southern nearshore of the central basin, with sample locations largely concentrated near river mouths (Krieger 1984).

Compared to more coordinated efforts seen in other areas of the Great Lakes, including Lake Huron (Nalepa et al. 2003) and Lake Michigan (Nalepa et al. 1998), recent surveys and consistent monitoring strategies of Lake Erie benthic invertebrates have been limited. Three lake wide surveys were reported for Lake Erie greater than a decade prior to the arrival of *Dreissena*. The University of Toronto Great Lakes Institute (GLI) surveyed the lake between 1963-1965. The chironomid, oligochaete and sphaeriid data from the 1963 GLI survey was originally reported by Brinkhurst et al. (1968) and later reported by Barton (1988a) in greater taxonomic detail including the 1963-1965 data. Under the Federal Water Pollution Control Administration, the U.S Public Health Service conducted their own survey in 1963-1964 (FWPCA 1968) and in 1978/79 the Canada Centre for Inland Waters (CCIW) completed a survey of benthic fauna in conjunction with a surficial sediment survey initiated under the Canada-United States

Agreement on Great Lakes Water Quality (1972) (Dermott 1994). Regrettably, the FWPCA report on benthic macroinvertebrates lacked taxonomic detail and was far too brief to assess invertebrate distributions even to the family level of classification. Additionally, the GLI and CCIW surveys have data of questionable quantitative value related to sample handling procedures in the former survey and the retrieval of only one replicate sample in both. Despite these shortcomings, the qualitative characteristics of the benthic community is consistent with earlier studies of Lake Erie fauna (Barton 1988a, Dermott 1994).

The limited number of benthic macroinvertebrate studies conducted on Lake Erie in the early 1980s, just prior to the arrival of *Dreissena* mussels, are suggestive of improved sediment and water quality resulting from nutrient and pollution abatement practices since the 1960s. Using oligochaete fauna and a tubificid trophic index refined for use in the Great Lakes (Milbrink 1983), Schloesser et al. (1995) observed a decline in the numbers of oligochaetes and changes in the relative numbers of indicator oligochaete taxa consistent with decreased pollution levels nearest to major river mouths in western basin Lake Erie. Conversely, changes in oligochaete communities at offshore sites indicated increased area of moderate pollution, suggesting that both the oligochaete community and pollution status were in a state of transition between 1961 and 1982. In Cleveland Harbour between 1978 to 1989, Krieger and Ross (1993) reported increased numbers of taxa at all sites, increased sphaeriid clam and chironomid abundance, reduced proportions of oligochaetes and increased frequency of *Oecetis* sp. caddisflies (Trichoptera) as evidence of improved sediment quality.

The often cited and most readily apparent evidence of improved conditions in Lake Erie in recent decades is from the reestablishment of populations of *Hexagenia* spp. in the soft sediments of the west basin. *Hexagenia* mayflies (Ephemeridae) have been recovering from a dramatic population decline after a series of hypoxic/anoxic events in the 1950s and 1960s as a result of cultural nutrient enrichment combined with meteorological conditions favourable to the establishment of a persistent thermocline late in the summer (Britt 1955a, Britt 1955b, Carr et al. 1965). *Hexagenia* were not commonly retrieved from benthic samples until the early 1990s and it wasn't until 1995 that burrowing mayflies were again being found throughout the basin (Krieger et al. 1996, Schloesser et al. 2000).

1.2 Benthic invertebrate distribution and impact of dreissenids on zoobenthos

As the number of exotic species in the Laurentian Great Lakes continues to rise over recent decades and threaten native species and ecosystem function (Mills et al. 1993b, Vanderploeg et al. 2002, Munawar et al. 2005), there is a rising complexity in the interactions between aquatic invasive species, changing nutrient levels and other anthropogenic influences on the benthic community. Trends of benthic (Krieger and Ross 1993, Schloesser et al. 1995) and pelagic (Charlton et al. 1999, Charlton 2001) cultural eutrophication were beginning to reverse in Lake Erie following abatement strategies adopted through international water quality agreements (IJC 1978) when two Ponto-Caspian bivalves, the zebra mussel, (*Dreissena polymorpha*) and the quagga mussel (*D. rostriformis bugensis*) arrived in the Laurentian Great Lakes. The zebra mussel was first detected from Lake St.Clair in June of 1988, in the western and central basin of Lake Erie later that year (Hebert et al. 1989) and then in eastern Lake Erie by 1989 (Griffiths et al. 1991). The quagga mussel was identified as a second *Dreissena* species, at first reported from Lake Ontario in 1991 (May and Marsden 1992) with sightings as early as 1989 in eastern Lake Erie (Mills et al. 1993a).

While ecologists began to synthesize knowledge of the biological and ecological importance of *Dreissena spp*. (Nalepa and Schloesser 1993) and document the distribution, population structure and initial *Dreissena*-mediated ecosystem effects in Lake Erie (Dermott and Munawar 1993, Mills et al. 1993a), two additional exotic species of concern were observed. The round goby, *Neogobius melanostomus*, was first collected from sites along the St.Clair River in 1990 (Crossman et al. 1992, Jude et al. 1992) and reported in the central basin of Lake Erie by 1994 (Haas and Tyson 2001). The amphipod, *Echinogammarus ischnus*, was dicovered near the mouth of the Detroit River in 1995 (Witt et al. 1997), appearing at survey sites throughout Lake Erie the following year (Dermott et al. 1998). With most exotic species introductions, the impact on native biodiversity and productivity are of primary concern and their discovery has prompted numerous studies of the putative impacts of *Dreissena* and other recent invaders on the biological integrity and energy pathways of Great Lakes ecosystems (Vanderploeg et al. 2002, Hecky et al. 2004).

Dreissenid mussels, when described as ecosystem modifiers (sensu Jones et al. 1994, Crooks 2002) exert biotic and abiotic influences on benthic macroinvertebrate communities by either excluding or facilitating various taxa (Strayer et al. 1999, Gutiérrez et al. 2003). However, these interactions are complex, not fully understood, and in some cases, the traditional interpretation of trends in trophic status based on benthic biological data in the Great Lakes have been complicated by the influence exerted by dreissenid mussels (Lang 1999, Nalepa et al. 2000). Experimental and mensurative studies of trends in zoobenthic density and distribution generally indicate a positive relationship between the presence of dreissenids and species richness, abundance and biomass of other benthic invertebrate species (Ward and Ricciardi 2007). Enhanced habitat heterogeneity and complexity contributed by mussel shells (both living and dead) increases surface area available for colonization, attachment and grazing, and interstitial spaces may provide smaller invertebrates with refuge from predation and wave induced disturbance (Dermott et al. 1993, Griffiths 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a, 1998c, Gonzalez and Downing 1999, Stewart et al. 1999, Bially and MacIsaac 2000). Taxon-dependent increases of non-dreissenid benthic invertebrates have been attributed to increases in nutrient rich biodeposits of faeces and pseudofaeces (Wisenden and Bailey 1995, Botts et al. 1996, Ricciardi et al. 1997, Roditi et al. 1997, Stewart et al. 1998a, 1998b, 1998c, Kuhns and Berg 1999, Stewart et al. 1999, Bially and MacIsaac 2000, Mayer et al. 2002, Szabo 2004). The retention of deposited particulate organic matter may also be enhanced by the mussel shell complex, prolonging its availability to the benthic invertebrate community (Roditi et al. 1997, Stewart et al. 1998a, 1999).

1.3 Predation and the Impact of Round Gobies

In addition to the considerable influence *Dreissena* can have in shaping the benthic community, predators may additionally regulate invertebrate composition and abundance (Stewart et al. 1999). Round gobies were first reported from the St. Clair River in 1990 (Crossman 1991, Jude et al. 1992) and have since expanded their range to Lake Erie (Haas and Tyson 2003) and across the Great Lakes basin. As juveniles (<12 cm total length), round gobies are known to feed voraciously on small, soft bodied invertebrates including amphipods, chironomids and zooplankton,with a subsequent ontogenetic shift in diet by larger gobies to include mollusks, particularly *Dreissena* (Ghedotti et al. 1995, Jude et al. 1995, Ray and Corkum 1997, Djuricich and Janssen 2001, French and Jude 2001, Janssen and Jude 2001, Skora and Rzeznik 2001). Although round goby diet preferences are well documented (Stewart et al. 1999, Pothoven et al. 2000, French and Jude 2001, Andraso 2005) their effects on *Dreissena* and benthic communities are only recently being demonstrated to cause reductions in *Dreissena* and some non-*Dreissena* invertebrate densities (Kuhns and Berg 1999, Barton et al. 2005) and affect invertebrate population size distributions (Patterson et al. 2005, Lederer et al. 2006). Of critical concern is the prospect of reduced endemic biodiversity, the degradation of benthic community assemblages and alteration of foodweb structure and trophic dynamics by round goby predation and *Dreissena* range expansion.

1.4 Thesis Objectives

The goal of my study was to report on the distribution of benthic macroinvertebrate fauna of Lake Erie with the following objectives:

1) On basin and lake-wide scales, quantify and compare:
    a) density distribution, relative abundance and biomass of Zebra mussels (*Dreissena polymorpha*) and Quagga mussels (*Dreissena bugensis*) from nearshore (≤20 m) vs. offshore sites with respect to depth and substrate.
    b) density and relative abundance of non-dreissenid benthic macroinvertebrates of nearshore and offshore regions with respect to depth and substrate.
    c) impacts of *Dreissena spp.* density on non-dreissenid macroinvertebrate community structure and abundance.
2) Compare objectives 1a-c with historical data and comment on temporal and spatial trends in dreissenid and non-dreissenid zoobenthic species distribution.

Objective 1a and 2 are addressed in Chapter 2 of my thesis, which was published in The Journal of Great Lakes Research (Patterson et al. 2005) as part of the Lake Erie Trophic Status Collaborative Study (Matisoff and Ciborowski 2005). Objectives 1b, 1c and 2 are fulfilled in Chapter 3.

Chapter 2 – The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002

2.1 Introduction

Since their discovery and proliferation in the Laurentian Great Lakes, zebra (*Dreissena polymorpha*) (Hebert et al. 1989) and quagga (*Dreissena bugensis*) (May and Marsden 1992) mussels have been implicated as modifiers of nutrient dynamics and biological integrity of lake ecosystems (see reviews in Strayer et al. 1999, Vanderploeg et al. 2002). Hecky et al. (2004) proposed a conceptual model that describes several mechanisms by which dreissenids reallocate nutrients from the water column to benthic habitats. A fundamental requirement for the accurate assessment of the effects of dreissenids on nutrient cycling is data on the abundance and distribution of mussels. When abundant, dreissenids unquestionably have significant influences on water quality and epibenthic characteristics in shallow water areas (Nicholls and Hopkins 1993, Lowe and Pillsbury 1995, Stewart et al. 1998a, Vanderploeg et al. 2001). Dreissenids had become abundant in the central basin of Lake Erie by 1990. By this time, loadings of total phosphorus to Lake Erie had been reduced to below 11,000 Tonnes/y, the level thought to be adequate to improve water quality and reduce the frequency of anoxic events in the central basin (Makarewicz and Bertram 1991). Marked increases in epilimnetic water clarity in the early 1990s (Nicholls and Hopkins 1993) and continuing apparent declines in open water total phosphorus concentrations (Millard et al. 1999) were ascribed to dreissenid activity. However, more recent evaluations of water quality trends through the 1990s indicate poorer correlations between some of these parameters and the advent of dreissenids. Makarewicz et al. (2000) found little difference in nutrient trends in the first 10 y since dreissenids had become established in L. Erie and the period immediately preceding their arrival. Barbiero and Tuchman (2004) reported that turbidity levels in Lake Erie have tended to increase over the interval during which dreissenids have been present. Nevertheless, when increased total phosphorus concentrations were observed in the central basin during spring monitoring in the late 1990s (Rockwell et al. 2005), questions about the role of dreissenids in internal nutrient dynamics and a potential link to hypolimnetic anoxia in the central basin stimulated the coordinated research program reported in this volume (Matisoff and Ciborowski 2005). If dreissenids have a direct effect, there should be a measurable relationship between changing densities of mussels at epilimnetic and metalimnetic depths and temporal patterns of total phosphorus concentrations and frequency of central basin hypolimnetic anoxia.

The biomass of *Dreissena* species in Lake Erie increased between 1992 and 1998 (Jarvis et al. 2000), as *D. bugensis* became increasingly abundant relative to *D. polymorpha* in the central and eastern basins (Dermott and Munawar 1993, Mitchell et al. 1996a, Dermott and Kerec 1997, Mills et al. 1999, Jarvis et al. 2000, Johannsson et al. 2000). Zebra mussels remained dominant in the western basin (Berkman et al. 2000, Bially and MacIsaac 2000, Jarvis et al. 2000). The two species were originally expected to partition the habitat, with *D. polymorpha* colonizing hard substrates in shallow water, and *D. bugensis* confined to soft sedimentary environments in the colder profundal zone (>30 m) (Dermott and Munawar 1993). Recent field observations, however, indicate a continued expansion of the quagga mussel into progressively shallower regions as well as soft offshore sediments in Lake Erie (Coakley et al. 1997, Berkman et al. 1998, Berkman et al. 2000, Haltuch et al. 2000, Coakley et al. 2002).

These observations suggest it is unlikely that recent densities reflect a long-term stabilization of abundance. Therefore, the objective of this study was to describe the distribution, density, and abundance of dreissenid species throughout Lake Erie in 2002, in order to evaluate the potential role of mussels in nutrient dynamics and anoxia, and to document continuing change in the benthic community.

2.2 Methods

From 15 May through 8 September 2002, benthic samples were collected during three surveys that included a total of 107 stations throughout Lake Erie (
Figure 1).

The West Basin Grid survey was conducted between mid-May and mid-August; five petite Ponar (0.0225 m^2) samples were collected from each of 38 stations in the west basin. Station depths ranged from 3.6 to 11.5 m. Secondly, three Petite Ponar samples were collected from each of 17 stations (6.1 to 61.8 m depth) along four transects visited by the USEPA Research Vessel 'Lake Guardian' during a cruise from 17 to 21 August 2002 (Guardian survey). (No benthic samples were taken at EPA sites '55' or 'Sandusky'.) The third survey covered 50 stations along 18 transects perpendicular to the north shore in the west, central and east basins (Northshore survey). Stations were located at depths of 2, 5 and 10 m on most west and central basins transects and 2, 5, 10 and 20 m in the east basin. Three samples were collected at each station during August 2002. A petite Ponar grab sampler was used at west and central basin sites. Rocky substrata at depths ≤10 m in the east basin were sampled with an airlift (0.0314 m^2) by divers. An Ekman grab (0.0225 m^2) was used for the 20-m sites. Hard substrata prevented sampling at two 2-m sites in the west basin (Plum Point, Kingsville). Two 10-m (Comet, Colchester) stations could not be sampled due to poor weather.

All samples were immediately sieved through 250 µm Nitex mesh and the material retained was preserved in 10% buffered formalin. Depth, substrate and GPS coordinates were recorded at all stations.

2.3 Sample Processing

Upon return to the laboratory, the preserved Northshore and Guardian samples were rinsed with water through 250-µm aperture screen and examined under a dissecting microscope. All macroinvertebrates were removed to 70% ethanol. Northshore and Guardian samples that contained very large numbers of animals were subsampled by dividing the residues into eighths and removing organisms from two, nonadjacent subsamples. If the numbers of organisms in the eighths differed by >10%, additional subsamples were sorted. West Basin Grid samples were washed through a set of nested brass sieves (4-mm, 1-mm, 0.5-mm and 0.25-mm apertures), then dreissenids were counted from each fraction. Large mussels (>1 mm) were found at only six of the West Basin Grid sites and these dreissenids were identified to species. Nine sites yielded only a few individuals (<533 mussels/m^2), all of which were too small to be identified reliably; values of density and mass for these 9 sites were treated as zeros during subsequent species-specific analyses.

The relationships among shell length, wet (with shell) mass and shell-free dry tissue mass were determined using dreissenids from one sample from each Guardian and Northshore station. Valve lengths were determined to the nearest 0.01 mm using electronic calipers, and all individuals >1 mm long were identified to species. Wet mass was determined following the procedures of Jarvis et al. (2000), then soft tissue was removed from the shell, dried at 50°C for at least 48 h, and weighted to the nearest 0.01

mg. Mussels <1 mm were enumerated from all samples, but omitted from further analysis.

2.4 Data Analysis

Areal dry mass of *Dreissena* at each sample station was estimated using a regression model of individual shell-free dry tissue mass versus shell length, combined with length-frequency distributions. Mean values for each station were used in a second regression of dry mass against whole wet-mass so that measurements (shell included) reported in previous studies of Lake Erie (Jarvis et al. 2000) could be converted to shell-free dry mass. The whole-lake 1992-1998 survey of Jarvis et al. (2000) was used for historical comparison with *Dreissena* abundance and dry biomass distribution in our study.

All mass and density data were log-transformed prior to analysis of patterns of distribution relative to basin, depth and substrate type. The unit of replication was a sampling site, and the variates consisted of the mean values of the three or five samples collected at each site. Two statistical analyses were performed. One incorporated the entire data set (all three surveys) using a multiple regression approach to test for differences among basins, and among classes of depth and substrate type, all treated as dummy variables. The second analysis evaluated variation in dreissenid abundance and mass among depths within Northshore transects. Analyses were performed using Statistica® Version 5.8 (Statsoft Inc. 2000).

Because the numbers of sites sampled throughout the lake varied disproportionately among basins, depth classes and substrate classes, multiple regression analysis was used to determine how dreissenid density and mass differed among locations. Classes of the independent variables depth (<4 m, 4-8 m, >8-15 m, >15-24 m, and >24 m), basin (east, central, west), and substrate (mud, sand/silt, sand, coarse material, hard) were treated as binary dummy variables against which densities and mass of each dreissenid species were regressed. Thus, a total of four regression analyses was performed. Both Northshore and offshore data were combined for these analyses.

The Northshore collections alone were analysed by treating each transect as a block and performing randomized block ANOVA to evaluate the significance of overall differences among depths (2, 5, 10 m) blocked by transect. We substituted Ponar grab sample values collected from the nearest Western Basin Grid station for two western basin transects where the 10-m depth had not been sampled. Data for one missing 2-m station were replaced by a value of zero (equivalent to values at the 2-m depth of adjacent transects on either side). A planned comparison test was performed to determine whether expected differences between the shallow vs. deeper sites (2 m vs. 5 & 10 m) were statistically significant.

2.5 Results

Of the 1,100 specimens of *Dreissena* used to describe the relationship between shell length and tissue dry mass, only 28 were *D. polymorpha*. Removal of these individuals from the analysis made no difference to the to the pooled regression results ($p>0.05$), so they were omitted from analysis. Valve length of mussels used for allometric models ranged from 4.9 mm to 38.5 mm, however no mussels collected from the west basin from either the Northshore or Guardian surveys were large enough to allow direct biomass measurements. Relationships between dry tissue mass (g) and shell length (mm) for mussels from the central and eastern basin at each depth class revealed three distinct groups: central basin, east basin 2-20 m and east basin >20 m. When coefficient *a* was constrained to be shared among these three groups, coefficient *b* differed significantly between regression equations for mussels collected from the three locations, so that each is described by a different regression equation ($F_{2,1069}=290.9$, $p<0.0001$, Bonferroni, $p<0.001$). Therefore, three separate regression models were used to estimate dry tissue mass from shell length for individual mussels collected from these areas of the lake (Patterson M.W.R. and Barton, D.R, unpublished data). The allometric equations for central basin dreissenids were applied to west basin mussels because too few mussels large enough for biomass measurement were found at the west basin Northshore and Guardian survey sites.

$$\text{dry tissue mass (g)} = 1.659\times10^{-5}(\text{shell length (mm)})^{2.463}\ (R^2=0.82).$$

This equation was used to estimate dry tissue mass from shell length distributions for all samples collected in 2002.

We used the following relationship between site mean dry tissue weight and site mean whole wet weight of dreissenids to convert values of mass (as wet weights with shell) reported by Jarvis et al. (2000) from surveys done from 1992 through 1998 to dry mass (tissue only) for comparison with our data:

$$\text{shell-free dry mass (g)} = 0.0265 * \text{whole wet mass (g)} \quad (R^2 = 0.96).$$

2.5.1 2002 Dreissenid Distribution

Dreissenids were present at 57 of the 107 sites surveyed in 2002 (Table 1, Figure 2), including all of the 17 stations in the east basin and about 44% of the stations in the central and west basins. The mean (±standard deviation) lake-wide density and dry mass of *Dreissena* spp. were 2,025±5,665 individuals/m^2 and 24.7±71.3 g dry tissue/m^2 (Table 1). Numerical densities did not differ significantly between the west (601.1 mussels/m^2) and central (635 mussels/m^2) basins, but were an order of magnitude greater in the east basin (9,481 mussels/m^2) (Table 2).

Dreissena bugensis was the dominant species in Lake Erie (Table 1), accounting for approximately 87% of the mussels identified from all three surveys, and was significantly more abundant in the east basin than in the west or central basins (density: $p<0.001$, Table 2; biomass: $p<0.001$, Table 3). Both the density and biomass of *D. polymorpha* declined from west to east ($p<0.05$, Table 2): zebra mussels accounted for 45%, 3% and 0% of mean *Dreissena* density in the west, central and east basins, respectively. Mean zebra mussel dry mass calculated using all samples from the three surveys was only 0.80 g /m^2, compared to 23.43 g/m^2 for quagga mussels.

Densities of zebra mussels were greatest at depths of 4 - 8 m lake-wide. In contrast, maximum densities and biomass of quagga mussels occurred at depths of 15-24 m (Table 2). Differences in density among depth intervals were not significant for either species for the combined surveys (Tables 2 and 3), except that *D. polymorpha* was almost completely restricted to the shallow western basin. However, analysis of the transect-specific Northshore data indicated that both species were significantly more abundant at depths of 5 and 10 m than at 2 m ($p<0.05$; Table 4). The distribution of mussel mass exhibited the same pattern. Mass of *D. bugensis* was lowest in the shallowest depth class

(<4 m) and greatest biomass occurred in the 15-24-m depth class of the eastern basin (Table 1). Because biomass was highly variable among samples, the difference in biomass relative to the shallowest depths only approached (but didn't achieve) statistical significance for the 8-15 m depth class ($p<0.08$, Table 3).

Part of the difference in mussel abundance among basins is due to differences in substratum. All sites sampled in the east basin at depths ≤10 m were on bedrock, boulders or cobbles; airlift samples yielded 6,334±4,441 quagga mussels/m^2 (Figure 3). Similar hard substrata in the western basin were not sampled as efficiently with the Ponar grab used for the West Basin Grid. Fine-grained sediments (mud, silt, sandy silt) were sampled effectively by the grab in all basins and supported high densities of mussels (1,599±5,937/m^2), but numbers of individuals were extremely variable both among stations and among replicate samples at most stations. This was especially true in the west basin where the mean density of dreissenids was 601±2,110/m^2, and the maximum was 13,822/m^2. Densities of *D. bugensis* on coarse and hard substrates were significantly greater than on mud ($p<0.05$, and $p<0.01$, respectively, Table 2). There were no significant differences in density of *D. polymorpha* with respect to substrate texture (Table 2). *Dreissena bugensis* biomass was significantly greater on hard (bedrock) substrate than on mud ($p<0.01$; Table 3). Although greater mass also occurred on coarse substrate than on mud, that difference was not statistically significant. Mass of *D. polymorpha* did not vary significantly among substrate classes (Table 3).

2.5.2 Changes in *Dreissena* spp. Distribution: 1992-2002

The lakewide mean density of *Dreissena* spp in 2002 (2,025/m^2) was 53% lower than in 1998 (3,791/m^2), but dry mass was 1.7 times as great (24.6 g/m^2 vs.14.5 g/m^2) (Figure 4). Neither of these differences was statistically significant ($p>0.05$) because of the large variability among stations and replicates in both years. The change in biomass was attributable to quagga mussels, whose mean areal mass increased significantly ($p<0.01$) from ca. 1.7 g/m^2 in 1992, to 13.2 g/m^2 in 1998, and 23.4 g/m^2 in 2002, despite a decrease from 3,478 to 1,860 individuals/m^2 from 1998 to 2002 (Figure 5A, Figure 6A). The change in zebra mussel abundance in the same period was also not statistically significant ($p>0.05$), even though mean lake-wide zebra mussel density decreased from ~2,096 individuals (5.5 g)/m^2 in 1992, to 131 individuals (0.8 g)/m^2 in 2002 (Figure 5B,

Figure 6B). *Dreissena bugensis* dry mass was consistently greatest in the eastern basin across all years. However, mass and density increased disproportionately through time in the eastern basin, whereas decreases have occurred in the western and central basins (Figure 5, Figure 6). Dry mass of *D. bugensis* increased from 13.2 g/m^2 in 1998, to 23.4 g/m^2 in 2002 but increased from 17.8 g/m^2 to 104.2 g/m^2 within the eastern basin considered alone. The overall decline in density of quagga mussels while total mass increased from 1998 to 2002 is attributable to a change in the size frequency distribution of mussels. For example, stations E3 and 933 from Jarvis et al. (2000) correspond very closely to our Port Ryerse 10-m and Evans Point 20-m stations. The virtual absence of individuals between 3 and 12 mm in length (Figure 7) at these stations in 2002, was typical of stations throughout Lake Erie.

2.6 Discussion - 1992-2002 Distribution

The results of benthic surveys in 2002 suggest that the distribution and size structure of dreissenid populations in Lake Erie is still evolving. After initially appearing on softer, offshore sediments (Dermott and Munawar 1993, Mills et al. 1993a, Mills et al. 1996, Jarvis et al. 2000, Martel et al. 2001), *D. bugensis* has become increasingly dominant throughout Lake Erie, completely displacing *D. polymorpha* in the eastern basin, and accounting for 43% of the mussels in samples from the west basin as of 2002. The total density of dreissenids appears to have decreased slightly, while mass has increased.

This shift in dominance from *D. polymorpha* to *D. bugensis* likely reflects differences in assimilation efficiency and respiration rates which make the quagga mussel a superior competitor at high densities and low food concentrations (Baldwin et al. 2002, Stoeckmann 2003). The early success of quagga mussels in deeper water is thought to reflect higher growth rates at low food concentrations (Diggins 2001, Baldwin et al. 2002) and a lower tolerance of high temperatures (Domm et al. 1993, Spidle et al. 1995, Thorp et al. 1998). Both food availability and temperature should be higher in shallow, more turbulent waters, and *D. polymorpha* is still common in the western basin of Lake Erie. However, water temperatures in the western basin rarely approach the upper lethal limits for either *Dreissena* species. Food concentrations in the nearshore of the eastern basin (0.5-4.0 µg Chl *a*/L; Depew (2003)) are within the range known to favour quagga over zebra mussels (Baldwin et al. 2002), and are somewhat higher in the western basin

(MacDougall et al. 2001). Perhaps even more significantly, mussels have limited access to the water column during much of the summer in the shallow (≤6m) nearshore zone of the eastern basin because of the dense growths of *Cladophora glomerata* that completely blanket all hard substrates from May through mid-August (Higgins et al. 2005). *Cladophora* coverage is less extensive in the west and central basins because of the limited availability of hard substrates and the higher turbidity caused by resuspension of sediments during strong winds. We suggest that the complete replacement of *D. polymorpha* by *D. bugensis* in the eastern basin has been facilitated by the combination of low concentrations of phytoplankton and a luxuriant carpet of benthic algae. These conditions are themselves a result of the establishment of dreissenids in Lake Erie, and their subsequent effects on the distribution of nutrients (Hecky et al. 2004).

Given the general west to east decline in primary production in Lake Erie (MacDougall et al. 2001), it is somewhat surprising that the abundance of *Dreissena* spp. now increases from west to east. Some of this pattern is directly attributable to the high densities of quagga mussels we collected in airlift samples from the extensive areas of rocky substrata along the north shore of the east basin. MacIsaac et al. (1992) reported very high densities of *D. polymorpha* (ca. 250,000/m^2), most of which were ≤5 mm in length, on rocks in western Lake Erie in 1991, but methodological differences preclude direct comparison with our results. Hard substrates account for about 15% of the bottom of the west basin (Coakley et al. 1997), but grab samplers are ineffective on rock so the densities of mussels on this substrate in 2002 are unknown.

All other sampling sites visited by the Northshore survey in the west and central basins had substrata consisting of fine gravel or sand at depths ≤5 m (Coakley 1972, Gelinas and Quigley 1973, Thomas et al. 1976), and finer-grained sediments in deeper water. Frequent disturbance by wave action strongly limits the abundance of mussels on sand and gravel in shallow water, and the few mussels collected in these samples were almost all <6 mm in length, suggesting they had settled recently. Colonization of softer sediments in deeper water largely depends on the availability of larger particles to which initial colonists can attach (Coakley et al. 1997, Berkman et al. 1998, Berkman et al. 2000, Haltuch et al. 2000, Coakley et al. 2002). Long-term survival of mussels in such habitats can be limited by episodic anoxia of the bottom waters and deposition of sediment (Dermott and Munawar 1993, Coakley et al. 1997, Bially and MacIsaac 2000), both of which are common in the central and west basins. Hypolimnetic anoxia has not been recorded in the much deeper eastern basin. Sediment inputs to the east basin are also proportionally less because of the rocky shoreline, which limits shore erosion (Quigley and Tutt 1968), and the small number of tributary streams. Consequently, the colonization of softer, offshore sediments has been uninterrupted in the east basin, resulting in high densities of mussels. The impacts of episodic anoxia and sediment deposition are evident in the lower and more variable densities of mussels on soft sediments in the west and central basins.

The apparent decline in the lake-wide density of *Dreissena* spp. between 1998 and 2002 is consistent with frequently observed population dynamics of invasive species (Sakai et al. 2001). The increase in biomass during that time interval, however, suggests that the dreissenid populations in Lake Erie are still in a state of flux. When the size-frequency distributions of mussels collected in 2002 are compared with those from previous surveys (e.g., Dermott and Munawar 1993, MacIsaac 1996b, Coakley et al. 1997, Jarvis et al. 2000), the disappearance of animals in the 3 to 12 mm size classes is striking. This is the size range preferred by round gobies (Ray and Corkum 1997). The average size and proportion of adult quagga mussels appears to have increased over time, but especially since 1998, and this is the interval during which round gobies invaded eastern Lake Erie. These observations suggest that predation by gobies is having a strong impact on the recruitment of mussels to the juvenile and adult stages (Barton et al. 2005). Quagga mussels that have achieved a shell length >12mm may be largely free of goby predation. The consequences of this are difficult to predict without information about round goby abundance and the longevity of quagga mussels once they have reached adult size.

While our observation of replacement of zebra mussels by quagga mussels is not novel, the marked increase in mean areal dry mass, especially in the eastern basin over the last decade, is. Increased biomass and filtering capacity by dreissenids, stimulates nutrient cycling and storage through benthic habitats (Arnott and Vanni 1996, Dobson and Mackie 1998, Ackerman 1999, Covich et al. 1999, Strayer et al. 1999, Ackerman et al. 2001, Conroy et al. 2005) driving strong benthic-pelagic linkages (Schindler and

Scheuerell 2002). While *D. bugensis* has been shown to remove and retain phosphorus from the water column more efficiently than does *D. polymorpha* (Conroy et al. 2005), internal loading and cycling of phosphorus will be intensified with greater densities of mussels of either species. Hecky et al. (2004) hypothesized that dreissenids are re-engineering the nearshore environment; the high densities of mussels in the profundal zone of eastern Lake Erie suggest these effects may not be limited just to the nearshore.

The biomass of *D. bugensis* increased substantially in the east basin of Lake Erie between 1992 and 2002, but it is not clear that this trend can be expected to continue. Obviously, there must be an upper limit set by the total energy inputs to Lake Erie, but in the shorter-term, the absence of mussels in the 3-12 mm length class suggests that predation is limiting recruitment to the adult population at depths ≤20 m. Whether or not this intensity of predation will continue also remains to be seen but seems unlikely based on the observations reported by Barton et al. (2005).

The estimates of abundance of dreissenids reported here are summaries of the samples collected in 2002. If we weight and sum our estimates for each basin according to the relative area of depths and types of substratum available, almost 90% of the total mass of mussels in Lake Erie in 2002 occurred in the east basin (Ciborowski, Barton & Krieger, unpublished data). This is inconsistent with conjectures that the recent increase in frequency and severity of hypoxia in the central basin (Charlton et al. 1999, Rockwell et al. 2005) is a direct consequence of the establishment of *Dreissena* species, because most of the mussels are presently downstream of the central basin. Therefore, if there are direct links among dreissenid activity, altered nutrient dynamics and central basin hypoxia, either eastern basin quagga mussels are influencing central basin processes (gyres can theoretically circulate water from the eastern to the central basin (Leon et al. 2005), or there must be a substantial time lag between the (past) influence of dreissenids on particle and nutrient dynamics and biological oxygen demand in the hypolimnion of the central basin.

Chapter 3 - Lake Erie Benthic Macroinvertebrate Community, 2002

3.1 Introduction

Through efficient filter feeding, dreissenid mussels have been widely implicated in the reallocation and sequestering of energy and nutrients from the water column to benthic habitats, coupling pelagic resources with benthic food webs (Holland et al. 1995, Klerks et al. 1996, Mitchell et al. 1996b, Johannsson et al. 2000, Ackerman et al. 2001, Hecky et al. 2004, Szabo 2004). The deposition of high quality, organically-rich biodeposits is a major energy flux to the sediment (Klerks et al. 1996, Roditi et al. 1997, Dobson and Mackie 1998), which largely benefits deposit-feeding invertebrates in rocky habitats (Stewart et al. 1998a, 1998b, Kuhns and Berg 1999, Mayer et al. 2002). Benthic foodwebs now appear to dominate Lake Erie's energy pathways as a product of dreissenid-induced energy diversion of pelagic resources to the benthos, coupled with increased benthic secondary production (Dahl et al. 1995, Johannsson et al. 2000). With *Dreissena* dry biomass increasing in Lake Erie by almost four-fold between 1992 to 2002 (Patterson et al. 2005), this represents a major alteration of energy and nutrients to the benthos.

Filter-feeding and deposit-feeding profundal invertebrates on the other hand typically experience declines in abundance as a result of seston being intercepted by *Dreissena* (Dermott and Munawar 1993, Dahl et al. 1995, Dermott and Kerec 1997, Strayer et al. 1998, Johannsson et al. 2000). Evidence of reduced benthic invertebrate diversity and abundance following *Dreissena* colonization have been reported from sites in eastern Lake Erie (Howell et al. 1996) and western Lake Ontario (Haynes et al. 2005). The former keystone species *Diporeia hoyi* appears to have been extirpated from Lake Erie (Dermott and Kerec 1997) and experienced steep declines in other areas of the Great Lakes (Dermott 2001, Lozano et al. 2001, Dermott et al. 2005, Nalepa et al. 2005a, Nalepa et al. 2005b). The response of sphaeriid clams to mussel infestation has been variable, but population declines have been observed in Lake Erie (Dermott and Kerec 1997), Lake Ontario (Kilgour et al. 2000, Dermott 2001, Lozano et al. 2001) and Lake Michigan (Nalepa et al. 1998, Lauer and McComish 2001). The extirpation of unionid mussels has also been accelerated by dreissenid infestation (Nalepa et al. 1996, Ricciardi et al. 1998), although there is evidence this trend was occurring in Lake Erie prior to

Dreissena spp. introduction (Nalepa et al. 1991). These effects are not just limited to the offshore. Nearshore, filter-feeding hydropsychid caddisflies and heptageniid mayflies have become rare where they were previously abundant (Ratti and Barton 2003). Recovery and maintenance of *Hexagenia* (Ephemeridae) populations in the west basin as an indicator of ecosystem health is also of great concern (Reynoldson et al. 1989, Krieger et al. 1996, Madenjian et al. 1998, SOLEC 1999, Edsall 2001, Krieger 2002, Edsall et al. 2005).

The concept of decreased faunal diversity and abundance, in conjunction with the recently proposed "invasional meltdown" hypothesis, whereby previously established invaders mediate the recruitment of new, non-endemic species, suggest the possibility of weakening the stability of benthic communities and the homogenization of benthic assemblages in the Great Lakes (Lodge et al. 1998, Simberloff and Von Holle 1999, Ricciardi 2001, Rahel 2002). For example, early indications suggested that *Gammarus fasciatus* was being replaced by the Ponto-Caspian invasive amphipod *Echinogammarus ischnus* on rocky habitats in the Laurentian Great Lakes, including Lake Erie (Dermott et al. 1998, Van Overdijk et al. 2003), but this trend was not seen in eastern Lake Erie (Barton et al. 2005).

In terms of ecosystem and biodiversity management, the interactions between mussel generated habitat complexity, *Dreissena*-induced energy diversion and the impacts of round gobies on zoobenthic structure and abundance should be better understood. Data from active monitoring of dreissenids and other benthic invertebrates on a lakewide scale are crucial to the interpretation of the impact of exotic species introductions, the allocation of resources to benthic secondary production and nutrient cycling processes, all of which are being viewed with increasing importance in lake management strategies and energy budgets (Vanderploeg et al. 2002, Hecky et al. 2004) and ecological models (Leon et al. 2011).

To help address several concerns of the long term effects of *Dreissena* spp. on benthic invertebrate community structure and dynamics, the objectives of the Lake Erie 2002 synoptic survey were to: 1) quantify and compare benthic invertebrate abundance and composition in Lake Erie's nearshore (<20 m) and offshore on a variety of substrates in all three basins, 2) and to make inferences as to historical changes in benthic community structure and abundance since the establishment of *Dreissena* and the round goby.

3.2 Methods

3.2.1 Sample Collection

Lake Erie is typically viewed as being comprised of three morphologically distinct basins, west, central and east, which deepen progressively from the west (mean depth 7.6, 17.8 and 27.0 m respectively; Burns 1976, Sly 1976). There is also an eastward gradient of declining total phosphorus and chlorophyll *a* concentrations from the productive west basin to the oligotrophic east basin (Dahl et al. 1995, Dermott and Munawar 2002). In the summer of 2002, benthic samples were collected during two surveys that included a total of 69 stations throughout Lake Erie (Figure 8, Appendix 1a). During the first survey (Guardian), three Petite Ponar (0.0225 m^2) samples were collected from each of seventeen stations (6.1 to 61.8 m depth) along four transects visited by the USEPA Research Vessel 'Lake Guardian' during 17 to 21 August 2002 (benthic samples were not taken at EPA sites '55' or 'Sandusky').

The second survey (Northshore), from 19 August to 8 September, covered 52 stations along 18 transects perpendicular to the north shore in the west, central and east basins (Figure 8). Triplicate samples were collected at depths of 2, 5 and 10 m on most west and central basins transects and at 2, 5, 10 and 20 m in the east basin. A Petite Ponar grab sampler (0.0225 m^2) was used at all depths at the west and central basin sites. In the east basin, sites with rocky substrate at depths ≤ 10m were sampled from 0.0314 m^2 quadrats with an airlift fitted with a 250 µm Nitex mesh collecting bag (Barton and Hynes 1978a) by SCUBA divers; an Ekman grab (0.0225 m^2) was used for 20 m sites. Hard substrata prevented sampling at the 2 m sites on the Plum Point transect in the central basin and Kingsville transect in the west basin. Two 10 m stations (Comet, Colchester) could not be sampled due to poor weather. Round gobies were observed at all sites sampled by SCUBA, but their abundances were not estimated. Estimates of round goby density were obtained from a companion study conducted along the Peacock Point transect at 2, 5, and 10 m depths (Barton et al. 2005).

All samples were immediately sieved through 250 µm Nitex mesh and the material retained was preserved in 10% buffered formalin. Depth, substrate type (i.e.

bedrock, gravel, sand, silt etc.) and GPS coordinates were recorded at all stations. For the purpose of this study the nearshore is defined as the area of the lake ≤20m deep, an area comprising 23 242.9 km^{-2}, approximatley 54 % of Lake Erie's surface area (M. Patterson, unpublished data). Sample stations were located away from known point sources of pollution and heavy anthropogenic activity. Given the large difference in the number of samples for each substrate type and depth within each basin (Appendix 1b), and following the recommendations of Barton (1988b), bedrock, cobble and gravel substrates were collapsed into a single "hard" substrate grouping. Sand, sand/silt, silt and mud sediments were combined into a "soft" substrate group to balance sample size for statistical analyses.

3.3.2 Laboratory Processing

Upon return to the laboratory, the preserved Northshore and Guardian samples were thoroughly rinsed with water through 250-µm aperture mesh, placed into a sorting tray and examined under a dissecting microscope. All *Dreissena* and other macroinvertebrates were removed and sorted into separate vials for each major taxonomic group (e.g. Amphipoda, Bivalvia, Chironomidae, Gastropoda, Oligochaeta etc.) and stored in 70% ethanol until identified. Northshore and Guardian samples that contained very large numbers of animals were subsampled by dividing the residues into eighths and removing organisms from at least two, nonadjacent subsamples.

Once separated from sediment residues, all dreissenids with valve lengths greater than approximately 4 mm were identified to species using external shell diagnostic features (Pathy and Mackie 1993, Rosenberg and Ludyanskiy 1994). Mussels with shell lengths of 1-4 mm were measured using the ZEBRA2 system (Allen et al. 1994) and identified under a dissecting microscope (Nichols and Black 1994, Claxton et al. 1997). Mussels <1 mm were enumerated from all samples, but not identified, and were omitted from analysis.

Chironomids were identified following Wiederholm (1983) and Epler (2001). *Gammarus fasciatus* and *Echinogammarus ischnus* were identified following Witt et al. (1997) while remaining Amphipods were identified according to Bousfield (1958). All other animals were identified following Sawyer (1972), Burch (1975, 1982), Edmunds et al. (1976), Williams (1976), Clarke (1981), Brinkhurst (1986), Wiggins (1996) and Thorp and Covich (2001). Animals were identified to the lowest practical taxonomic level, usually genus or species.

3.3.3 Historical Data

To facilitate historical comparison of pre-dreissenid zoobenthos abundance and distributions, data from a 1978/79 Lake Erie survey (Dermott 1994) were acquired from Ron Dermott (Department of Fisheries and Oceans Canada). The 1978/79 survey initiated through the Canada-United States Agreement on Great Lakes Water Quality (1972) was designed to provide baseline data on the abundance and species composition of benthic fauna in Lake Erie. Two Shipek grab samples were collected at each station, one for surficial sediment/geochemical analysis and one for zoobenthos. Of the original 260 geochemical sample stations analyzed (Thomas et al. 1976), 159 stations were analyzed for benthic invertebrates (Dermott 1994).

Invertebrate counts for the 159 benthic survey stations sampled in October 1979 were received as FORTRAN output to a MS Wordpad document with site headers, including depth, latitude and longitude in decimal degrees, and taxonomic variables and area standardized animal density (number of individuals m^{-2}). These data were imported to a MS Access database and exported to a MS Excel spreadsheet as a variable (column) by site (row) matrix. The original analysis included meiofauna (Nematoda, Copepoda and Ostracoda) most of which were not enumerated in the 2002 survey, so were deleted from further analyses. Identifications made in 1979 were revised to match current taxonomy if necessary. From the 1979 survey, Dermott (1994) reported reduced abundance of oligochaetes in the west basin as a result of improving water quality since the 1960's, but suggested there was little change in benthic community composition and abundance within the central or eastern basin.

To allow for meaningful evaluation of changes in zoobenthic composition between 1979 (pre-*Dreissena*) to 2002, a subset of the original 159 lake-wide sites from the 1979 survey were selectively reduced to the three nearest-neighbour sites to those from 2002 in ArcGIS (Beyer 2004, ESRI Inc. 2004). Since few sites in the 1979 survey corresponded closely in terms of depth or substrate to the 2002 Northshore survey, 41 sample points from the 2002 Northshore survey, mostly from the central basin, particularly sites ≤5m, were omitted from this comparison. In total, 35 sites from 1979 and 28 sites from 2002 were retained for analysis and are termed 1979-2002 “matched” sites (Figure 9). These data do not explicitly allow direct site to site comparison, but they do afford the opportunity to approximate any changes in the benthic fauna from comparable depths and habitats in Lake Erie in the last 23 years. Similar methods and comparison of unpaired sampling locations from historical data have proven informative in documenting changes in the benthic community of western basin Lake Erie (Reynoldson et al. 1989, Minns et al. 1996). Other than the exploratory use of rarefaction and correspondence analysis, no statistical tests of significance were performed between the 1979-2002 “matched” data, due to the small number of replicates in 1979 (n=1) and because invertebrate abundance was not standardized or corrected for sampling device efficiency or mesh aperture used in each survey (Flannagan 1970, Nalepa et al. 1988, Reynoldson et al. 1989, Schloesser and Nalepa 2002).

3.3.4 Data Analysis

Invertebrate mean density and richness (number of taxa per sample) were evaluated for differences among depths (5 classes: <2m, >2-5m, >5-10m, >10-20m & >20m), basins (west, central, east) and substrates (hard vs soft). Log(x+1) transformation failed to normalize abundance data or stabilize variance, so these data were analyzed using non-parametric Mann-Whitney *U* statistics and Kruskal-Wallis one-way analysis of variance by ranks with SPSS 13 and Dunn’s multiple comparison (Dunn 1964) using GraphPad Prism 4 where applicable.

The number of organisms and taxa collected at each site are inherently valuable measures of the community, however, the number of individual organisms retrieved at each site showed considerable variation. To standardize taxa richness between basins and years, individual-based rarefaction (± 95% confidence limits, Gotelli and Colwell 2001) was performed using EcoSim v7.0 (Gotelli and Entsminger 2005) to calculate the mean number of species expected for a given sample size. The mean number of species observed at each site was used as the unit of replication. EcoSim default abundance levels based on 1000 random samples (with replacement) were used for rarefaction curve estimation. The number of default abundance levels (S+1) calculated by EcoSim follows the approach suggested by Tipper (1979), where S is the number of species, and S+1 are equally spaced integer values between 1 and the maximum observed abundance, N.

Explicit rarefaction was also performed, based on the lowest mean number of individuals collected from each basin (or year) drawn randomly 1,000 times (with replacement) from the community data.

The use of trophic indices offers a method to detect changes in nutrient status based on oligochaete taxa (Howmiller and Scott 1977, Milbrink 1983, Lauritsen et al. 1985, Reynoldson et al. 1989, Schloesser et al. 1995). The trophic condition index of Milbrink (1983) is based on the number, identity and ecological tolerances of oligochaete taxa, and was calculated for both the 1979 and 2002 data using oligochaete trophic classifications of Mozley and Howmiller (1977) and Lauritsen et al. (1985). Values approaching 3.0 indicate eutrophic conditions, 0.6-1.0, mesotrophic conditions, and values less than 0.6 indicate more oligotrophic conditions.

Benthic community analysis was performed by correspondence analysis (CA, Hill 1973) using CANOCO (Version 4, ter Braak and Šmilauer 1998). CA simultaneously describes major gradients in species composition among sites, indicates locations of species maxima, is not effected by total abundance and has been demonstrated to be a robust, unimodal multivariate method when analyzing benthic invertebrate communities (Jackson 1993). CAs were scaled by species, since the configuration of species is our main interest. Scaling by species does not affect the order of points along the axis, only the relative scatter of points along the extracted ordination axis (Jongman et al. 1995, Legendre and Legendre 1998). This results in scatterplots on which species are plotted at the approximate centroid of the samples where they occur and the distance between species and sites approximates the chi-square distance. CA is also a recommended ordination method when data contain many null values, such as when species replace each other over long environmental gradients (Legendre and Legendre 1998). However, since CA ordination plots can suffer from distortion when rare taxa are included (Jongman et al. 1995), only those taxa accounting for >0.5% (2002 survey only) and >0.25% (1979-2002 "matched" data) of total adundance were retained. Additionally, since species abundance had a skewed distribution, with many small and some very high values, data were square-root transformed prior to CA.

3.4 Results

3.4.1 Invertebrate Distribution, 2002

Invertebrate Density and Richness

A total of 107 taxa was identified from the 69 stations sampled in 2002, with a lake-wide average density of 6426.5 ± 933.1 (±SE) individuals m^{-2} (Table 5). The most abundant organisms were D. r. *bugensis* (38%), Oligochaeta (33%), Chironomidae (18%), Sphaeriidae (2.7%), Amphipoda (2.3%) and Hydrozoa (2.2%). *D. r. bugensis* was collected at 40 sites lake-wide, with a mean density of 2436.8 ± 629.0 individuals m^{-2} and was the only dreissenid retrieved from the east basin, accounting for 60.7% of the invertebrates found there. *Dreissena polymorpha* was collected at 15 sites in the west and central basins, but represented <1% of the total invertebrate abundance.

Invertebrate density was significantly greater in the east (Figure 10 &Figure 11) than either the west or central basins (Table 6, $p<0.001$). Lake-wide, invertebrate density was lower at ≤2 m (5433.9±2781 m^{-2}) than >5-10 m depth class (7404.7±1433.3 m^{-2})(Appendix 2), although within the west and east basins there was no significant difference of invertebrate density between depth categories (Table 6). In the central basin, invertebrate density ranked significantly lower at 2m (552.7±204.9 m^{-2}) compared to all depths classes except >20 m (4177.3 m^{-2}, $p<0.001$), however there was only one site >20 m deep in the central basin.

Overall, median invertebrate density on hard substrate ranked higher than on soft substrates (Figure 12, Mann-Whitney U=237.5, $p<0.01$). On soft substrates, invertebrate density was lowest at ≤2 m (ie. sandy sites in the central basin) compared to >5-10, >10-20 and >20 m depths (H=22.20, df=4, Dunn's post test, $p<0.05$). Lake-wide, there was no significant difference in density between depths on hard substrates ($p>0.05$), however sites in the east basin at depths ≤5 m on bedrock and limestone supported the highest mean invertebrate densities (Figure 11).

Average non-*Dreissena* invertebrate density (3973.4 ± 539.6 m^{-2}) was dominated by Oligochaeta (53%), Chironomidae (28%), Sphaeriidae (4.3%), Amphipoda (3.7%) and Hydridae (3.5%) (Appendix 3). These other invertebrates were more abundant at sites colonized by *Dreissena* than at those without mussels (Mann-Whitney U=316.0, $p<0.01$), most notably on hard substrates in the east basin (Table 7). Unlike total invertebrate density, non-*Dreissena* invertebrate density did not differ significantly among basins, but did differ among depths (Table 6, Figure 11 inset). Lake-wide, non-*Dreissena* density was lowest at 2 m sites ranking below the >5-10 and >10-20 m depths because of the very small numbers of animals found at 2 m in the central basin. Similar to total invertebrate density, there were no significant differences in non-*Dreissena* invertebrate density between depths in the west or east basin, whereas non-*Dreissena* invertebrate density was significantly lower at 2 m than >5-10 and >10-20 m depths in the central basin.

The number of taxa observed was greatest in the central basin, with 69 taxa represented (Table 5). The number of taxa identified in the central basin was greater than found in the west basin (*H*=9.085, df=2, Dunn's post test, $p<0.05$), but not in the east ($p>0.05$) When taxon richness was evaluated by rarefaction for a mean sample size of 3037 individuals (mean number of invertebrates from west basin samples), richness estimates suggest that the number of species in the central basin was significantly greater than in both the west and east basins, with no significant differences in species richness between the west or east basins (Table 8). As would be expected, individual-based rarefaction curves for the three basins indicate significant differences in species richness between basins, even for small sample sizes (Figure 13). Within the west and central basin, taxa richness was lowest at 2 m, unlike the east basin, where invertebrate species richness was highest at 2 m and declined with depth (Figure 14).

Dreissena

Dreissena were collected from 58% of sites and accounted for 38% of the invertebrates collected, with a mean density of 2436.8±629 m^{-2} (Figure 15, Table 5) *D. r. bugensis* was collected from all sites in the east basin. *D. polymorpha* was found at 15 sites, but accounted for less than 1% of total invertebrate abundance with a mean density of 16.3±6.7 m^{-2} comprising 26% and 8.6% of all *Dreissena* from the west and central basins, respectively. *Dreissena* density ranked significantly higher in the east (8379.1±1909.3 m^{-2}) than the west (70.7±31.8 m^{-2}) or central (635.1±201.9 m^{-2}) basins (Table 6), but there was no significant difference in *Dreissena* density between depths, except in the central basin, where densities were significantly lower at 2 m than at >5-10 m (Table 6). In the east basin, *Dreissena* density generally declined from 2 m to >20 m, except for an increase at sites >10-20 m (Figure 16).

Amphipoda and Isopoda

Amphipods were collected from 15% of the sites in the central basin and 65% of the sites in the east basin. No amphipods were collected in the west basin (Figure 15 & Figure 16). Amphipod density was significantly higher in the east basin (552.5±319.0 m^{-2}), especially on *Dreissena*-colonized hard substrates (898.3±579.7 m-^{2}, Figure 17), where *G. fasciatus* comprised 80% of the total amphipods, than in the central basin (19.33±9.9 m^{-2}, Mann-Whitney *U*=171.0, p<0.005). Within the east basin, amphipod density was much greater at 2 m (2366±1520 m^{-2}, Figure 16) than any other depth and was dominated by *G. fasciatus* (2071±1324 m^{-2}). However due to high variability in the number of individuals collected from sites at this depth, there was no statistical difference in amphipod density between depth classes (Table 6, p>0.05). *E. ischnus* occurred at 11 sites, including 10 sites along the Northshore transects and was dominant at two Northshore transects in the central basin (Figure 18). *E. ischnus* was the only amphipod found at 4 sites in the east basin, but total densities at these sites were <45 individuals m-2. Within the east basin, *G. fasciatus* was the dominant amphipod at ≤5 m (88%) and >20 m (100%), while *E. ischnus* was dominant at >5-20 m (70%), but at relatively low densities (Figure 19). Amphipods were also more abundant in association with *Dreissena*, primarily on hard substrates in the east (Figure 17).

No *Diporeia hoyi* were collected from any site during this survey. Isopods were most abundant in the central basin at >5-10 m (234.3±214.4 m^{-2}) and >10-20 m depths (140.7±81.9 m^{-2}, Figure 16) and at sites associated with *Dreissena* in the central basin (Figure 17). There were no significant differences in isopod density among basins or depths (Table 6).

Chironomids

Chironomids were nearly ubiquitous in Lake Erie, being collected at 67 stations with a mean density of 1130.7 ± 204.3 individuals m^{-2}, and were dominated by *Tanytarsus* and *Chironomus*, representing 5.6% and 4.5% of total invertebrate density, respectively (Figure 15, Table 5). As a percentage of total invertebrates, chironomids were relatively more abundant in the west (38.3%) and central basins (27.3%) than the east basin (7.4%), but densities did not differ significantly among the three basins (Table 6). *Cryptochironomus* and *Procladius* were common throughout the lake, occurring at 40 and 31 sites, respectively (Figure 20). *Procladius* had a similar distribution to that of *Chironomus*, but was less abundant. *Dicrotendipes* and *Polypedilum* were also relatively common. *Polypedilum* was rare in the west basin and only found at >2-5m sites in the central basin (Figure 21). *Dicrotenipes* occured mostly in the east basin nearshore. *Heterotrissocladius* occurred at a single site (11 m depth) in the east basin.

In the east basin, chironomid density was greatest at 2 m and declined with increasing depth (Figure 16), however the differences in density between depths were not significant (Table 6). Chironomids at eastern 2m sites were mostly represented by *Dicrotendipes* and *Tanytarsus*, (Figure 20, Figure 21). *Chironomus* was dominant at depths >2 m. In the central basin, chironomid density was highest at >5-10 m and was significantly lower at 0-2 m than at >5-10 m and >10-20 m (Figure 16, Table 6). *Chironomus* density increased with increasing depth in the central basin, but was absent for the three deepest sites (≥40 m) in the east basin (Figure 20). *Tanytarsus* declined in density between depths of 5-10m to >20 m in the central basin. *Coelotanypus*, *Chironomus*, *Cryptochironomus* and *Pseudochironomus* were all relatively abundant in the western basin (Figure 20, Figure 21), although the density of *Coelotanypus* was strongly influenced by the large numbers collected from a single sandy site with little apparent organic material (Colchester 5m). *Cryptochironomus* were rare at sites deeper than 10 m, but were common at nearshore transect sites in the west and central basin.

Chironomids were generally more adundant on soft sediments than hard, regardless of the presence of *Dreissena*, except in the east basin, where chironomids were most dense on *Dreissena*-colonized bedrock (Figure 17). In the central basin, densities of chironomids were similar on hard and soft substrates, either with or without *Dreissena*, but little hard substrate was found in either the west or central basins. *Polypedilum* were most dense at sites without *Dreissena* in the central basin (701.5 m^{-2}, 2-5 m depth) compared to sites with *Dreissena* (2.1 m^{-2}), but were present at Northshore sites in the east basin with *Dreissena*.

Oligochaetes

Oligochaetes were collected from 66 sites, with an average density of 2125.7 ± 344.6 individuals m^{-2} and were the numerically dominant organisms of the west and central basins (Table 5, Figure 16). Most were Tubificidae, largely represented by immature tubificids without hair setae (22% of total invertebrates) and *Potamothrix* (2.4%). *Stylodrilus herringianus* and *Tubifex tubifex* were only collected in the east basin, and *Limnodrilus hoffmeisteri* (<1% of total invertebrate density) was also most abundant at >20m in the east (Figure 22 & Figure 23). Naididae accounted for 4.3% of total invertebrate abundance, with *Nais* spp. and *Piguetiella michiganensis* being most abundant in the central and west basins, respectively.

In the central basin, oligochaete density increased with increasing depth, then declined at depths >10 m (Figure 16). Numbers of *Spirosperma ferox* also increased with depth in the central basin (Figure 23). In the central basin alone, oligochaetes accounted for 42.4% of total invertebrate abundance, compared to 25% in the east basin. Despite the lower relative contribution of oligochaetes to east basin abundance, oligochaete density was significantly higher in the east basin than the west or central basins (Table 6), accounting for 64% of east basin non-*Dreissena* invertebrates (Appendix 3). There were no significant lake-wide differences in oligochaete densities with respect to depth, except that densities were significantly lower at 2 m in the central basin than at >5-10 m (Table 6). Oligochaetes were typically more abundant at sites with soft sediments either with (2374.9 ± 402.9) or without *Dreissena* (1781.9 ± 605.7, Figure 17).

In the west basin, immature tubificids without hair chaeta, *Piguetiella michiganensis*, *Uncinais uncinata*, *Aulodrilus* spp. and *Limnodrilus* spp. were the dominant oligochaetes (Table 5, Figure 22 & Figure 23). *P. michiganensis* and *U. uncinata* had similar distributions in the west and central basins: the greatest density of both species was at 2 m in the west basin and they were also found at nearshore sites (≤5 m) in the central basin. *Aulodrilus* was most abundant at depths >2-5 m in the west basin (Figure 23).

Potamothrix vejdovskyi, *Spirosperma ferox* and *Nais* spp. were the dominant oligochaetes in the central basin (Figure 22 & Figure 23). *P. vejdovskyi* was most dense at 10 m nearshore sites at Port Burwell and Clear Creek. *S. ferox* was not present at depths less than 5m in the central basin northshore transects, but density increased with depth at sites >5m. *Nais* spp. occurred frequently at >5-10 m central basin northshore sites.

Stylodrilus heringianus and *Tubifex tubifex* were collected only in the east basin, and *Limnodrilus hoffmeisteri* (<1% of total invertebrate density) and *Vejdovskyella* were also most abundant at >10m in the east. Immature tubificids, especially those lacking hair chaeta, were generally most abundant in the east basin littoral zone (<5m) and at >10-20m depths.

Gastropods and sphaeriids

Gastropods were collected in low densities and were generally rare (Table 5, Figure 15 & Figure 16), except in the east basin where density was highly variable (110.7±74.1 individuals m^{-2}) and small-bodied Hydrobidae (*Amnicola limosa* and *Marstonia decepta*) were most frequently encountered and numerous. Gastropods were also more abundant on *Dreissena* colonized hard substrates in the east basin (168.0±135.5 m^{-2}) than on soft sediments or at sites without *Dreissena* (Figure 17). There was no significant difference in gastropod density between basins or depths (Table 6).

Sphaeriid densities were greatest in the west (273.4 ± 103.4 m^{-2}) and central basins (215.3 ± 81.5 m^{-2}) and were significantly greater in the west than the central and eastern basin, although sphaeriid density was greatest within the central basin at depths >10-20 m (Figure 16). In the western and central portions of the lake most sphaeriids were *Pisidium*, while *Sphaerium rhomboidium* was the only sphaeriid found in the east basin, occurring at a single offshore site. Within the central basin, sphaeriid density was significantly higher at >10-20 m than at 2-10 m (Table 6) and *Pisidium* density was three times that of *Sphaerium*. Sphaeriids were most abundant on soft substrates (236.7 m^{-2}) and at sites where *Dreissena* densities exceeded 4310 individuals m^{-2} (Figure 17). No unionids were collected.

Insects and Miscellaneous

Ephemeroptera were generally rare and only two genera were identified. *Caenis*, was found in the central and east basin at sites <5 m. *Hexagenia* was collected from 4 sites, all at depths >2-10 m in the west basin, accounting for 8.8% of west basin density.

The highest mayfly densities were observed in the west basin and there was no significant difference in mayfly density with depth (Table 5 & Table 6, Figure 16).

Optioservus sp. and *Stenelmis* sp. (Coleoptera) were both collected from a single 5m site in the west basin. *Oecetis* sp. (Trichoptera) was collected from both the central and east basins, but was rare (Table 5). *Hydroptila* sp. was also collected in the east basin, from 2 m and 5 m sites (Appendix 2). Flatworms (Platyhelminthes) and *Hydra* were most abundant in the central basin at 5-10 m depths colonized by *Dreissena*. Leechs (Hirudinea) were predominately represented by the tolerant *Helobdella stagnalis*. These were most abundant at >5-10 m sites in the west and >5-20 m in the central basin regardless of the presence of *Dreissena*.

3.4.2 Community Analysis: 2002

Patterns and complexity of the benthic community are summarized by scatterplots of CA site and species scores (Figure 24). The first two axes combined account for >30% of the variation in the benthic community. The first axis is best explained by a west-east/substrate association, with relatively low invertebrate density on sand/gravel sites in the west, dominated by *Coelotanypus*, sphaeriids and the presence of *Hexagenia*, to the *D. bugensis* and gammarid dominated bedrock and limestone sites in the east basin. The second axis, is best described by a combination of depth and substrate: from deep, soft-bottom, sphaeriid-dominated offshore sites in the central basin (Guardian sites 43, 42, 30, 31, 32) to the poorly colonized, sandy, wave-zone sites along the central basin (Alma 2m, Palmyra 2m , Wheatley 2m etc.). This interpretation was partially confirmed *ad hoc* by canonical correpondance analysis (CCA, ter Braak 1986) of the same data using basin (west, central, east) and substrate (hard, soft) as 'dummy' variables, and depth and *Dreissena* density as environmental variables (Figure 25). *Dreissena*, 'east' and hard substrate were highly correlated with the first axis and depth was approximately equally correlated to the first two axes (Table 9). The environmental variables included also account for a moderate portion of the variation in the species data (Table 10). In both plots *G. fasciatus* and *E. ischnus* associate closely with *D. bugenesis* in ordination space, as do Chironominae, Tanytarsini and Naididae. Hydridae are also in close proximity to *D. bugensis* in CA, but not in CCA. Immature tubificids and *Potamothrix vejdovskyi* are located near the origin because of a high relative abundance at >5-10 m sites in the central basin, while *S. ferox*, *Pisidium* and other sphaeriids associate more closely with central basin offshore Guardian sites.

3.4.3 Changes in Benthic Community: 1979-2002

Based on the "matched" sites used for comparison between 1979 and 2002, mean total invertebrate density increased from 5166.3±545.7 individuals m^{-2} (±SE) in 1979, to 7210.6±1229.2 individuals m^{-2}, while non-*Dreissena* invertebrate density declined to 4704.4±843.8 in 2002 (Table 11, Figure 26). The change in the abundance of non-*Dreissena* invertebrates was greatest in the east basin. Densities were similar in both years in the central basin. In the western basin, both total density and non-*Dreissena* density were greater in 2002 than in 1979, but these values are potentially biased by a small sample size (n=3) in the west basin in 2002. The most notable differences in relative abundance between years was the decline in percentage of sphaeriids and amphipods and the increase in chironomids, especially in terms of non-*Dreissena* abundance (Table 12). Percent contribution of oligochaetes to total density also declined during this interval, but exhibited little difference in terms of non-*Dreissena* percent density.

Individual-based rarefaction, with a sample of 4704 individuals (mean number of non-*Dreissena* invertebrates in 2002) indicated that there was no significant difference in species richness between years, either with or without *Dreissena*, despite an overall increase in taxa richness from 54 species in 1979 to 63 species in 2002 (Table 13) Rarefaction curves also showed no difference in richness between years, except at large sample sizes (>15 000 individuals, Figure 27).

Amphipods and Isopods

Amphipod mean density (351.4±156.8 m^{-2}) represented 6.8% of the animals collected in 1979, but in 2002 contributed <1% (51.9±39.6 m^{-2}) to invertebrate density at corresponding locations (Table 12, Figure 28). In 1979, amphipods were dominated by *Diporiea* (6.4% of the invertebrates), with the greatest numbers in the east basin (1290.0±481.6 m^{-2})(Figure 29). No *Diporiea* were found in 2002. The greatest amphipod densities were found in the east basin in both years (1350.0±488.1 m^{-2} in 1979 and 119.9±106.7 m^{-2} in 2002. Isopod density and frequency of occurrence also declined between years as a result of reduced abundance at deeper sites in the central basin and apparent absence from the east basin (Figure 30). Similar to 1979, no isopods were collected in the west basin.

Chironomids

Chironomid mean density tripled between 1979 and 2002 and 10 chironomid taxa were identified in 2002 that were not present at comparable sites in 1979 (Table 12, Figure 31). The relative contribution of chironomids to total density in 2002 was greater than twice that from 1979. Chironomids showed an almost four-fold increase in relative abundance when *Dreissena* were omitted from the 2002 data, despite a lower frequency of occurrence. The biggest increase in average density was observed in the central basin, where chironomid density increased from 467.4±174.3 m^{-2} in 1979 to 1980.8±590.9 m^{-2} in 2002 (Figure 31). In 1979, *Chironomus* (141.4±41.9 m^{-2}) represented 2.7% of the total invertebrates, but in 2002 (481.8±99.1 m^{-2}) accounted for 6.7% of total invertebrate or 10.2% of non-*Dreissena* density (Figure 32). Similarly, *Tanytarus* (22.3±7.4 m-2) comprised <1% of 1979 density, and 8% of invertebrate density or 12.2% non-*Dreissena* density in 2002. In the west and east basins, mean chironomid density increased by 144% and 75%, respectively. In 2002, intolerant Orthcladiinae, *Epiocladius* and *Heterotrissocladius*, were found at a single site each in the west and east basin, respectively, but were not reported in 1979. No chironomids were found at the two deepest sites (42 m and 61 m) in 2002.

Oligochaetes

Mean and relative density of oligochaetes decreased from 1979 to 2002, yet percent abundance of worms among all non-*Dreissena* invertebrates indicated oligochaete contribution was relatively unchanged (Table 12, Figure 33). Lake-wide mean and relative density of *Stylodrilus heringianus*, *Aulodrilus*, *Limnodrilus* spp., *Spirosperma ferox* and *Tubifex tubifex* (Figures 34-38) and immature tubificids with hair chaetae were all lower in 2002, however, immature tubificids without hair chaetae increased slightly during this time (Table 12). Mean oligochaete density was greater in the west basin in 2002 than in 1979, and percent *Limnodrilus hoffmeisteri* and *Branchiura sowerbyi* (of total oligochaetes) declined slightly (Table 14). In the central basin, percent *Limnodrilus* spp. and immature tubificids (with hair chaetae) declined slightly, while *Nais* spp. and immature tubificids (without hair chaetae) increased in relative abundance. The density distribution and relative contribution of *S. ferox* in the central basin changed very little between years, whereas percent *Aulodrilus* spp. declined. *S. herringianus* was not found in the central basin in 2002, where it had previously accounted for 4.1% of oligochaete abundance.

S. ferox, *T. tubifex* and *Potamothrix vejdovskyi* were relatively less abundant in the east basin in 2002 than in 1979 and percent density of *L. hoffmeisteri* remained relatively unchanged (Figures 37-39 & Table 14). *S. herringianus* density declined from 707.3±283.7 m^{-2} to 91.6±84.4 m^{-2} and percent *S. herringianus* of total oligchaetes declined 15% in the east basin between 1979 and 2002. Immature tubificid (without hair chaetae) percent density was greater in the east basin in 2002.

The mean (±SE) oligochaete trophic index values in 2002 showed a small increase over those values from 1979 (Table 15). According to Milbrink's (1983) criteria, these values would indicate similarly meso-eutrophic conditions in all basins in 2002 (Figure 40). When comparing 1979 and 2002 survey years, there appears to be little difference in the trophic index in any of the basins.

Gastropods and sphaeriids

Gastropod distribution and abundance was similar in 1979 and 2002 (Figure 41) but *Amnicola* and *Valvata* were replaced by *Bithynia tentaculata* and *Amnicola* as the most abundant species in 2002 (Table 12, Figures 42-44).

Sphaeriids occurred at 33 of the sites retained from the 1979 survey, accounting for nearly 17% of invertebrate abundance. Sphaeriids were less common in 2002, being found at 12 stations lake-wide, representing 4.7% of the total animals collected, with the most notable declines in the east basin (Table 12, Figure 45). Mean sphaeriid densities were similar between 1979 and 2002 at matched sites in the west basin. Fewer sphaeriids were collected from northshore sites in the central basin in 2002, but densities offshore and along the southern shoreline, mostly *Pisidium*, were similar to those observed in 1979 (Figure 46). In the east, *Sphaerium* spp. declined from 166.7 m^{-2} to 1.35 m^{-2} between 1979 and 2002, occuring at only a single site (Figure 47). *Pisidium* spp. had a mean density of 320.0 m^{-2} in 1979, but were not collected from corresponding sites in the east basin in 2002.

Insects and Miscellaneous

In 1979 and 2002, *Hexagenia* were found at relatively low density at a single, similarly located site in the west basin near the mouth of the Detroit River (Figure 48). Density was higher in 2002 than in 1979, yet still represented <1% total abundance, even when *Dreissena* have been excluded. Hydridae were not reported from Lake Erie in 1979, but had a mean density of 65 individuals m^{-2} in 2002 (Table 12). Acari also occurred more frequently and with greater mean density in 2002.

3.4.5 Community analysis: 1979-2002

Correspondence analysis of 1979-2002 "matched" sites indicated a clear change in species composition between basins and years (Figure 49a). The first two axes account for 28.6% of the variation in species composition, with a distinct separation of survey sites between years along the first axis and a west-east/depth gradient on the second axis. The gradient on the first axis is largely influenced by the presence of *D. bugensis* and *E. ischnus* in 2002, and the abundance of *Diporiea* in the east basin in 1979 on both the first and second axis. Since the absence of species between years (ie. no *Diporiea* in 2002 and no *Dreissena* in 1979) had considerable influence on the first two axes, these species were deleted and the CA repeated. The variation explained on the first axis remained the same, and the second axis explained less variation after deletion of *Diporeia*, yet the configuration of the site- and species-scores remained relatively unchanged (Figure 49b). With only *Dreissena* removed prior to CA, the relative orientation of sites and taxa between years revealed the influence of *Dreissena* on the 2002 data (on the first axis), reflecting a 3% loss of explained variation (Figure 49c, note the influence now of *Dreissena*-associated Naididae): *Diporeia* in the east basin in 1979 now defined the first axis. With both *Diporeia* and *Dreissena* omitted from the CA, the first two axes account for a similar amount of variation, and are strongly influenced by the presence of *E. ischnus* and *Dreissena*-associated Naididae at nearshore sites in the east basin (Figure 49d). There is a less distinctive gradient along the first two axes, but still clear separation between years. Finally, to alleviate any possible artifacts of the presence/absence of species extirpated or introduced since 1979, *Dreissena*, *Diporeia,* and *E. ischnus*, as well as *Dreissena*-associated Naididae (anomalously high relative abundance at a single site in the east basin) were omitted from the CA. The scatter observed in the preceding plots due to extreme relative abundance of a few taxa between years (such as when species are replaced over long gradients or through succesion) and outliers has been relieved. Despite the removal of these taxa, the first two axes account for close to 25% of the variation in the community data, with relatively less separation of 1979 and 2002 sites along the second axis (Figure 49e). Generally, *Nais*, *Chironomus* and *Tanytarsus* have higher relative abundance at central and east basin sites in 2002, while *Gammarus*, *Potamothrix* spp., *S. herringianus* and *Tubifex* co-occurred in similar proportions at many of the east basin sites in 1979 and 2002. *Limnodrilus* was relatively more abundant at several sites in the central basin in 1979. Sphaeriids occurred in higher relative numbers in the central basin in 1979 than in 2002. *Hydridae* and *Nais* appear as outliers because of their relatively high numbers at two sites in 2002.

3.5 Discussion

3.5.1 Invertebrate Distribution

Benthic community composition and abundance in 2002 appear to reflect the depth and basin-specific effects of *Dreissena*-generated habitat complexity and eutrophication of Lake Erie's benthos combined with round goby predation on benthic macroinvertebrates. Both *Dreissena*-colonized and non-colonized locations generally appear to be supportive of dense zoobenthos either through providing habitat heterogeneity or nutrient rich biodeposits. However, confirming a direct cause and effect relationship and quantifying continued *Dreissena*-mediated impacts is made difficult by the combined influence of changing nutrient levels, the dynamics of trophic interactions, differential sensitivity of invertebrate feeding guilds, life history and the inherent patchiness of benthic invertebrate distributions.

By 1979 improvements in surface water quality in Lake Erie were already being seen following nutrient load reductions (Yaksich et al. 1985, Charlton et al. 1993, Charlton et al. 1999), indicating that continued recovery might also be observed in the benthic fauna (Krieger and Ross 1993, Schloesser et al. 1995). It is important to keep in mind that the interval between 1979-2002 was not a period of stable nutrient concentrations in Lake Erie, with *Dreissena* being implicated for changes in many water quality trends (Bertram 1993, Charlton et al. 1993, Holland et al. 1995, Charlton et al. 1999, Nicholls et al. 1999b, Makarewicz et al. 2000, Charlton 2001, Nicholls et al. 2001, Charlton and Milne 2004). Benthic community composition and abundance in 2002 do not explicitly reflect nutrient reductions or improved water quality in Lake Erie.

Nevertheless, general patterns typical of *Dreissena*-altered food webs continued to be observed. These include an apparent increase in total invertebrate density (namely *Dreissena*), yet non-dreissenid density decreased from 1979 levels with no significant change in taxa richness, except perhaps for the Chironomidae. Dreissenids are the dominant benthic organisms in the lake, followed closely by oligochaetes, chironomids, sphaeriids and amphipods. *D. r. bugensis* remains the dominant (only) dreissenid observed in the east basin on all substrates and depths, with the highest densities on stable rocky substrates in the nearshore. Since 1979, sphaeriid clams, amphipods and isopods have all declined in relative density, both in terms of total invertebrates, and total invertebrates excluding *Dreissena*, while chironomid relative density increased more than three-fold (*Dreissena* excluded) at the sites used for pre-*Dreissena* comparison. Gastropod and oligochaete relative density have experienced negligible changes in this time. The historically dominant mayfly, *Hexagenia*, continues to be observed in the west basin following population recovery whereas, in the east, sphaeriid density appears to be in decline and *Diporeia* has disappeared.

In 2002, total invertebrate density was three times greater in the east basin than in the west or central basins, but this was almost exclusively due to the abundance of *Dreissena* in the east basin. Sites with and without *Dreissena* support dense zoobenthos in Lake Erie, however *Dreissena*-colonized sites may support more taxa. The influence of *Dreissena* appears to be dependent on basin-specific habitat characteristics such as depth and substrate stability. Non-*Dreissena* invertebrate density is generally higher on bedrock (eg. amphipods, gastropods and chironomids) than on fine substrates (eg. oligochaetes) in the east basin. In the central basin, non-*Dreissena* invertebrate density appears to be slightly higher on *Dreissena* colonized habitats or on soft substrates in the sub-littoral zone (>5-10 m) without *Dreissena,* although this difference is best described on a taxa specific basis. In the west basin, non-*Dreissena* invertebrate density is similar on both *Dreissena*-colonized and non-colonized habitats. However, conclusions regarding non-dreissenid density with respect to *Dreissena* presence and substrate type my be biased by a small sample size on hard surfaces in the west basin. Compared to *E.*

ischnus, *G. fasciatus* retains its status as the dominant amphipod in the lake, however amphipod density and percent abundance are relatively low, likely a result of heavy predation pressure from the round goby. Gastropod numbers were also relatively low, except at depths of 2m on hard surfaces in the east basin, but even here gastropod density is highly variable. Aside from the Chironomidae, insect taxa richness and density are also low at most sites expected to have a richer insect fauna.

The highest non-*Dreissena* densities were in the east basin, but species richness was highest in the central basin. Within the central basin, communities from fine particulate offshore sediments are typically comprised of *Dreissena*, chironomids, oligochaetes, and sphaeriids, in comparison to the central basin wave zone which is uninhabitable to many taxa. The larger number of taxa found in the central basin, is undoubtedly due to a larger sample size. The greatest number of taxa occured at >5-10m, and invertebrate abundance and species richness were lowest at 2m sites, typical of invertebrate richness and distributions reported for the central basin northshore as dictated by habitat stability (Barton and Hynes 1978a, Barton 1988b). Most nearshore sites in this part of the lake are characterized by unconsolidated sand in a high energy wave-zone environment (St. Jacques and Rukavina 1973, Thomas et al. 1976, Rukavina and St. Jacques 1978) with characteristically low organic C and P (Thomas et al. 1976, Williams et al. 1976) and high inputs of terrestrial fine-grained sediments (Kemp et al. 1976, Rukavina and Zeman 1987) all under the influence of longshore currents (Beletsky et al. 1999) limiting habitat suitability for many taxa. Great Lakes nearshore macroinvertebrate densities are typically greater on stable substrates than soft, fine particulate sediments (Goforth and Carrnan 2005).

The increase in mean invertebrate density in Lake Erie over the past 23 years is similar to previously reported trends in the benthic community of the lower Great Lakes since the arrival of *Dreissena*. Between 1979 and 1993, benthic biomass increased substantially in Lake Erie, but 90-99% of benthic invertebrate biomass and >90% of benthic secondary production was from dreissenids in 1993 (Dahl et al. 1995, Johannsson et al. 2000). Dahl et al. (1995) and Johannsson et al. (2000) observed greater benthic biomass and production, dominated by *Dreissena*, at nearshore sites than offshore with little change in non-*Dreissena* biomass between 1979-1993, suggesting that dreissenid production added to benthic production, and not at the cost of lowered production of the remaining benthic fauna. Non-*Dreissena* invertebrate density however, appeared to have declined to below 1979 levels in this study.

In the east, taxa richness was greatest at 2m and declined with depth, as might be expected from classical zoobenthic distributions in deep lakes (Brinkhurst 1974). Densities of *Dreissena*, amphipods, gastropods, chironomids and oligochaetes are generally greatest on stable nearshore bedrock in the east basin. In contrast, fine substrates offshore are much more homogeneous and are predominantly comprised of *Dreissena*, oligochaetes and relatively fewer chironomids. Nearshore habitats in the east basin were also generally taxa rich, with *Dreissena*, amphipods, isopods, gastropods, chironomids and a few other insects. Ratti and Barton (2003) reported a significant decline in total invertebrate richness, mostly by a loss of insects in the wave-zone (<1.8m) of northeast Lake Erie between 1974/75 and 2001, citing the establishment of *Dreissena* as the primary cause. The dominance of *D. r. bugensis*, oligochaetes, chironomids and amphipods in the present study are consistent with the findings of Barton et al. (2005) from a rocky nearshore transect sampled in the east basin throughout the summer (May-August) of 2002. Aside from the Chironomidae, insect taxa richness and density were lower than might be expected at nearshore sites. It is likely that in very shallow water, *Dreissena* may support higher chironomid taxa richness by providing habitat and food resources for littoral zone invertebrates. Between 1979 and 1993, total non-*Dreissena* invertebrate density increased with the largest increase attributed to nematodes and other meiofauna (ostracods and harpacticoids), but non-*Dreissena* invertebrate biomass decreased (namely *Diporeia*, chironomids, and *Pisidium*) in the profundal (Dermott and Kerec 1997). From a long term study in southwestern Lake Ontario, Haynes et al. (2005) found similar or reduced diversity and abundance of non-*Dreissena* taxa between 1983 and 1999/2000 following *Dreissena* colonization, noting a rise, however in the years between 1983 and 1991/92.

Correspondance analysis of 2002 survey data highlights a close association between *Dreissena* and *G. fasciatus*, *E. ischnus*, and some chironomid and oligochaete taxa. The influence of *Dreissena* is also closely related to a substrate effect, which is expected given the higher than average *Dreissena* densities on the northeast rocky nearshore. The differences in community composition at spatially matched sites between 1979 and 2002 were greatly influenced by the disappearance of *Diporeia*, the introduction of the non-native *E. ischnus*, and the dominance of *D. bugensis*. Only once these taxa were removed from the correspondence analysis did the separation of sampling sites become more reflective of the underlying compositional changes of the non-dreissenid community.

Dreissena

D. r. bugensis was the only dreissenid identified in the east basin in 2002, displaying a gradient of declining relative abundance and replacement by *D. polymorpha* progressing to the west. In 1998, *D. bugensis* comprised 37%, 99.9% and 85% of the driessenids in the west, central and east basins, respectively and was the only dreissenid found at depths >30 m (Jarvis et al. 2000, Dermott and Munawar 2002). In 2002, *D. bugensis* accounted for 55%, 86%, and 100% of the dreissenids from west to east. Similarly, zebra mussels have not been collected at an east basin rocky shoal (Peacock Point) from 2001 to 2004 (Barton et al. 2005). This observation of a progressive increase in the relative proportion of the quagga mussel over the zebra mussel is consistent with earlier reported trends from Lake Erie (Jarvis et al. 2000) and Lake Ontario (Mills et al. 1999, Haynes et al. 2005).

Increasing density of *D.r. bugensis* has been observed in the east basin since 1992, while west and central basin densities have declined despite an increase in biomass (Jarvis et al. 2000, Patterson et al. 2005). Low densities and patchy distribution in the west basin likely reflects the limited availability of hard substrate (Rasul 2002), waves and episodic weather events creating elevated turbidity (Alexander et al. 1994, Summers et al. 1996, Madon et al. 1998, Schneider et al. 1998) and sediment instablilty on soft (Bially and MacIsaac 2000) and hard substrates (MacIsaac 1996a). Athough *D.r. bugensis* density remains largest on the rocky east basin northshore, there are signs that *Dreissena* densities may be declining on rocky habitats in eastern Lake Erie attributed to round goby predation (Barton et al. 2005, Patterson et al. 2005).

Amphipods and Isopods

Lake-wide amphipod density comprised only 2.3% of the invertebrate community, a nearly 85% decline in mean density from sites examined in the 1979-2002 comparison. This decline was accounted for by the obvious disappearance of the deep-water, burrowing amphipod *Diporeia hoyi* from the east basin despite a history of dense populations in the cool, oligotrophic water of the east basin (FWPCA 1968, Veal and Osmond 1968, Flint and Merckel 1978, Barton 1988b, Dermott 1994). The initial decline in Lake Erie's *Diporeia* population was documented in 1992-93, only 2-3 years following the arrival of *D. bugensis* in the east basin (Dermott and Kerec 1997). By 1993, *Diporeia* densities in the east basin (218.0 m^{-2}) were already significantly lower than in 1979 (1843.8 m^{-2}), when they had accounted for 9% of the total invertebrates and 38% of the east basin benthic invertebrate biomass. By 1998, *Diporeia* were no longer being observed in the east basin (Dermott and Munawar 2002).

Declining or extirpated *Diporeia* populations in Lake Erie and elsewhere in the Great Lakes (Nalepa et al. 1998, Nalepa et al. 2000, Dermott 2001, Lozano et al. 2001, Nalepa et al. 2005a, Nalepa et al. 2006) is generally viewed as being related to the invasion of *Dreissena* and their interception of food particles, depleting the amount of settling algal material made available to *Diporeia* in the profundal zone (Dermott and Kerec 1997, Madenjian et al. 2002, Dermott et al. 2005, Nalepa et al. 2005a, 2005b). Although *Diporeia* are also known to feed regularly on sediment bacteria (Guiguer and Barton 2002), which are more abundant (Izvekova and Lvova-Katchanova 1972) and productive (Roditi et al. 1997) on organic-rich *Dreissena* biodeposits, and thus providing a food resource for *Diporeia*, the specific cause of the extirpation of *Diporeia* from Lake Erie still remains unclear.

The lack of amphipods in the west basin in 2002 was typical of the very low abundance and occurence recorded from earlier surveys (Shelford and Boesel 1942, Carr and Hiltunen 1965, FWPCA 1968, Veal and Osmond 1968, Keeler 1981, Barton 1988a, Dermott 1994), but was unexpected given the availability of suitable habitat and the observed increase in *Gammarus* biomass in the west basin between 1979 and 1993 (Johannsson et al. 2000). Stewart et al. (1999) also reported relatively high amphipod density from experimental mussel density treatments in the west basin. Regardless, the status of amphipod populations in the west basin in 2002 is uncertain given the small number of sites sampled in this study.

In the central basin, amphipods were collected in relatively low numbers at 6 of 41 sites and were limited to nearshore sites irrespective of the presence of *Dreissena*. Of these sites, *G. fasciatus* was the only amphipod collected from four sites and the introduced *E. ischnus* was clearly dominant at the remaining two sites. Similarly low frequency of occurrence of *Gammarus* was reported from the central basin in 1963-1965 (Barton 1988a) and 1967 (Veal and Osmond 1968). However Barton (1988a) reported increasing occurence from west to east while Veal and Osmond (1968) reported declining frequency. In a survey restricted to the eastern portion of the central basin from Port Glasgow to Long Point in 1972/73 (Barton 1988b), *Gammarus* was also considered rare. Conversely, Barton and Hynes (1978a) reported *G. fasciatus* as the most frequently collected animal during an intensive qualitative nearshore (≤2.0 m) survey of Lake Erie in 1974. However, by 1979 *Gammarus* density in this section of the the lake was greatly reduced but no explanation was given to account for the reduced numbers (Dermott 1994). It is likely the establishment of dense populations of amphipods in the central basin is limited by availability of preferred hard substrates.

In 2000, *E. ischnus* was reported to be the dominant amphipod in western Lake Erie, displacing *G. fasciatus* on shallow (0.5-3.6 m) rocky habitats (Van Overdijk et al. 2003). In 2001, the relative abundance of *E. ischnus* and *G. fasciatus* together in eastern Lake Erie (depths <2m) were comparable to pre-*Dreissena* (1974) *G. fasciatus* relative abundance alone (Ratti and Barton 2003). In field experiments, Stewart et al. (1998a, 1998b) found a similar increase in *E. ischnus* density in western Lake Erie on shallow hard substrates. Haynes et al. (2005) reported that *E. ischnus* replaced *G. fasciatus* as the most abundant non-dreissenid invertebrate in southwestern Lake Ontario during an interval when round gobies were not present. They observed that combined density of *G. fasciatus* and *E. ischnus* in 1999/2000 equaled *G. fasciatus* density observed in 1983 on a shallow (5-7 m) artificial reef, but *G. fasciatus* doubled its pre-*Dreissena* density on cobble substrates during the same time.

My data did not show increasing dominance of *E. ischnus* in 2002. *G. fasciatus* remained the dominant amphipod, nearly 3.5 times more abundant than *E. ischnus*. In the east basin, the relative density of *G. fasciatus* was four-fold greater than *E. ischnus* and the two species were somewhat spatially segregated. *G. fasciatus* was the dominant amphipod on *Cladophora*-dense rock at 2-5m and at >20m sites (88% and 100% of amphipod density, respectively), while *E. ischnus* was dominant at intermediate depths (>5-20m, 70%). Ratti and Barton (2003) also report higher *G. fasciatus* percent abundance than *E. ischnus* from similar depths and habitat in Lake Erie. This study suggests that the native Gammarids are maintaining their populations, while the invasive *E. ischnus* may be filling a specific niche.

In the eastern basin, amphipods comprised 10.2% of non-*Dreissena* invertebrate density and densities were most abundant on *Cladophora*-covered, rocky 2m sites (2366.0 m^{-2}). The association of *G. fasciatus* with *Cladophora* is well known (Barton and Hynes 1976, Delong et al. 1993, Stewart and Haynes 1994, Summers et al. 1997, Gonzalez and Burkart 2004) and is related to habitat and food resources. *G. fasciatus* densities have been reported as high as 10,000 m^{-2} on *Cladophora* covered nearshore habitats but as low as 10-100 m^{-2} on *Cladophora*-free hard substrates (Barton and Hynes 1976, 1978c). However, this is considerably lower than reports of over 20,000 individuals m^{-2} shortly following the establishment of *Dreissena* in shallow, northeastern parts of the lake (Dermott et al. 1993). The relationship between amphipods and *Dreissena* is also well documented and is due to microhabitat stability and food availability provided by the mussels (Dermott et al. 1993, Griffiths 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts et al. 1996, Ricciardi et al. 1997, Dermott et al. 1998, Stewart et al. 1999, Bially and MacIsaac 2000, Gonzalez and Burkart 2004). Gut content and stable isotope analysis of the nearshore benthic community in eastern Lake Erie revealed that *G. fasciatus* feeds predominantly on *Cladophora* and associated epiphytic diatoms when readily available, while *E.ischnus* relies mostly on *Dreissena* biodeposits (Szabo 2004), which explains the distributions of the two amphipod species in 2002. Conflicting stable isotopic results from a similar study in the nearshore (0-2m) rocky habitats of western Lake Erie suggest that *E. ischnus* does not feed on *Dreissena* faeces/pseudofaeces, but this was based on very limited data (Limnén et al. 2005).

Szabo (2004) found similar densities of *G. fasciatus* along a single east basin transect (Peacock Point) sampled repeatedly through the summer of 2002 (June-October). *G. fasciatus* biomass was at its maximum (1766.33 mg m^{-2}) the same day the transect was sampled for this survey, but quickly declined to 397.86 mg m^{-2} 10 days later. Therefore, it is likely that the relatively low density found in the east basin during the present survey represents a seasonal amphipod density maxima. Sampling *Cladophora* covered nearshore habitats in late-August to early September may subsequently lead to lower density estimates given that seasonal *Cladophora* die-off in late summer (Higgins et al. 2005) is presumed to minimize habitat suitability for *Gammarus* (Van Overdijk et al. 2003).

Shorltly after the arrival of *Dreissena*, biomass and productivity of *G. fasciatus* were greatest at a rocky nearshore site in the east basin compared to other nearshore and offshore stations in Lake Erie (Dahl et al. 1995, Johannsson et al. 2000). Amphipod densities reported from 2002 are considerably lower than reports of up to 24,000 individuals m^{-2} shortly following the establishment of *Dreissena* in the shallow, northeastern part of Lake Erie (Dermott et al. 1993). A progressive decline in amphipod density has recently been documented in Lake Erie's eastern northshore (2-10m depth), principally as a result of round goby predation (Barton et al. 2005). *G. fasciatus*, which were not found at sites deeper than 11 m in 1979, were found at two sites deeper than 20 m in 2002, suggesting that *Gammarus* may either be expanding its range to deeper water exploit *Dreissena* colonized habitats or to avoid competition for nearshore habitats with the recent invader *E. ischnus*. Ratti and Barton (2003) also report higher *G. fasciatus* percent abundance than *E. ischnus* from similar depths and habitat in 2001. Between 2001 and 2004, the proportion of *E. ischnus* at east basin nearshore sites declined from 26.7% to 6.8% (Barton et al. 2005). Therefore, any effect that *Dreissena* or *Cladophora* may have on increasing amphipod abundance by improving habitat or food availability may be lost to round goby feeding. The low density of amphipods in the central basin in 2002 was also likely being diminished by round gobies, especially in the absence of suitable refugia to avoid predation. From this study it is difficult to make a distinction between the effects of *Dreissena* colonization, the rate of invertebrate consumption by round gobies and competition with *E. ischnus* on populations of native gammarids in Lake Erie.

As expected, the differences in community composition at neighbouring sites between 1979 and 2002 were greatly influenced by the disappearance of *Diporeia*, the introduction of the non-native *E. ischnus*, and the dominance of *D. bugensis*. Only once these taxa were removed from the correspondence analysis did the separation of sampling sites between years become more reflective of the underlying compositional changes of the non-dreissenid community, with less distinction between basins and years.

Isopods were largely limited to limestone bedrock with *Dreissena* in the east basin or stable areas of relatively low wave energy predominately associated with *Dreissena* at nearshore sites at intermediate depths (>5-20) in the central basin, typical of their historic distribution in Lake Erie prior to the arrival of *Dreissena* mussels (Barton and Hynes 1976, Britt et al. 1980, Barton 1988a, 1988b, Dermott 1994). The positive association of isopods with *Dreissena* has also been observed in transplant (Bially and MacIsaac 2000) and *Dreissena* density manipulation experiments (Kuhns and Berg 1999, Stewart et al. 1999).

Chironomids

Chironomid density was relatively high in 2002, especially on rocky, *Dreissena*-colonized nearshore habitats, an observation supported by a temporal survey of one of the transects in northeastern Lake Erie in 2002 (Szabo 2004, Barton et al. 2005). Unlike amphipod density, chironomid density was greater in 2002 compared to historic records. At 'matched' 1979-2002 sites, the density of chironomids in 2002 was 2.5, 4 and 1.7 times greater than in 1979 in the west, central and east basins, respectively. The greatest increase in relative abundance since 1979 was from *Tanytarsus* and *Chironomus*. At least with respect to dominant taxa, proportions of chironomids were similar from 1979 and 2002. Ratti and Barton (2003) found proportions of chironomids were similar between 1974 and 2001. Chironomid density remained relatively high in 2002, an observation supported by a recent study in northeastern Lake Erie in 2002 (Szabo 2004, Barton et al. 2005). No chironomids were found at the two deepest sites in the east basin in 2002.

In the west basin, relatively pollution intolerant *Coelotanypus* and *Pseudochironomus* were found at shallow sandy-gravel sites along with moderately tolerant *Cryptochironomus*. *Chironomus*, regarded as highly tolerant of organic pollution and low oxygen levels, were found further offshore (>6m depth) on finer sediments, but not at sites associated with higher dressenid density (>200 *Dreissena* m^{-2}). *Coelotanypus, Chironomus* and *Cryptochironomus* were all historically abundant in the west basin (Shelford and Boesel 1942, Carr and Hiltunen 1965) where chironomid densities were relatively stable from the early 1960s to the mid-1970s (Reynoldson et al. 1989). The pollution tolerant predator *Procladius* was also relatively abundant historically (Shelford and Boesel 1942, Carr and Hiltunen 1965), but densities were comparably low (25 m^{-2}) in the west basin 2002. Similar to the 1978/79 survey, *Coelotanypus* was the dominant chironomid in the west basin in 2002, likely due to the warm water temperature in the shallow west basin (Dermott 1994).

In the central basin, chironomid density was highest at sites ≥10 m deep where wave energy is reduced and sediments are more stable. At shallower depths, substrates are composed of shifting sand and are subject to longshore currents (St. Jacques and Rukavina 1973, Thomas et al. 1976, Rukavina and St. Jacques 1978, Beletsky et al. 1999) limiting availability of suitable habitat for settling dreissenids and non-dreisenid invertebrate taxa. Offshore stable, depositional zone sediments composed of fine silt and higher organic content may be more supportive of a diverse and dense fauna (Rasmussen and Rowan 1997). Dahl et al. (1995) and Johannsson et al. (2000) found a greater than three fold increase in chironomid productivity at an offshore station in the west-central basin compared to a sandy nearshore site, however total benthic productivity was higher at the nearshore station due to high *Dreissena* abundance.

Procladius was observed at 40% of the sites in the central basin, compared to >70% of the sites in the eastern part of the central basin in 1972/73 (Barton 1988b), however this difference is likely due to the greater number and density of sites in the 1972/73 survey. *Tanytarsus* distribution was relatively unchanged, being found at all offshore sites in the central basin. Higher relative densities of *Chironomus* and *Tanytarsus* in the central basin in 2002 than in 1979 could be indicative of increased availability of planktonic and algal material and improved DO conditions at the sediment-water interface. The lack of *Pseudochironomus* in the central basin is similar to that found by Barton (1988b). *Cryptochironomus* at shallow sites is consistent with their known habitat preference (Barton 1988b), however neither *Pseudochironomus* or *Cryptochironomus* were found in relatively high abundance in the central basin in 2002. *Polypedilum* were most dense in the central basin, similar to their known distribution (Barton and Hynes 1978a, Barton 1988b), at sites without *Dreissena* but were also found at east basin northshore sites with *Dreissena*. Conversely, Stewart et al.(1998a) found *Polypedilum* on bare tiles but not on shell or living *Dreissena* rocky habitat treatments.

Dermott and Kerec (1997) found reductions in the number of filter-feeding chironomids (*Chironomus* and *Tanytarsus*) in Lake Erie's east basin profundal zone between 1979 and 1993. Similarly, at depths >20 m in the east basin chironomid density was low (≤163 m^{-2}). Conversely, east basin *Chironomus* density (233.8 m^{-2}) was higher in 2002 than in 1979 (16.6 m^{-2}), with the greatest abundance occurring at depths <20 m densely colonized by *Dreissena*. No *Chironomus* were found at depths >20 m. Chironomid (mostly *Chironomus* spp.) contribution to Lake Erie benthic secondary productivity in 1993 was greater at nearshore stations in the west and east basins than further offshore (Dahl et al. 1995, Johannsson et al. 2000). The 'oligotrophic' indicators *Monodiamesa* and *Potthastia* were found along the Port Ryerse transect at depths <20 m. *Heterotrissocladius* was found at one site (Port Dover, 11 m) in the east basin in 2002, within a region of relatively high *Heterotrissocladius* density found in 1972/73 (Barton 1988b). *Potthastia* was found at one site in 1979, but no *Monodiamesa* or *Heterotrissocladius* were found in 1979 (Dermott 1994). *Monodiamesa* and *Heterotrissocladius* were also found in greater numbers in the east basin in 1993, suggestive of improved water quality since 1979 (Dermott and Kerec 1997). Unfortunately densities of these taxa were not presented by Dermott and Kerec (1997) so no comment can be made on the status of these chironomid populations since 1993.

Chironomids, more than other taxa, appear to respond postively to the biotic inputs of living *Dreissena*, that is, faeces/pseudofaeces and the associated microbial community, rather than the physical habitat generated by non-living shell material (Botts et al. 1996, Kuhns and Berg 1999, Stewart et al. 1999, Szabo 2004). Pseudofeces are agglutinated, undigested, filtered material expelled through the mussel's inhalant siphon, and as much as 90% of a mussels waste products can be comprised of pseudofeces (Reeders and Bij de Vaate 1992). Deposited pseudofecal material is a nutrient rich bacterial-detrital complex which has been found to have higher bacterial densities than settling seston (Izvekova and Lvova-Katchanova 1972). High in organic matter, chlorophyll *a* and nitrogen, *Dreissena* biodeposits also support high rates of bacterial production (Roditi et al. 1997) and are a valuable food resource for chironomids

(Izvekova and Lvova-Katchanova 1972, Szabo 2004) but can be easily resuspended in littoral habitats and so may have a short residence (Roditi et al. 1997) unless settled deep within mussel bed interstices. Chironomids may also be responding to a shift from pelagic to more accessible periphytic diatom species which are resistant to *Dreissena* filtering and which may become more adundant under low light conditions produced by *Cladophora* shading (Pillsbury et al. 2002).

Oligochaetes

Oligochaete density was second only to *Dreissena* and demonstrated an increase from west to east, opposite to the pattern classically associated with basin trophic status (Brinkhurst 1969b). A similar eastward trend of increasing oligochaete density was found in the 1979 data set used in this study. Total oligochaete densities increased in the west and decreased in the central and eastern basins since 1979. Oligochaetes typically exhibit a positive response to the presence of *Dreissena* (Botts et al. 1996, Stewart et al. 1999, Bially and MacIsaac 2000), although long term studies also document declines in oligochaete density after the arrival of *Dreissena* (Dermott and Kerec 1997). Sediment burrowing oligochaetes almost certainly respond to the increased accumulation of POM generated by *Dreissena* as both a source of food and habitat.

In 1993, Johannsson et al. (2000) found that oligochaetes contributed more to benthic productivity in Lake Erie than any other non-dreissenid taxon at a hypolimnetic station in the east basin compared to the central basin. In the east basin nearshore benthic production by amphipods and chironomids was more important (Dahl et al. 1995, Johannsson et al. 2000). However, it must be said that ascribing oligochaetae abundance and distribution in 2002 solely to putative factors such as higher *Dreissena* densities and associated enhanced deposition of detrital material in the east is problematic given the importance of depth and substratum in oligochaete distributions (Stimpson et al. 1975, Barton 1988b), the lack of sediment chemical and nutrient data and small sample size in the west basin.

Oligochaete communities or taxocenes have widely been used to assess sediment and water quality in the Great Lakes (Brinkhurst 1966a, 1966b, Brinkhurst et al. 1968, Brinkhurst 1969b, Howmiller and Scott 1977, Milbrink 1983, Lauritsen et al. 1985, Reynoldson et al. 1989, Schloesser et al. 1995) and oligochaetes are a suggested indicator of ecosytem health for the Great Lakes (SOLEC 1999). Oligochaetes, specifically the Tubificidae, are regarded as having taxonomically diverse physiological tolerances to organic pollution and dissolved oxygen. "Oligotrophic" indicators (e.g. *Stylodrilus herringianus*) are typically more abundant on sand (Barton 1988b), usually of low organic content or bacterial abundance (McMurty et al. 1983), while "eutrophic" indicator taxa (*Limnodrilus* spp. and *Tubifex tubifex*) are inherently more common on organic-rich silt and mud in their preferred food particle size (Rodriguez et al. 2001). The dominance of *Limnodrilus hoffmeisteri* with few other oligochaete taxa is typical of areas of intense eutophication, but when found together with several other abundant taxa can signify the onset of organic pollution (Brinkhurst 1966a, 1966b, 1969b, Howmiller and Scott 1977, Milbrink 1983). Schloesser et al. (1995) indicated a reduction in the percent composition of *L. hoffmeisteri*, from 21.5% in 1961 to 3.9% in 1982, as evidence of recovery from sediment organic pollution in the west basin. Similarly, between 1979 and 2002, percent *L. hoffmeisteri* in the west basin also declined slightly, from 13.1% to 9.2%. In the west basin, "mesotrophic" taxa were more abundant at depths ≤5m on sand and gravel (*Piguetiella michiganensis)* or silty sand (*Aulodrilus* spp.), while *Limnodrilus* spp. were found in low abundance on fine sand/silt at 5-10m. *Aulodrilus* spp. are often associated with mesotrophic or slightly enriched habitats (Howmiller and Scott 1977, Milbrink 1983). Based on the relative abundance of *L. hoffmeisteri* in 2002, there appears to be some improvement in sediment quality in the west and central basins since 1979 ('matched' data only) and a considerable improvement in sediment pollution levels compared to those seen in the 1960's and earlier (Carr and Hiltunen 1965, Hiltunen 1969). There was little change in sediment quality in the east basin between 1979 and 2002. However, the areas of highest *L. hoffmeisteri* abundance in the whole 1979 survey (Sandusky Basin area) were not covered by the 2002 survey, so the indication of improving sediment environment based on *L. hoffmeisteri* in the central basin should be viewed with some uncertainty.

S. heringianus was absent from all locations sampled in Lake Erie in 2002, except on fine sediments at depths >20m in the east basin, where it was found along with relatively low densities of *L. hoffmeisteri*, *T. tubifex* and moderately high total oligochaete densities (mostly immature tubificids lacking setae). The presence of *S.*

heringianus is generally accepted to indicate areas of minimal organic enrichment (Brinkhurst 1969b) and dense populations in Lake Erie have typically been restricted to the east basin (Flint and Merckel 1978, Dermott 1994). The absence of *S. heringianus* in the west and central basin in 2002 was typical of their observed distribution in 1973/74 (Britt et al. 1980) and 1978/79 (Dermott 1994). In 1979, Dermott (1994) reported *S. heringianus* from only 3 of 69 sites in the central basin, unlike the relatively high frequency observed in the eastern part of the central basin in 1972/73, where they were observed at close to 50% of the sites (Barton 1988b). Incidentally, the three sites reported by Dermott (1994) to have *S. heringianus* were within the nearshore zone analyzed by Barton (1988b). The lack of *S. heringianus* in the central basin and the decline in percent abundance of *S. heringianus* in the east basin provides some evidence of reduced substrate quality in both these locations since the 1970's.

In the central basin, oligochaete density increased with increasing depth to 10m, then declined in deeper water. Similar to their pre-*Dreissena* distribution (Barton 1988b), *S. ferox* density increased with depth in the central basin. Barton (1988b) suggested that given the broad range of sediments this "mesotrophic" species can occupy, *S. ferox* is particularly useful as an indicator of trophic conditions. Between 1979 and 2002 in the central basin, there was very little change in the distribution and mean density of *S. ferox;* the persistence of which might suggest the presence of surficial sediment-water quality levels in 2002 similar to those in 1979. A decline in the percent of *S. heringianus*, *L. hoffmeisteri* and total oligochaete density since 1979 may suggest a minor improvement, or at least the maintenance of a long-term mesotrophic condition, in the central basin offshore. *S. ferox* is typically rare in the west basin (Carr and Hiltunen 1965, Schloesser et al. 1995), so its apparent absence from the west basin and relatively low density in the east basin in 2002 tend to suggest slightly more eutrophic than mesotrophic conditions in these areas of the lake.

Schloesser et al. (1995) found a marked improvement in the most heavily polluted areas near river mouths (Carr and Hiltunen 1965, Hiltunen 1969) in the west basin between 1961 and 1982 using indices derived from oligochaete abundance, but there was little change between 1979 and 2002. In 2002, the oligochaete trophic index suggests a minor increase of eutrophic conditions in the west basin and relatively unchanged conditions in sediment quality in the central basin. At the few sites available for comparison in the east basin, areas of the offshore appear marginally improved since 1979. Conflicting indications based on total oligochaete density, relative abundance of "indicator" taxa and trophic condition index, given the limited number of samples stations used for comparison, suggest that Lake Erie's oligochaete community has changed very little since 1979. Seasonal variation in the abundance of mature and identifiable tubificids and differences in sampling device efficiency (Flannagan 1970) may quantitatively limit the applicability of using oligochaetes in making informed conclusions regarding sediment quality in this study, and so qualitative comparisons and evaluation of relative abundance of oligochaete taxa are a preferred method of assessing water quality.

Gastropods and sphaeriids

A general increase in gastropod abundance associated with *Dreissena* is characteristic of nearshore rocky substrates (Stewart et al. 1998b, 1999), but not universal (Wisenden and Bailey 1995). Much like the post-*Dreissena* gastropod density reported for the wave-zone (<0.5-1.8 m) of eastern Lake Erie (Ratti and Barton 2003), this study found relatively high, but variable, gastropod density limited to 2m sites on *Dreissena*-colonized, hard substrate in the east basin. At sites deeper than 2m, gastropod abundance was low. Similar gastropod densities were also reported by Haynes et al. (2005) at 5-7m cobble and reef sites prior to the appearance of round gobies in southwestern Lake Ontario. The increase in gastropods and other littoral grazers is attributed to enhanced benthic primary productivity as a result of improved post-*Dreissena* nutrient and nearshore light environment (Lowe and Pillsbury 1995, Higgins et al. 2005).

Compared to other synoptic surveys there appeared to be little change in the low gastropod densities typical of the central basin (D.R. Barton, 1972/73 unpublished data, Barton 1988a, Dermott 1994). Sphaeriid distribution in the central basin in 2002, and historically (Barton 1988a, Dermott 1994), indicates a predominance of *Pisidium* spp, which borrow soft sediments for food and fill a functional role as bioturbators (McCall et al. 1995, Vaughn and Hakenkamp 2001) in the offshore (>10 m). In the west basin, sphaeriid abundance fluctuated between the 1960s and late 1980s (Reynoldson et al. 1989). The relatively high densities of sediment-burrowing sphaeriids observed in the productive west and central basin are considered to be a result of reduced competition with *Dreissena* for available settling food particles in the offshore of the west and west-central basins. The northshore (≤10 m) of the central basin formerly supported high densities of *Pisidium* (Dermott 1994, D.R. Barton, 1973/73 unpublished data), which now appear to have been greatly reduced, likely as a result of competiton with *Dreissena*, which are better equipped to attach bysally and aggregate on the abrasive, semi-consolidated sediments of the dynamic nearshore environment.

The decline in sphaeriid abundance in Lake Erie since 1979 (Dermott 1994) and their almost complete absence from the east basin in 2002 is in keeping with current trends (Dermott and Kerec 1997, Dermott and Munawar 2002). In a mechanism similar to that causing losses of *Diporeia* populations, *Dreissena* appear to be out-competing sphaeriid clams for newly settled seston in the offshore zone, either directly through filter feeding or through utilization of non-suspended food resources (Nichols et al. 2005). *Pisidium* spp. were formerly the dominant sphaeriid in the east basin (Dermott and Kerec 1997). This is in contrast to the declining, yet persistent, offshore (31-50m) sphaeriid (mostly *Pisidium*) population in southern Lake Michigan despite relatively high *Dreissena* densities (Nalepa et al. 1998, Nalepa et al. 2000). Nalepa et al. (2000) suggest that *Pisidium* may be feeding on *Dreissena* biodeposits directly or on associated microorganisms and that the trend in declining sphaeriid populations was being observed after reductions in phosphorus loads, but prior the arrival of *Dreissena*. Given the low number of Sphaeriidae collected in 2002, this seems an unlikely mechanism to sustain sphaeriid populations in eastern Lake Erie.

Hexagenia

Hexagenia are informative indicators of ecosystem health because of their i) intolerance to environmental stress associated with organic pollution and low dissolved oxygen levels ii) historical abundance in mesotrophic, unpolluted, soft-bottomed habitats, iii) capacity to recover from disturbance, and iv) their contribution to bioturbation and integration of benthic and pelagic resources (Eriksen 1963, Fremling 1964, Nebeker 1972, Corkum et al. 1997, Edsall 2001). *Hexagenia* were adundant in the west basin between the 1930s and mid-1950s when invertebrate composition was dominated by a "*Hexagenia-Oecetis*" community (Shelford and Boesel 1942, Carr and Hiltunen 1965, Manny 1991). After the 1950s there was a shift to a chironomid and oligochaete dominated community, where *Hexagenia* represented <1% of their former adundance: organic pollution and anoxia were blamed for their aberrantly low densities (Shelford and Boesel 1942, Britt 1955a, 1955b, Carr et al. 1965, Carr and Hiltunen 1965, Reynoldson and Hamilton 1993, Schloesser et al. 1995, Krieger et al. 1996). *Hexagenia* densities remained low until 1993-1997, when pollution abatement programs and the appearance of *Dreissena* were credited with providing amenable conditions for *Hexagenia* recolonization, approaching or meeting densities high enough to satisfy management objectives (Reynoldson et al. 1989, Krieger et al. 1996, Corkum et al. 1997, Schloesser et al. 2000).

In the current survey, *Hexagenia* were collected exclusively in the west basin (4 of 11 stations) on preferred substrates of clay/sandy silt and soft, cohesive mud (<8.5 km from shore and depth <6 m) with a mean density of 266.6 individuals m^{-2} and maximum density of 1,822 individuals m^{-2} at a single site. Although the rate of *Hexagenia* recolonization since the 1990s may have been accelerated by the diversion of planktonic food resources to the lake bottom via *Dreissena* biodeposits (Krieger et al. 1996, Schloesser et al. 2000, Cavaletto et al. 2003), *Hexagenia* were only found at sites with very low *Dreissena* (<325 m^{-2}) density and no direct correlation between *Hexagenia* and *Dreissena* was evident. Schloesser et al. (2000) reported relatively high frequency, but variable densities, of *Hexagenia* at nearshore and offshore (<7.5 km and >7.5 km from shore, respectively) sites between 1995-1998, with significantly greater densities occurring nearshore. Given the limited sample size of the present survey and the annual and seasonal variation seen in *Hexagenia* populations in recent years (Schloesser et al. 2000, Schloesser and Nalepa 2001), the magnitude and direction of *Hexagenia* population increase in the west basin is uncertain. However, densities in 2002 were within the range of 34 to 2,100 individuals m^{-2} observed from 1997-1999, which were reported as the highest densities documented in almost 50 years (Schloesser and Nalepa 2001) and slightly higher than densities (range: 0-364.3 m^{-2}, mean=98.5 m^{-2}) reported in 2001 (Edsall et al. 2005). Timing of annual and seasonal sampling for *Hexagenia* is important as mature nymphs (approx. >20 mm) typically emerge from late June to early July and *Hexagenia* recruitment can be variable between years (Reynoldson and

Hamilton 1993, Schloesser et al. 2000, Edsall 2001, Schloesser and Nalepa 2001). Individuals collected in late summer (post-emergence) of 2002 were all approximately 10-20 mm (personal observation), representative of a 2001 cohort exhibiting a 2-year life cycle (Schloesser and Hiltunen 1984, Manny 1991, Schloesser and Nalepa 2001). Although the status of the *Hexagenia* population indicates recovery, continued monitoring is required in order to objectively define management criteria related to *Hexagenia* population health (Krieger 2002, Edsall et al. 2005) and their susceptibility to sporadic episodes of thermal stratification and oxygen depletion in the western basin (Bartish 1984, 1987).

Other taxa

Another typical pattern associated with long-term changes in *Dreissena*-impacted communities is a decline in insect abundance and richness characteristic of rocky nearshore habitats. Numbers of case-building (Leptoceridae) and net-spinning caddisflies (Hydropsychidae and Polycentropodidae) often decline (Ratti and Barton 2003), although these results can be variable (Wisenden and Bailey 1995, Ricciardi et al. 1997). Ratti and Barton (2003) found declines in relative abundance of heptageniid mayflies (Ephemeroptera) and hydropsychid caddisflies in the east basin wave-zone and suggested that mussel biodeposits accumulate within the interstices and undersides of rocks, fouling these microhabitats, eventually turning anoxic. Conversely, the microcaddisfly *Hydroptila* appears to benefit from *Dreissena* shell as habitat, perhaps taking advantage of oxygen rich siphonal currents and grazing periphyton from shells (Stewart et al. 1998b). Haynes et al. (2005) reported decreases in both chironomid and Trichoptera abundance in Lake Ontario between 1983 to 1999/2000.

A notable, but generally innocuous change seen in 2002 is the apparent increase of hydrozoans that frequently colonize *Dreissena* occupied sandy (Botts et al. 1996) and rocky (Stewart et al. 1999) habitats, likely taking advantage of mussel generated substrate stability and feeding currents to intercept small prey. *Helobdella stagnalis* (Hirudinea) density appeared to be similar between 1979 and 2002, and densities were highest in the west and central basin. Dermott and Kerec (1997) reported that this predatory leech averaged 25 m^{-2} in the east basin in 1979 but were not collected in 1993, suggesting that it's predatory role may have been assumed by the nemertean *Prostoma*. In 2002, flatworm (Platyhelminthes) density was greatest at sites with relatively high *Dreissena* density. Flatworms have been observed to respond positively to *Dreissena* in descriptive and experimental field studies (Botts et al. 1996, Stewart et al. 1999).

3.5.2 Lake Erie's Changing Benthos

By 1979 improved surface water quality was being seen in Lake Erie following nutrient load reductions (Yaksich et al. 1985, Charlton et al. 1993, Charlton et al. 1999). This improvement was also being observed in the benthic fauna (Krieger and Ross 1993, Schloesser et al. 1995). Of important consideration is that the interval between 1979-2002 does not represent a period of stable nutrient concentrations in Lake Erie, with *Dreissena* being implicated for effecting many water quality trends (Bertram 1993, Charlton et al. 1993, Holland et al. 1995, Charlton et al. 1999, Nicholls et al. 1999b, Makarewicz et al. 2000, Charlton 2001, Nicholls et al. 2001, Charlton and Milne 2004), however, benthic community composition and abundance in 2002 do not explicitly reflect nutrient reductions or improved water quality observed in Lake Erie. Nevertheless, general patterns typical of *Dreissena*-altered food webs continue to be observed. These include an apparent increase in total invertebrate density (namely *Dreissena*), yet non-dreissenid density appears to have decreased (from 1979 levels) with no significant change in taxa richness, except perhaps for the Chironomidae. Dreissenids are the dominant taxa, followed closely by oligochaetes, chironomids, sphaeriids and amphipods. *D. bugensis* remains the dominant (only) dreissenid observed in the east basin on all substrates and depths. Sphaeriid clams, amphipods and isopods have all declined in relative density, while chironomid relative density has more than doubled between the sites used for pre-*Dreissena* (ca. 1979) comparison. Gastropod and oligochaete relative density have experienced negligible changes in this time. The historically dominant mayfly, *Hexagenia*, continues to be observed in the west basin following population recovery, whereas in the east, sphaeriid density appears to be in continued decline and *Diporeia* seems to have been extirpated.

These effects are not just limited to the offshore. The nearshore waters of the Great Lakes are increasingly being viewed as important integrators of lake processes (Edsall and Charlton 1997, Hecky et al. 2004). Recently, nearshore filter-feeding hydropsychid caddisflies and heptageniid mayflies are rare where they were previously abundant (Ratti and Barton 2003). Strayer et al. (1998) suggests that benthic community responses to *Dreissena* are very much dependent on physical charactersitics of the habitat (substrate, depth, nutrient concentration, etc.), a supposition that is evident in the current study. Nearshore benthic invertebrate taxa and feeding guilds respond differently to increased physical habitat complexity, organic matter, nutrient availability, increased water clarity and associated benthic primary producitivity, and the flourishing growth of *Cladophora*, such as found on hard substrates in the east basin nearshore (Higgins et al. 2005). Despite the added habitat heterogeneity provided by dreissenid mussel colonies on hard substrates or in druses on soft substrates, accelerated biodeposition of organic matter by *Dreissena* (Klerks et al. 1996, Dobson and Mackie 1998, Stewart et al. 1998a) and subsequent transport to profundal zones (ie. through proposed 'nearshore shunt' model, Hecky et al. 2004) may result in communities with relatively high abundances of tolerant species (*sensu* Thienemann).

Short-term studies performed in shallow water on hard substrates relate the local presence of *Dreissena* to increased non-dreissenid abundance and biomass (Wisenden and Bailey 1995, Ricciardi et al. 1997, Thayer et al. 1997, Stewart et al. 1998a, 1998b, Kuhns and Berg 1999, Stewart et al. 1999) sustained by deposition of *Dreissena* faeces and pseudofaeces (Botts et al. 1996, Stewart et al. 1998a, Mayer et al. 2002). Aside from increased invertebrate density or biomass, taxa generally observed to respond positively to *Dreissena* generated habitat include hydriods, triclads, small gastropods (ie. *Amnicola limnosa*, *Physella*) and amphipods (*G. fasciatus*, *E. ischnus*) (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a, 1998b, 1999). The responses of various chironomid and oligochaete taxa, while usually positive, are more varied and seem to be a matter of habitat (ie. depth, substrate) or study area, and so comparison with other regional surveys or habitats not represented in the current survey may be spurious. For example, abundance of the algae- and detritus-feeding *Microtendipes* has been reported to increase (mean density 798 m^{-2}) with increasing *Dreissena* density in west basin nearshore habitats in Lake Erie (Stewart et al. 1998a, 1998b, 1999). However, in 2002, *Microtendipes* were found at only three sites (density ≤ 127 m^{-2}), all in the east basin nearshore (2 m), which also happen to correspond well to the limited range of this taxon observed in 1972/73 (≤ 931 m^{-2}, Barton 1988b) and 1979 (≤ 90 m^{-2}, Dermott 1994).

Furthermore, local-scale observational and experimental studies are of limited comparative use if several of the most dominant and ecologically informative chironomid and oligochaeta taxa from Lake Erie are not present. This loss in taxonomic informarion is intensified when family or higher level identification is used in other studies (Wisenden and Bailey 1995, Botts et al. 1996, Stewart et al. 1998a, Bially and MacIsaac 2000).

Problematically, several studies on the impacts of *Dreissena* colonization on the benthic community were of relatively short duration (1 month to 1 year) so may not reflect the long-term *in situ* effects of *Dreissena* mussels on benthic invertebrate community dynamics (Wisenden and Bailey 1995, Stewart et al. 1998a, 1999). From a long term study in southwestern Lake Ontario, Haynes et al. (2005) found similar or reduced diversity and abundance of non-*Dreissena* taxa between 1983 and 1999/2000 following *Dreissena* colonization, noting a rise, however, in the years between 1983 and 1991/92. Similarly, a decade-long (1981-2004) study of western Lake Erie found that abundance of tubificid and naidid oligochaetes and chironomids declined >70%, suggesting systemic changes in trophic dynamics since the arrival of *Dreissena* (Soster et al. 2011). However, this study was limited to only 4 long-term monitoring stations on soft substrates. Variability in short-term versus long-term effects of dreissenids and other introduced species on native benthic fauna may be a result of local conditions, time-scale or duration of study, reinforcing the importance of long-term, lake-wide biological monitoring. For example, older mussel colonies may support more invertebrate species than newly established colononies (Tsuchiya and Nishihira 1986).

Moderately organic tolerant species may temporarily benefit from the supplemented food supply, so invertebrate abundance and taxa richness rise. This would be an expected macroinvertebrate response, as suggested by whole-lake nutrient enrichment experiments (Clarke et al. 1997). Organically tolerant collector-gatherers will be favoured in the nearshore (ie. chironomids) and offshore (ie. oligochaetes), while suspension and filter feeding taxa decline in both habitats as a result of direct competion with *Dreissena* for food and space. *Diporeia* and Sphaeriidae, relying largely on pelagic primary production and freshly settled detritus, were the groups worst affected by *Dreissena* in sublittoral and profundal Lake Erie (Dermott and Kerec 1997, Johannsson et al. 2000), Lake Ontario (Haynes et al. 1999), Lake Michigan (Nalepa et al. 1998, Lauer and McComish 2001) and Saginaw Bay, Lake Huron (Nalepa et al. 2003). Nearshore, intolerant heptageniid mayflies and filter-feeding hydropsychid caddisflies are rare where they were previously abundant, either through being out-competed for food and space (Hydropsychidae) or loss of microhabitat (Heptageniidae, Ratti and Barton 2003).

As biodeposits accumulate and sediment nutrient levels rise at an accelerated rate associated with *Dreissena* population growth, only more organic tolerant species and those feeding on organic-rich material and associated bacteria would remain in this niche, usually with a subsequent taxa- and habitat-specific decline in diversity to pre-*Dreissena* levels (Haynes et al. 1999, Haynes et al. 2005). This may represent a resource dependent shift in taxa occurence. In southwestern Lake Ontario, Haynes et al. (2005) found that benthic communities were more closely related between 1983 (7 years pre-*Dreissena*) and 1999-2000 (7-9 years post-*Dreissena*) than to the 1991/92, reporting higher non-*Dreissena* abundance from 1991/92, only 1-2 years post-*Dreissena*.

As *Dreissena* densely populates the nearshore, they intercept a major component of pelagic productivity and sequester more of this material and nutrients from the offshore pelagic, either as new *Dreissena* biomass (see Chapter 2), or as coarse aggregate particles carried by longshore currents to be discharged to the outflow, or are retained as depostional material that resists frequent resuspension, only to be transported directly to the offshore profundal zone (Hecky et al. 2004). Pelagic algal communities change to indicate oligotrophic conditions (Dahl et al. 1995) and chl *a*:P ratios become uncoupled (Nicholls et al. 1999a).

3.5.3 Effects of Hypolimnetic Oxygen Depletion on Invertebrate Distribution

Johannsson et al. (2000) reported low benthic productivity, low *Dreissena* abundance and the dominance of low DO tolerant oligochaetes, chironomids (mostly *Chironomus*) and *Pisidium* at their west-central offshore station in 1993, typical of the pre-*Dreissena* hypolimnetic community (Brinkhurst et al. 1968, Britt et al. 1980, Barton 1988a, Dermott 1994). This is similar to the benthic community observed in the current study along a similarly located transect in the west-central basin (extending south from Port Alma to Cleveland). Distributions of oxygen sensitive benthic invertebrates (eg. *Hexagenia*) have been historically limited by low dissolved oxygen below the thermocline (Reynoldson and Hamilton 1993). Paleo-biological data reveal that *Hexagenia* were distributed along the central basin shoreline, but were absent from large areas below the thermocline (>20m) due to periodic hypoxia/anoxia in his region of the lake, despite suitable substrates (Reynoldson and Hamilton 1993). *Dreissena* density in the central basin hypolimnion is commonly below lake-wide average or *Dreissena* are absent altogether (Dermott and Munawar 1993). In 2002, *Dreissena* density was <650 individuals m^{-2} at any site where seasonal hypoxic/anoxic conditions have been reported (Bertram 1993, Charlton and Milne 2004), including the 2002 study year (Burns et al. 2005). The prevalence of low DO tolerant chironomid, oligochaete and sphaeriid taxa and the paucity of dreissenids at offshore sites may be evidence of oxygen limitation on *Dreissena* abundance and distribution by seasonal or periodic episodes of hypoxia/anoxia. Several profundal sphaeriid taxa are known to be tolerant of periodic hypoxia and anoxia during summer stratification (Jonasson 1972, McMahon and Bogan 2001).

In 1979, the high density and biomass of *Chironomus plumosus*, along with the abundance of *Limnodrilus hoffmeisteri* in the western section of the central basin (Sandusky sub-basin), were likely caused by a period of hypolimnetic anoxia that occurred there in late summer (Charlton et al. 1993, Dermott 1994, Dermott and Munawar 2002). The Sandusky sub-basin was not sampled in 2002, but *Chironomus* spp. density was higher at three west-central basin offshore sites in 2002 than in 1979, suggesting the possibility of low hypolimnetic dissolved oxygen at these sites, however *L. hoffmeisteri* abundance at these three sites remain low.

D. polymorpha are much less tolerant of hypoxia (<2-3 mg O_2 l^{-1}) and anoxia compared to other bivalves, especially at progressively warmer temperatures (Matthews and McMahon 1995, Johnson and McMahon 1998, Matthews and McMahon 1999, McMahon and Bogan 2001, Alexander and McMahon 2004); a physiological constraint presumed to restrict their distribution in Lake Erie (Dermott and Munawar 1993, Johannsson et al. 2000) and elsewhere (Mihuc et al. 1999, Yu and Culver 1999). Yu and Culver (1999) documented 100% mortality of zebra mussels from the hypolimnion of a small lake with a summer DO concentration <1.0 mg O_2 l^{-1}. Matthews and McMahon (1999) reported 100% sample mortality of *D. polymorpha* from 8-61 days at a partial pressure of oxygen (P_{O_2}) less than 5 Torr (≈0.4 mg O_2 l^{-1} at 10°C, standard central basin hypolimnion temperature, after Rosa and Burns 1987) depending on acclimation (5°, 15°, 25°C) and test temperature (5°, 15°, 25°C), compared to 3, 4 and 6 days reported by Mikeev (1964) at 23-24°C, 20-21°C, and 17-18°C, respectively. The rapid mortality observed by Mikeev (1964) was explained by acute toxicity caused by the build up of anaerobic metabolic by-products and toxins produced from excreted or decomposing material in a closed system (Matthews and McMahon 1999). NO_3-N concentrations can be higher and DO concentrations up to 2 mg O_2 l^{-1} lower at the base of a *Dreissena* colony (Burks et al. 2002) caused by cascading effects of *Dreissena* ammonium excretion and increased rates of bacterial nitrification in the presence of mussels (Lavrentyev et al. 2000). Yu and Culver (1999) suggest that elevated ammonia concentrations in the hypolimnion may also exacerbate *Dreissena* mortality. Furthermore, sediment oxygen levels can affect nitrification-denitrification, the accumulation of toxic H_2S and the liberation of sediment bound P (Newell 2004) which together are influenced by bioturbators, which make up the majority of the benthic community in the central basin hypolimnion.

There is also evidence that byssal thread production is inhibited at a P_{O_2} of 40 Torr (≈2.87 mg O_2 l^{-1} at 10°C) (Matthews and McMahon 1999, McMahon and Bogan 2001). Matthews and McMahon (1999) noted that mussels attached to other individuals' shells during the oxic acclimation period, subsequently released their byssal attachments during the hypoxic treatment well prior to death. Therefore, it appears that persistence of hypolimnetic DO concentrations as low as ≈3 mg O_2 l^{-1} can cause respiratory and metabolic stress to *Dreissena* in the warm hypolimnetic water of the central basin. While larger *D. polymorpha* are more tolerant of low DO than smaller individuals (Matthews and McMahon 1999), mussels <7 mm (shell length) comprised >94% of the animals collected at the west-central offshore transect. This unusual size frequency distribution compared to other sites in the lake suggest high mortality of larger individuals due to hypolimnion oxygen depletion or successive failed annual recruitment in the central basin hypolimnion due to high veliger mortality. Tamburri et al. (2002) found 82% mortality of 3-day-old *D. polymorpha* veligers at ≤0.8 mg O_2 l^{-1}. The small individuals observed in 2002 are likely to be young-of-the-year establishing themselves in this location following fall turn-over when dissolved oxygen has been replenished in the previous year. *Dreissena* themselves may be contributing to hypolimnetic biological oxygen demand directly through respiration, as documented for other systems (Effler et al. 1998, Caraco et al. 2000) or indirectly by supporting bacteria respiration.

3.5.4 Predation and the Impact of Round Gobies

In addition to the considerable influence *Dreissena* can have in shaping the benthic community, predators may additionally regulate invertebrate compostion and abundance (Stewart et al. 1999). The diet of juvenile round gobies (<9-13 cm TL) is dominated by small, soft-bodied invertebrates, including amphipods, chironomids and zooplankton, and larger round gobies additionally feed heavily on mollusks, including dreissenids (Ghedotti et al. 1995, Jude et al. 1995, Ray and Corkum 1997, Djuricich and Janssen 2001, French and Jude 2001, Janssen and Jude 2001, Skora and Rzeznik 2001, Szabo 2004, Barton et al. 2005, Andraso et al. 2011), causing significant reductions in *Dreissena* and non-*Dreissena* invertebrate densities (Kuhns and Berg 1999) and potentially effecting population size distributions (Patterson et al. 2005, Lederer et al. 2006).

Round gobies are opportunistic feeders, exploiting whichever food resource is in highest relative supply. Optimal foraging theory (MacArthur and Pianka 1966) might suggest a cost-benefit initially for the round goby to feed on readily available non-dreissenid food resources. Round gobies have been shown to prefer amhpipods to *Dreissena* on bare substrate in aquaria and will readily consume more amphipods as they are presented, but that increased habitat complexity and reduced visibility will shift round goby prey preferences towards *Dreissena* (Gonzalez and Downing 1999, Diggins et al. 2002). Diggins et al. (2002) further suggest that the substantial contribution of dreissenids to round goby diets may not reflect their preference for *Dreissena*, but low frequency of encountering motile prey. While it is widely demonstrated that an increase in amphipod density generally accompanies the presence of *Dreissena* mussels (Dermott and Munawar 1993, Botts et al. 1996, Kuhns and Berg 1999, Stewart et al. 1999, Bially and MacIsaac 2000, Gonzalez and Burkart 2004), the relatively low amphipod density observed in 2002 compared to other studies may be attributed to heavy predation pressure from the round goby on this valuable prey item (Kuhns and Berg 1999, Gonzalez and Burkart 2004, Barton et al. 2005). Additionally, it has been suggested that size distribution of amphipod populations is structured by predation (Stewart et al. 1998b), although Stewart et al. (1999) attributed reduced *E. ischnus* biomass to predation even prior to the arrival of the round goby at their test site.

In lab experiments and in the field, *E. ischnus* was more abundant than *G. fasciatus* on *Dreissena* colonized substrates, but *G. fasciatus* utilized macrophytes or *Cladophora* along with *Dreissena* (Van Overdijk et al. 2003, Gonzalez and Burkart 2004). While Van Overdijk et al. (2003) noted these differences in habitat preference in the absence of predators, Gonzalez and Burkart (2004) also attribute this difference to round goby and yellow perch feeding preferences, suggesting the possibility of predator-induced spatial variation in *G. fasciatus* and *E. ischnus* distribution. Additionally, there is evidence that *G. fasciatus* use *Cladorphora* and associated diatoms as food whereas *E. ischnus* do not (Szabo 2004). Data from the present survey, in part, support both these findings, as *G. fasciatus* was the dominant amphipod (88%) at *Cladophora*-dense 2 m sites, while *E. ischnus* was dominant (70%) at sites >5-20 m deep, where *Cladophora* is less dense (Higgins et al. 2005). This suggests that in the presence of dense *Cladophora* on mussel beds, *G. fasciatus* will tend to be the dominant amphipod, as was observed in the current study. Round gobies tend to be more abundant at 10 m than 2-5 m sites in the east basin, and gut contents of round gobies captured from deep-littoral habitats in eastern Lake Erie contain fewer amphipods than fish from ≤5m (Szabo 2004).

There was little evidence to suggest an increase in abundance of large gastropods compared to recent or historical records in the nearshore, although the relatively high gastropod density in the east basin nearshore might reflect limited round goby predation in the very nearshore (≤2 m) by dense *Cladophora* growth. Gastropods, especially small bodied forms (i.e. *Amnicola*), may seek refuge from predatory fish (i.e. Pumpkinseeds, *Lepomis gibbosus*) (Turner 1996, Andraso 2005) by migrating to the interstices between mussel shells in dense growths of *Cladophora*. Regardless, any effect that *Dreissena* may have in supporting high densities of benthic grazers may be negated by specialzed round goby feeding on mollusks (Ricciardi et al. 1997, Gonzalez and Burkart 2004, Barton et al. 2005). Likewise, it is difficult to conclusively attribute the changes in benthic algal grazers to algal abundance or other environmetal conditions.

Due to their smaller size, chironomids are better suited to avoid predation by retreating into the small interstices between rocks, mussel shell and within macroalgae. Kuhns and Berg (1999) and Lederer et al. (2006) found no detectable effect of round goby predation on midge larvae on rocky nearshore habitats of Lake Michigan. Lederer et al. (2006) suggest that increased habitat availability provided by filamentous algae may have limited the effect of goby predation on chironomids. The relatively high abundances of amphipods, chironomids and gastropods at 2m sites in the east basin in 2002 supports a nearshore refugia concept (Reed et al. 2004). As round goby size-class distribution shifts to larger fish capable of handling and consuming mollusk prey, gobies will begin to feed heavily on *Dreissena* (Szabo 2004, Barton et al. 2005). Between 2001 and 2004, east basin, rocky northshore *D. bugensis* densities declined by 94%, particulary apparent in a loss of individuals with a shell length of 3-15 mm (Barton et al. 2005, Patterson et al. 2005), the size prefered by round gobies (Ray and Corkum 1997). Haynes et al. (2005) speculate that as *D. bugensis* replaces *D. polymorpha* in large areas of the Great Lakes the size of interstitial spaces between individual mussels will become larger, providing less effective refugia for small, mobile invertebrates. Similarily, as populations of *D. bugensis* begin to show signs of reduced abundance and a shift in size distribution away from small size classes suitable for round goby consumption towards fewer large bodied individuals, available refugia for soft-bodied invertebrates may decline, accelerating loss of zoobenthic abundance and diversity, most notably at *Dreissena* colonized locations (Ricciardi 2001, Patterson et al. 2005). Evidence provided by gut contents and stable isotopes now suggests that as the availability of suitable size mussels becomes limited, chironomids and amphipods resume an important part of the goby diet (Barton et al. 2005). A decline in amphipod densities and relatively stable chironomid and oligochaete densities on east basin rocky habitats between 2002-2004 (Barton et al. 2005) is consistant with comparisons made between 1979 and 2002.

Round goby abundance has increased in Lake Erie since their establishment in the central basin in 1994, and gobies now comprise a large portion of predator fish diets in all areas of the lake (Deller et al. 2003, Trometer et al. 2004). Between 2001 and 2002, goby densities tended to decline throughout the lake, except in the offshore areas of Long Point Bay (Haas and Tyson 2003) and by 2001 round gobies were often the most numerically adundant forage fish caught by index trawling (Trometer et al. 2004). Goby density subsequently increased in most areas of the east basin in 2003, declined or stabilized in the other basins compared to 2002 and gobies generally remain absent from the offshore areas of the central basin (Haas and Tyson 2003, 2004). Round goby catches (CPUE) from the Long Point Bay Index Gillnetting Survey have declined averaging 40, 359, 1270, 204 and 202 between 2000 to 2004 (D. Greenwood, Lake Erie Management Unit, Ontario Ministry of Natural Resources, Port Dover). Round gobies were the most frequently observed fish at Peacock Point, Lake Erie in 2002 (M. Patterson and R. Szabo, personal observation). Conservative estimates of mean round goby density from Peacock Point (10m) range from 6.5 m^{-2} in 2001 to 14 m^{-2} in 2002, and 9 m^{-2} in August 2002 (2-5m, Szabo 2004, Barton et al. 2005) Similar diver counts suggested that round goby densities ranged from 0.3-19 m^{-2} in the Detroit River (Ray and Corkum 2001) and 0.6-6.9 m^{-2} in western Lake Erie (Johnson et al. 2005). Therefore, it is likely that round gobies were present in relatively high densities at most zoobenthic survey sites in 2002. Haynes et al.(2005) suggest that declines in non-*Dreissena* invertebrate abundance seen at their sites was due to declines in *Dreissena* density in the absence of round gobies. Unlike their reported situation, *Dreissena* densites were relatively high in Lake Erie in 2002, even in the presence of round gobies.

Prior to the rapid dispersal of the round goby in Lake Erie it was suggested that the diversion of pelagic resources to the benthos (Mitchell et al. 1996b) and increases in post-*Dreissena* benthic secondary productivity may directly benefit native benthivorous fishes such as whitefish (*Coregonus clupeaformis*), freshwater drum (*Aplodinotus grunniens*), yellow perch (*Perca flavescens*) and rock bass (*Ambloplites rupestris*) (Stewart et al. 1998b, Johannsson et al. 2000). However, round goby diets overlap considerably with commercially and recreationally important yellow perch, walleye (*Stizostedion vitreum*), bluegill (*Lepomis macrochirus*), logperch (*Percina caprodes*) smallmouth bass (*Micropterus dolomieui*) and rock bass (Stewart et al. 1999, Pothoven et al. 2000, French and Jude 2001, Andraso 2005). Given the growth of the round goby population it is likely that more energy from benthic secondary productivity will contribute to goby biomass and respiration (Szabo 2004) and gobies now comprise an increasingly large portion of predator fish diets in all areas of the lake (Deller et al. 2003, Trometer et al. 2004). However given the current data it is difficult to directly quantify the impacts of the round goby or other benthivorous predators on invertebrate density and composition.

Chapter 4 - Conclusions

As indicated by invertebrate distributions, Lake Erie appears to maintain it's typical gradient of decreasing nutrient concentrations from west to east. Aside from the readily apparent declines in unionid clams and *Diporeia* attributed to the colonization of *Dreissena* in Lake Erie, there appear to have been several subtle changes in the benthic community. Evidence from the benthic macroinvertebrate community in 2002 suggests that the west basin retains its status as being more organically enriched relative to the central and east basins by a small margin. Given the resilience of the benthic community (Reynoldson et al. 1989) and other indicators of ecosystem health (Charlton et al. 1993, Munawar et al. 2002), it is likely that the response of the benthic environment to reduced nutrient loads and other cultural stresses was gradual or delayed as water quality was beginning to show signs of improvement following nutrient control measures in the 1970's and 80's (Yaksich et al. 1985). Although the years between 1979-2002 represent an interval of declining or fluctuating nutrient concentrations (Nicholls et al. 2001), the benthic community composition and abundance in 2002 did not characteristically reflect nutrient reductions or improved water quality. Recovery in abundance and composition of benthic communities may have been delayed due to the time needed for faunal recruitment and colonization or a lag in response to reductions in peak nutrient loads and producitvity (Nalepa et al. 2000). From a long term data set, Nalepa et al. (2000), observed peak total invertebrate densities at depths <50m in 1980, 5-10 years following peak nutrient loads in Lake Michigan; maximum densities in deeper water were delayed another 6-7 years and were less prominent. Unfortunately, there is a lack of data regarding the benthic community throughout Lake Erie in the 1980's and 1990's, so changes in benthic density and taxon diversity during the interval between reduced nutrient loads and the appearance of *Dreissena* are largely undetectable. As indicated by the oligochaete trophic index, the west basin retains its status as being more organically enriched relative to the central and east basins. Conflicting indications based on total oligochaete density, relative abundance of "indicator" taxa and trophic index provide little evidence as to the direction and magnitue of changes occuring in the benthic macroinverebrate community in Lake Erie in 2002.

Despite the food web disruption caused by *Dreissena*, mussels will likely have a long-term stabilizing effect on the benthic invertebrate community, by providing habitat, high quality particulate organic matter and refuge from predation and disturbance (Stewart et al. 1998b). Conversely, if previously established invaders mediate the recruitment of new exotic species, as predicted by the "invasional meltdown" hypothesis, it may decrease the stability of native benthic communities and expedite the homogenization of benthic assemblages in the Great Lakes (Lodge et al. 1998, Simberloff and Von Holle 1999, Ricciardi 2001, Rahel 2002). Early indications suggested that *Gammarus fasciatus* was being replaced by the Ponto-Caspian invasive amphipod *E. ischnus* on rocky habitats in the Laurentian Great Lakes, including Lake Erie (Dermott et al. 1998, Van Overdijk et al. 2003), but this does not appear to be the case in the eastern basin (Barton et al. 2005) or throughout Lake Erie (this study). While *E. ischnus* may benefit from the establishment of *Dreissena* in stable nearshore environments, thus appearing to support the "invasional meltdown" hypothesis (Lodge et al. 1998, Simberloff and Von Holle 1999, Ricciardi 2001), the actual niche separation of *E. ischnus* and *G. fasciatus* is wider than suggested by early studies.

Nevertheless, with the increasing threat of introduced species, the Great Lakes will continue to be subject to a panoply of apparent, and some more subtle, changes in benthic community structure and dynamics. Palmer et al. (2000) and Vanderploeg et al. (2002) both acknowledge Ricciardi and Rasmussen (1998, 1999) and recommend that our empirical emphasis on pelagic systems should now turn to focus on the biota above and within the sediments as drivers of food web and ecosystem processes, in order to better understand the current and potential impacts of Ponto-Caspian invaders on biodiversity and benthic-pelagic dynamics in the Great Lakes.

Differentiating between *Dreissena*-induced effects, round goby predation, changing nutrient levels and other biological and physico-chemical variables on invertebrate abundance and community structure is challenging (Nicholls et al. 2011). The strength of these effects also varies with sediment particle size (Ward and Ricciardi 2007) and can change over time (Strayer et al. 2011).Density, distribution and diversity of the benthic invertebrate community can no longer be related solely to nutrient status but must also explicitly integrate measures of round goby predation in addition to the biotic and abiotic impacts of *Dreissena*. The benthic community of Lake Erie described in 2002 is unlikely to represent an equilibrium condition because at least one of these factors was clearly not stable.

Much of Lake Erie suffers intermittently from low hypolimnetic oxygen concentrations, further inhibiting benthic community recovery. It is hypothesized that sediment nutrient levels and biological oxygen demand similar to those observed shortly following nutrient abatement are likely being maintained by *Dreissena*-enhanced deposition and bacterial decomposition of dreissenid fecal and pseudofecal material. For example, the decline in relative numbers of the pollution intolerant lumbriculid *S. heringianus* in the central and east basin may be indicative of a continued accumulation of organic deposits in the deep parts of the basins, enhanced by *Dreissena* faeces and pseudofaeces deposited locally or transported from the nearshore (Hecky et al. 2004). The relative contribution of *S. ferox* to total oligochaete numbers in the central basin remained unchanged between 1979-2002, further suggesting a presistent or stable sediment environment.

Despite concerns of spatial equivalence, interannual variation or other methodological factors when comparing zoobenthic field studies (Barton 1989), the comparison of the 1979 and 2002 surveys has a robust qualitative descriptive value given the close agreement with previously reported broad-scale trends in pre/post-*Dreissena* zoobenthic communites observed in the Laurentian Great Lakes. However, some caution is advised in the interpretation of these results with respect to assessment of water quality. Even intensive surveys can be affected by spatial variation in the benthic community (Barton 1989), especially given the history of instability in the benthic community in Lake Erie (Reynoldson et al. 1989). The variablity of response seen in the zoobenthic community subsequent to *Dreissena* invasion undoubtedly has both a temporal (Haynes et al. 2005) and spatial dependence (Bailey et al. 1999, Mayer et al. 2002), such that duration and timing of sampling could be as important as the physical geographic coverage. Despite the temporal and spatial variablity typical of macrobenthic communites, this study does support previous reports describing *Dreissena* as an ecosystem engineer restructuring the benthic community of the lower Great Lakes**.**

Dreissena have unequivocally impacted the structure and function of Great Lakes benthic and pelagic communities and processess, however, it is uncertain to what magnitude *Dreissena* and round goby predation had altered benthic invertebrate community composition and abundance in 2002. Confirming a direct cause and effect relationship and quantifying continued *Dreissena*-mediated impacts with the present data is complicated by the combined influence of changing nutrient levels, the dynamics of trophic interactions, life history and physico-chemical sensitivity of invertebrate taxa, and the inherent patchiness of benthic invertebrate distributions.

Clearly, Lake Erie continues to be a lake in transition.

Figures

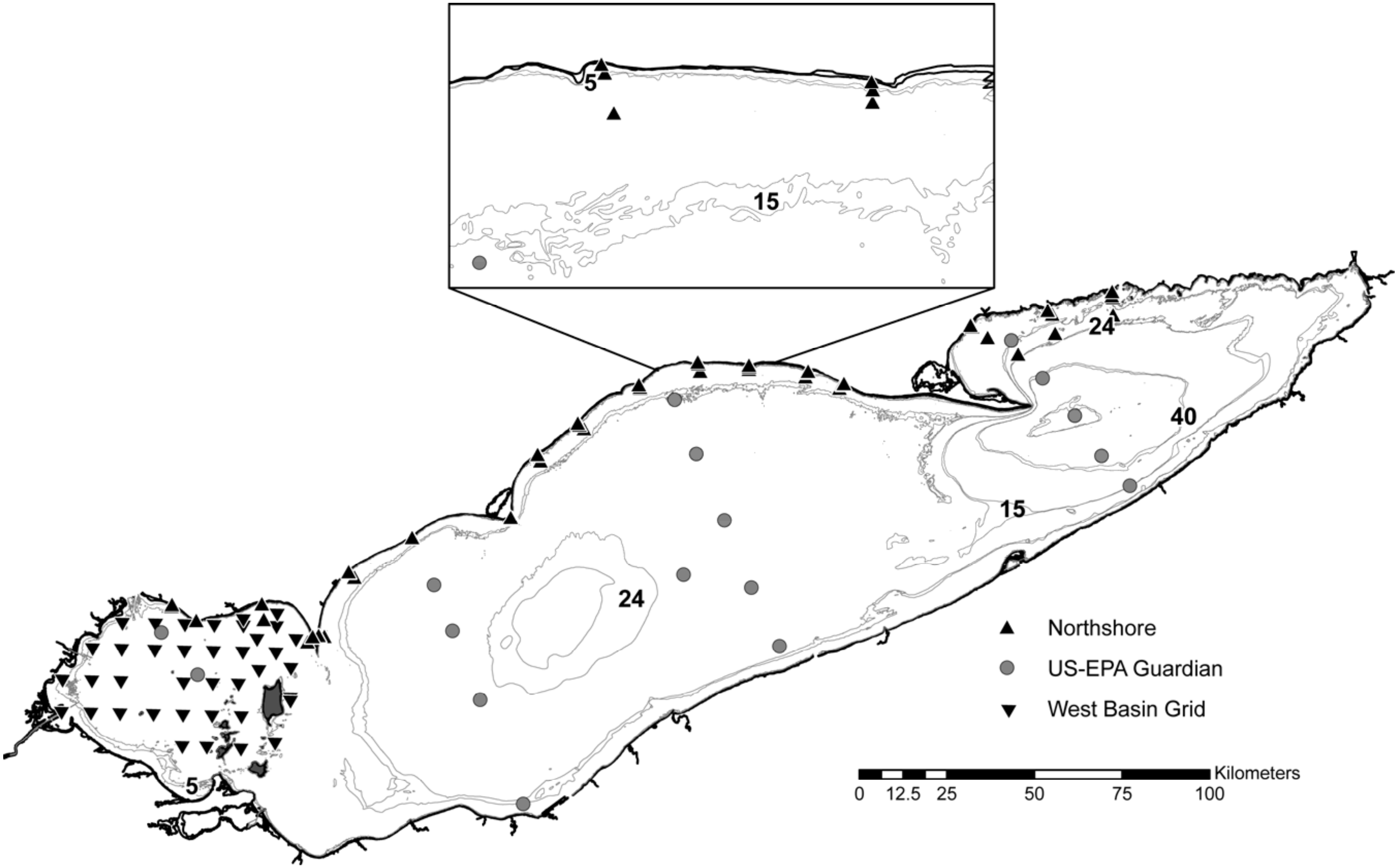

Figure 1. Lake Erie 2002 Dreissena survey sample stations. Numbers on isobaths indicate depth in meters.

Table 1. 2002 Lake Erie mean density (individuals m^{-2} ± standard deviation) and mean dry tissue biomass (g m^{-2} ± standard deviation) by basin and depth (m). N=no. of sites sampled, f=frequency of occurrence.

			D. bugensis Density			*D. polymorpha* Density			Total Density			Total Dry Biomass (g m^{-2})	
Basin	Depth (m)	N	f	Mean	±S.D.	f	Mean	±S.D.	f	Mean	±S.D.	Mean	±S.D.
West	0-4	4	2	153.3	250.9	1	257.8	515.6	2	180.0	303.6	2.4	4.8
	4-8	15	8	548.2	1378.5	7	588.2	1402.9	11	1253.2	3564.2	11.1	28.2
	8-15	30	4	126.7	485.5	2	112.3	510.3	10	331.2	953.7	3.6	14.4
	15-24		.	.	.	.	.	.	.	.	.	.	.
	>24		.	.	.	.	.	.	.	.	.	.	.
	Total	49	14	257.9	859.4	10	269.9	891.8	23	601.1	2110.4	5.8	19.3
Central	0-4	10	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0.0	0.0
	4-8	11	4	960.2	1587.6	3	22.9	50.2	4	983.1	1628.4	18.8	34.5
	8-15	13	8	1038.1	1610.5	4	9.1	17.7	8	1047.2	1613.6	28.6	48.8
	15-24	7	5	163.0	216.4	4	67.7	141.5	5	230.7	249.5	0.7	1.3
	>24		.	.	.	.	.	.	.	.	.	.	.
	Total	41	17	614.6	1279.3	11	20.6	65.3	17	635.2	1292.8	14.2	34.2
East	0-4	3	3	11002.6	4309.1	0	0.0	0.0	3	11002.6	4309.1	58.1	44.1
	4-8	3	3	3816.1	1103.4	0	0.0	0.0	3	3816.1	1103.4	37.4	24.9
	8-15	4	4	8218.9	8471.6	0	0.0	0.0	4	8218.9	8471.6	108.3	128.3
	15-24	4	4	17835.3	20375.1	0	0.0	0.0	4	17835.3	20375.1	233.9	250.2
	>24	3	3	4167.5	3438.8	0	0.0	0.0	3	4167.5	3438.8	38.6	29.9
	Total	17	17	9480.9	11173.1	0	0.0	0.0	17	9480.9	11173.1	104.2	146.6
Total	0-4	17	5	1977.7	4569.6	1	60.7	250.1	5	1984.0	4567.5	10.8	27.5
	4-8	29	15	1042.5	1701.5	10	312.9	1034.0	18	1415.9	2844.4	16.8	30.5
	8-15	47	16	1067.5	3245.0	6	74.2	408.5	22	1200.5	3273.5	19.4	52.0
	15-24	11	9	6589.2	14285.2	4	43.1	114.8	9	6632.3	14264.3	85.5	180.6
	>24	3	3	4167.5	3438.8	0	0.0	0.0	3	4167.5	3438.8	38.6	29.9
	Total	107	48	1859.9	5558.5	21	131.5	614.9	57	2025.0	5664.9	24.7	71.3

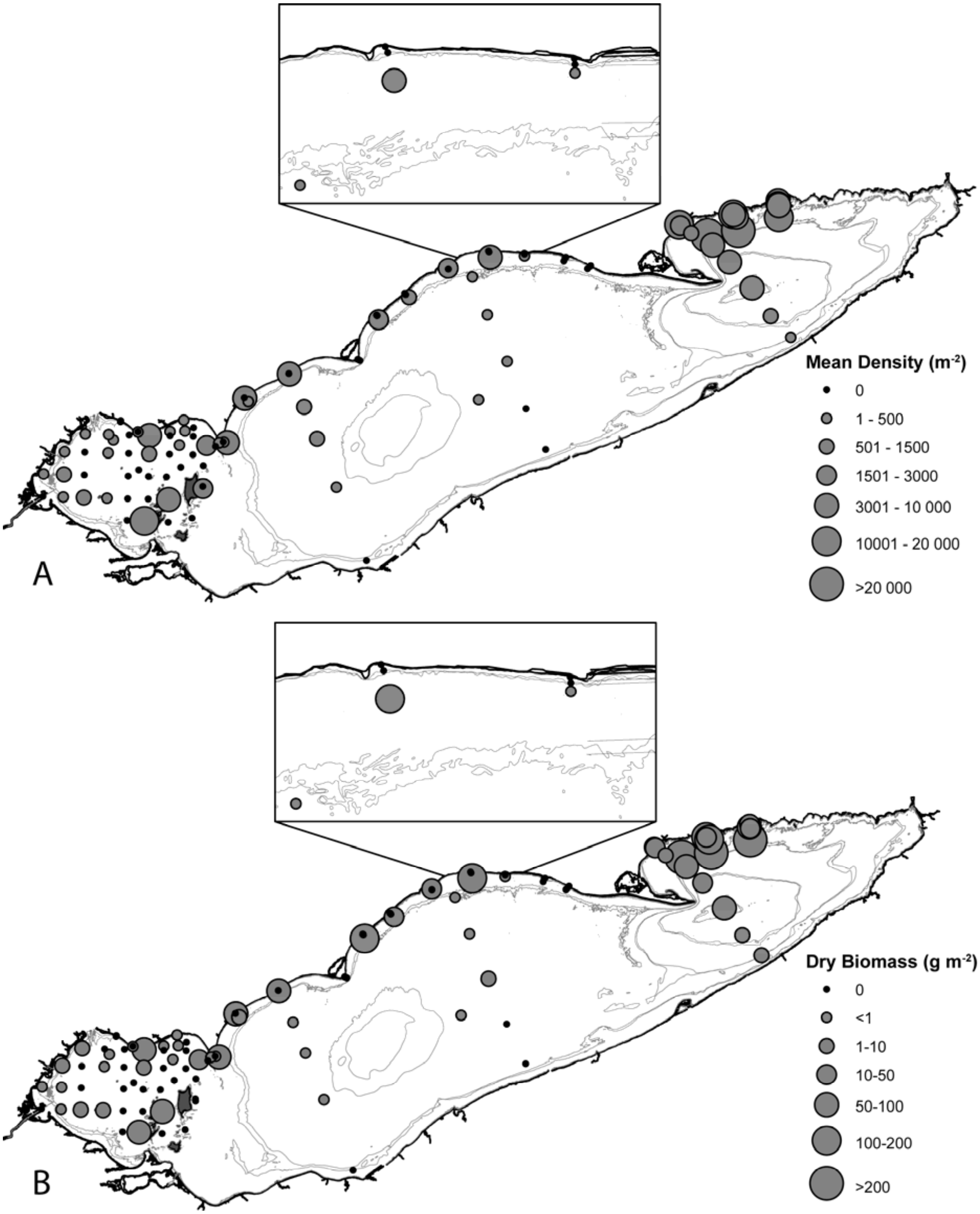

Figure 2. The distribution of *Dreissena* in Lake Erie, 2002: A) mean density (individuals/m^2) and B) dry tissue mass (g/m^2) distribution.

Table 2. Regression coefficients for dummy variables relating classes of depth, basin and substrate texture to density of *Dreissena bugensis* (cumulative R^2=0.56 $F_{[10,97]}$= 12.48, p<0.001), and *D. polymorpha* (cumulative R^2=0.15, $F_{[10,98]}$=1.75, p=0.08). Regression coefficient values for depth, basin and substrate class are expressed relative to <4 m, eastern basin and mud, respectively. + $p < 0.10$ (not significant), * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Dreissena bugensis		*Dreissena polymorpha*	
Variable	Reg. Coeff.±SE	*t*-value	Reg. Coeff.±SE	*t*-value
Intercept	1.907±0.630	3.03	-0.836±0.495	-1.69
Depth >4-8 m	0.656±0.357	1.84+	0.442±0.280	1.58
Depth >8-15 m	0.337±0.368	0.91	-0.022±0.289	-0.07
Depth >15-24 m	0.951±0.570	1.67+	0.652±0.448	1.46
Depth > 24 m	0.805±0.867	0.93	0.512±0.681	0.75
West Basin	-1.821±0.515	3.54***	1.161±0.405	2.87**
Central Basin	-1.881±0.409	4.60***	0.747±0.321	2.32*
SAND/SILT	0.753±0.393	1.91+	0.324±0.309	1.05
SAND	0.054±0.404	0.13	0.142±0.317	0.45
COARSE	1.224±0.566	2.16*	0.181±0.445	0.41
HARD	1.713±0.535	3.20**	0.693±0.421	1.65

Table 3. Regression coefficients for dummy variables relating classes of depth, basin and substrate texture to biomass of *Dreissena bugensis* (cumulative R^2=0.55 $F_{[10,94]}$= 11.53, p<0.001), and *D. polymorpha* (cumulative R^2=0.09, $F_{[10,98]}$=0.96, p=0.56). Regression coefficient values for depth, basin and substrate class are expressed relative to <4 m, eastern basin and mud, respectively. + $p < 0.10$ (not significant), * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Dreissena bugensis		*Dreissena polymorpha*	
Variable	Reg. Coeff.±SE	*t*-value	Reg. Coeff.±SE	*t*-value
Intercept	2.066±0.737		-0.111±0.341	
Depth >4-8 m	0.800±0.417	1.92+	0.120±0.198	0.61
Depth >8-15 m	0.831±0.430	1.93+	-0.061±0.203	0.30
Depth >15-24 m	1.125±0.680	1.65	0.316±0.315	1.01
Depth > 24 m	1.109±1.007	1.10	0.205±0.466	0.44
West Basin	-2.574±0.602	4.28***	0.395±0.283	1.40
Central Basin	-2.364±0.477	4.96***	0.066±0.227	0.29
SAND/SILT	0.166±0.467	0.36	-0.094±0.211	0.45
SAND	0.197±0.466	0.42	0.141±0.216	0.65
COARSE	0.868±0.655	1.33	-0.035±0.303	0.12
HARD	1.767±0.622	2.84**	0.072±0.294	0.24

Table 4. Analyses of variance of density and biomass of *Dreissena bugensis and D. polymorpha* distribution at depths of 2,5 and 10 m along transects from the Canadian side of Lake Erie.

Density

		Dreissena bugensis			*Dreissena polymorpha*		
	DF	MS	F	*p*	MS	F	p
Transect	17	4.5370	2.677	0.007	0.6173	1.292	0.255
Depth	2	5.7935	3.418	0.044	1.5338	3.211	0.053
[2 vs. (5+10)]	1	11.1545	6.581	0.015	2.5571	5.353	0.027
Discrepance	34	1.6949			0.4777		
Total	53						

Biomass

		Dreissena bugensis			*Dreissena polymorpha*		
	DF	MS	F	*p*	MS	F	*p*
Transect	17	0.9757	2.435	0.013	0.00012	0.995	0.486
Depth	2	0.8871	2.214	0.125	0.00025	2.137	0.134
[2 vs. (5+10)]	1	1.5450	3.856	0.058	0.00013	1.116	0.298
Discrepance	34	0.4007			0.00012		
Total	53						

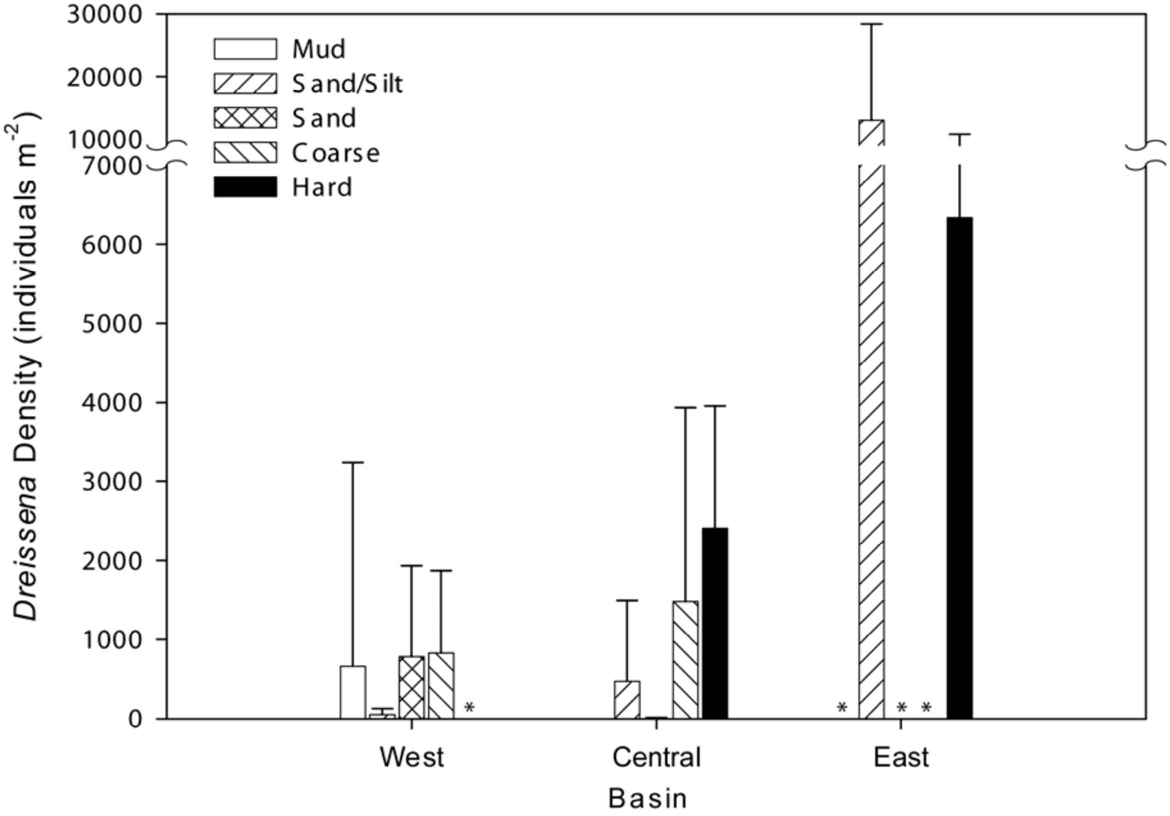

Figure 3. Mean density (individuals/m^2) of *Dreissena* in Lake Erie during 2002, by basin and substrate. Error bars indicate 1 standard deviation. * = category not sampled.

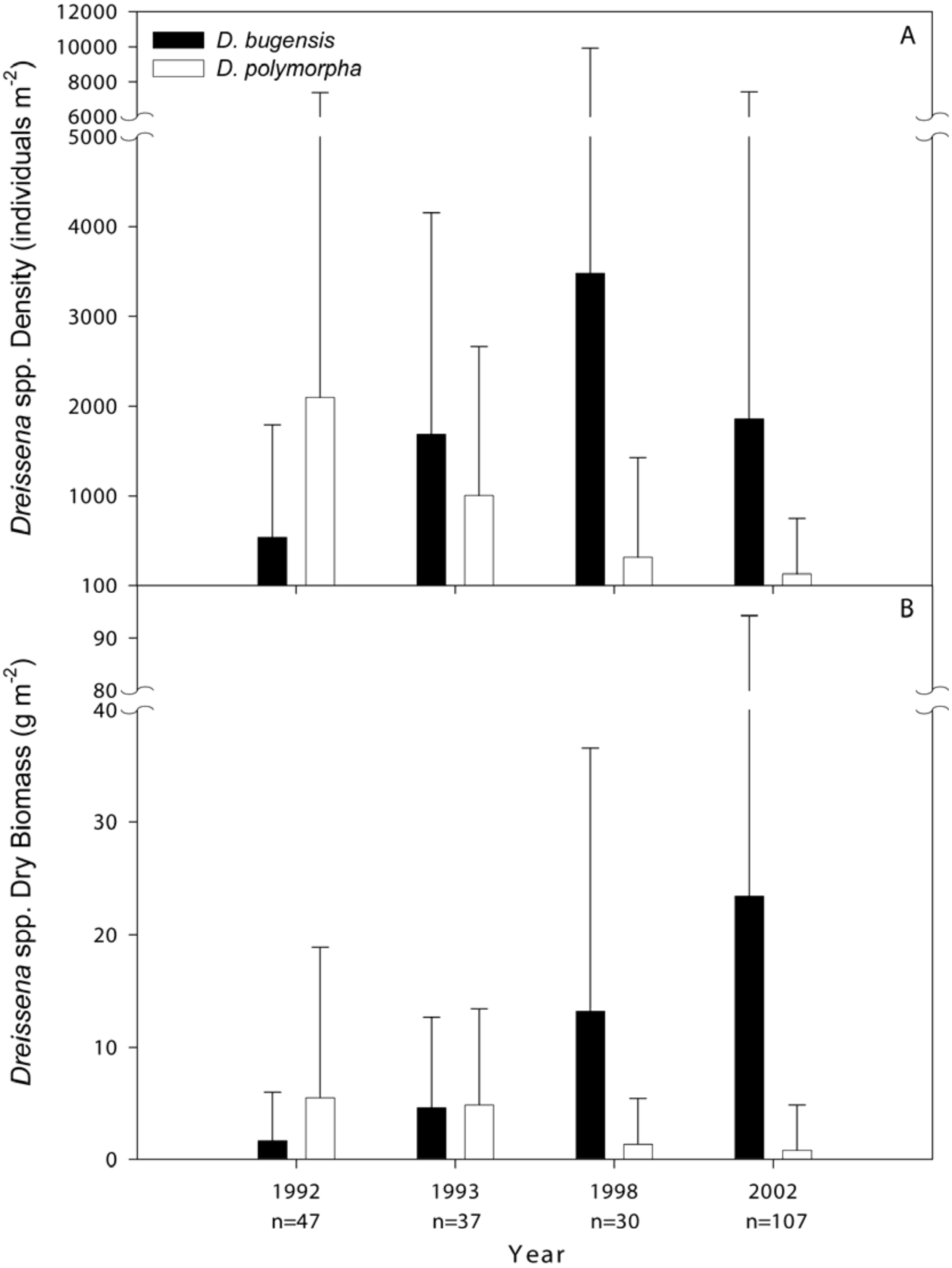

Figure 4. Mean density (individuals/m2) (A) and mean dry tissue mass (g/m2) (B) of *D. bugensis* and *D. polymorpha* from all sites surveyed during the years 1992, 1993, 1998 (data from Jarvis et al. 2000) and 2002. n = number of sites surveyed each year. Error bars indicate 1 standard deviation.

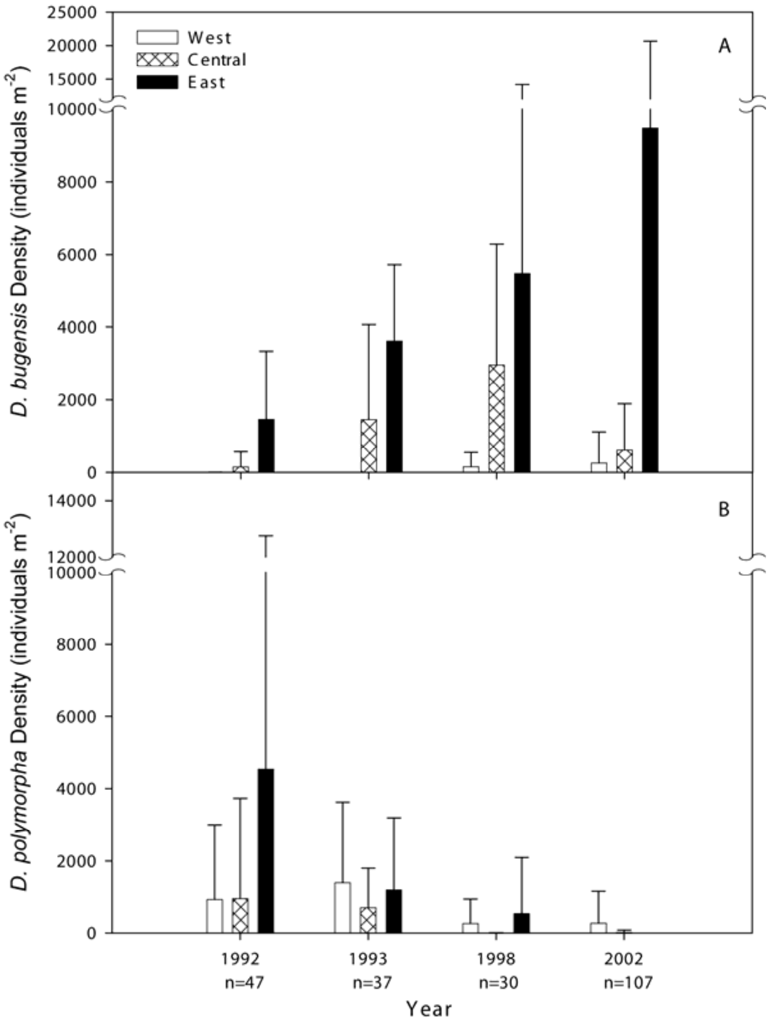

Figure 5. Mean density (individuals/m2) of *D. bugensis* (A) and *D. polymorpha* (B) by basin and year for all sites surveyed during the years 1992, 1993, 1998 (data from Jarvis et al. 2000) and 2002. Error bars indicate 1 standard deviation.

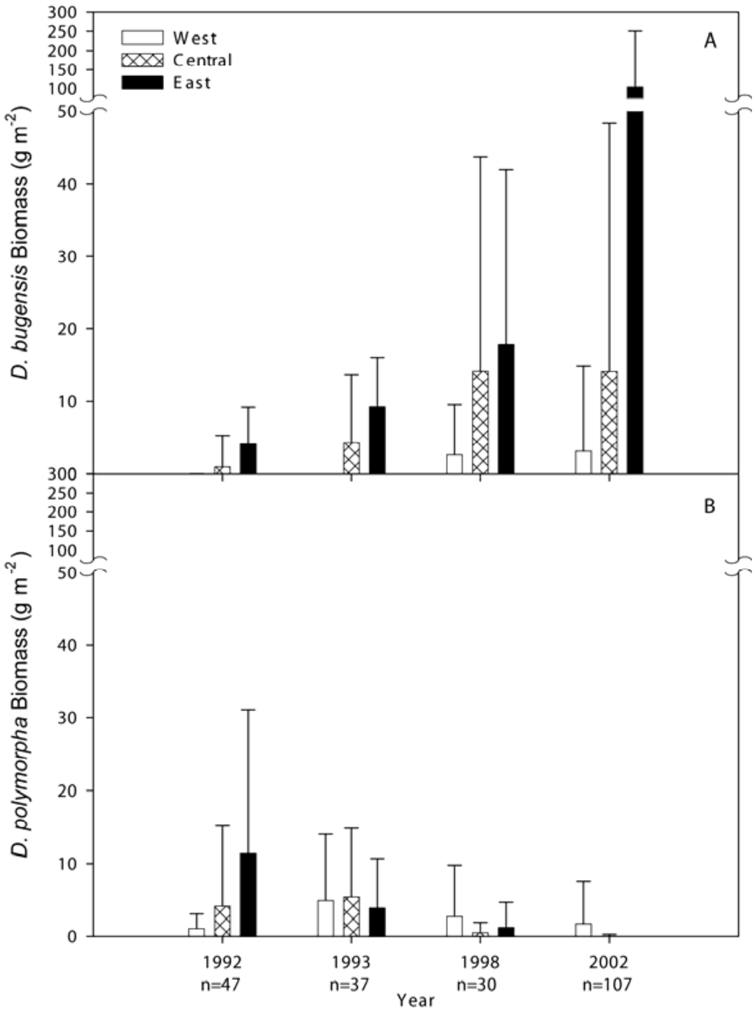

Figure 6. Mean dry tissue mass (g/m2) of *D. bugensis* (A) and *D. polymorpha* (B) by basin and year for all sites surveyed during the years 1992, 1993, 1998 (data from Jarvis et al. 2000) and 2002. Error bars indicate 1 standard deviation.

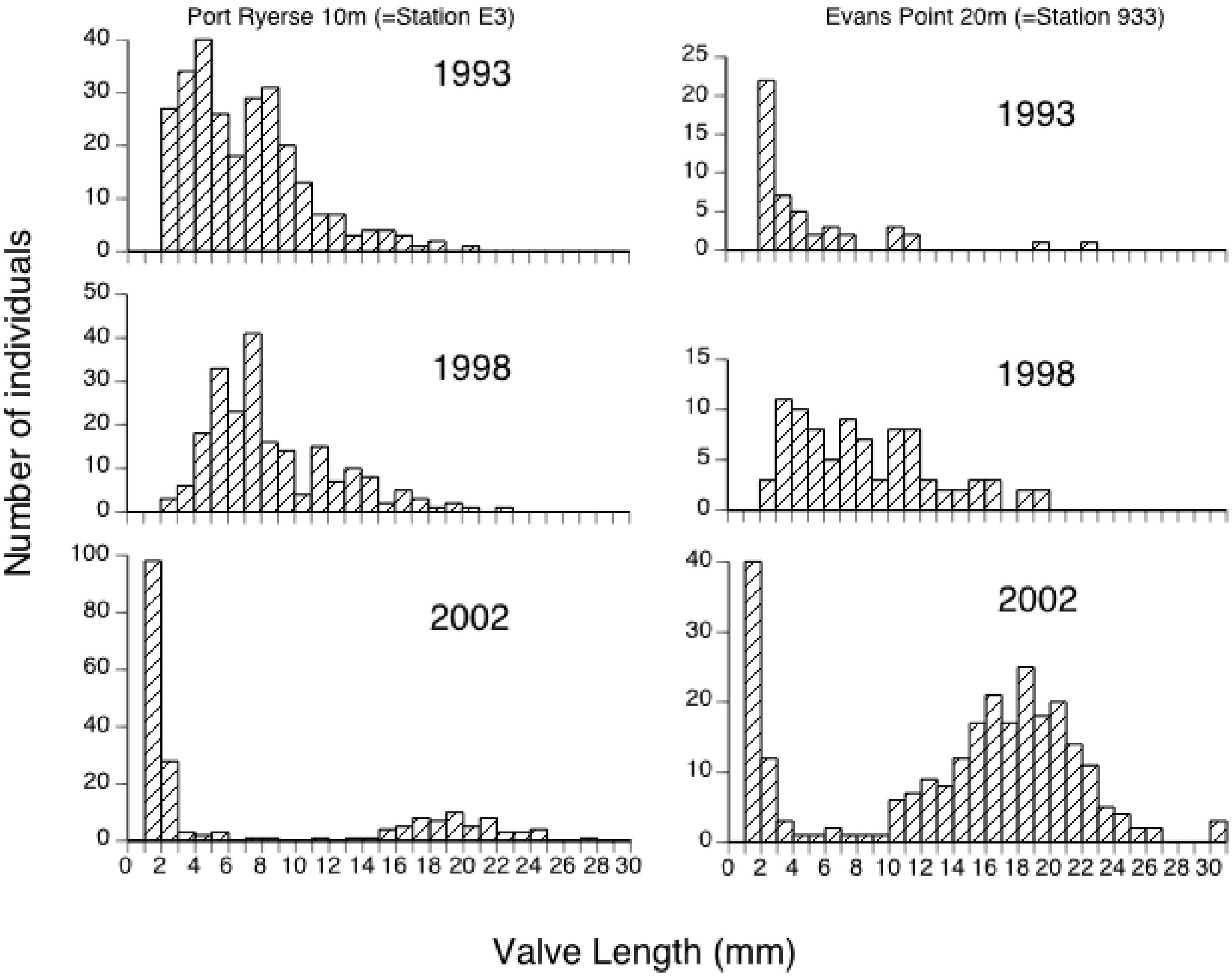

Figure 7. Length-frequency distributions of *Dreissena* spp. from stations E3 and 933 during 1993 and 1998 from Jarvis et al. (2000) and corresponding stations sampled in 2002 (Port Ryerse 10 m and Evans Point 20 m).

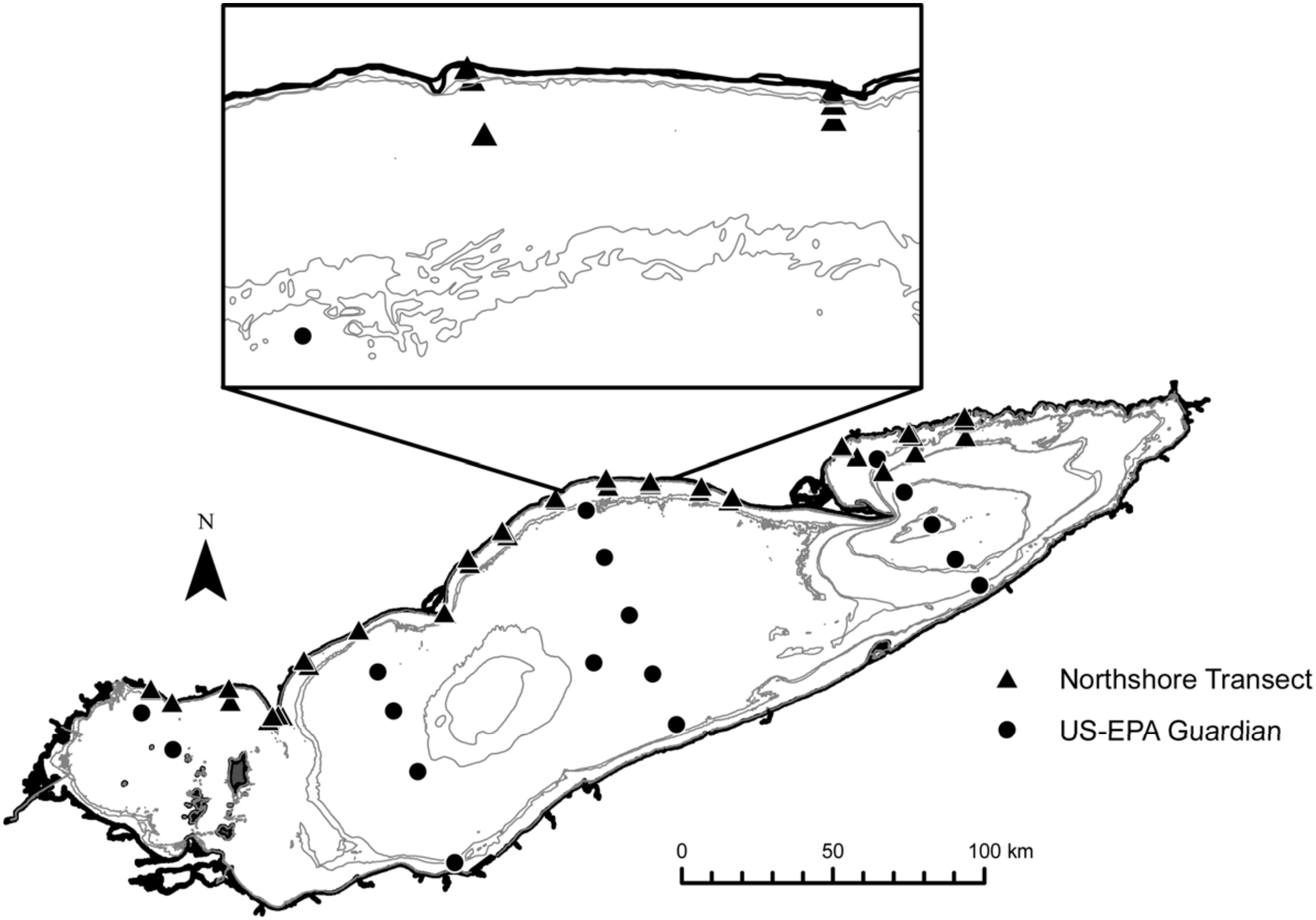

Figure 8. 2002 Lake Erie zoobenthic sample sites. Bathymetry data courtesy National Geophysics Data Center (1998).

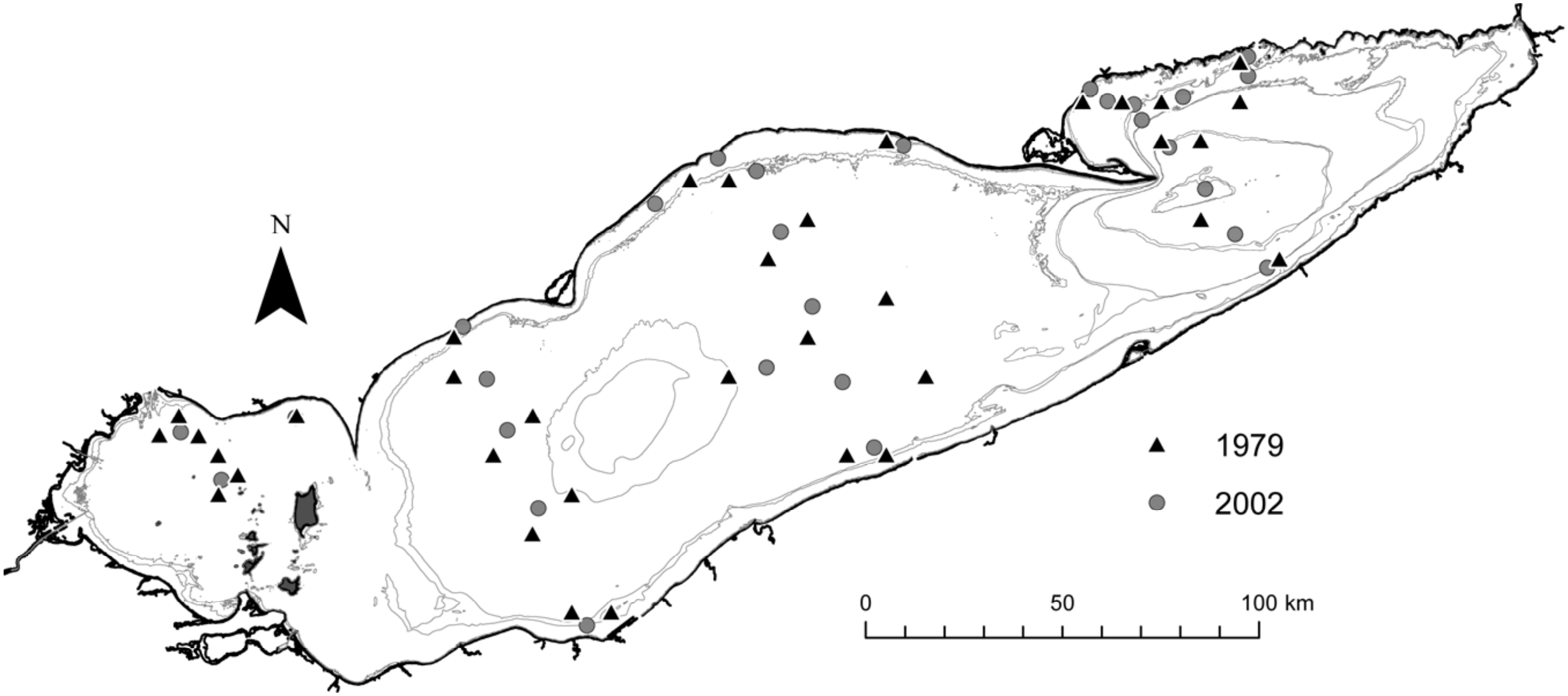

Figure 9. Lake Erie 1979-2002 'matched' sites.

Table 5. Basin and lake-wide frequency of occurrence (f), mean density (individuals m^{-2}), lake total and within-basin percent density of macroinvertebrates from Lake Erie, 2002. N=total number is sites sampled. Standard error of mean in parentheses.

			Basin														
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density
Cnidaria	Hydridae	*Hydridae*					10	230.1 (92.6)	2.1	5.4	4	19.4 (10.4)	<1	<1	14	141.5 (56.3)	2.2
Platyhelminthes	Tricladida	*Dugesia*									1	0.9 (0.9)	<1	<1	1	0.2 (0.2)	<1
		Planariidae	1	1.3 (1.3)	<1	<1	6	54.7 (38.8)	<1	1.3					7	32.7 (23.2)	<1
		Total Planariidae	1	1.3 (1.3)	<1	<1	6	54.7 (38.8)	<1	1.3	1	0.9 (0.9)	<1	<1	8	33.0 (23.2)	<1
	Proseriata	*Hydrolimax*									2	4.7 (3.3)	<1	<1	2	1.2 (0.8)	<1
		Turbellaria									1	58.0 (58.0)	<1	<1	1	14.3 (14.3)	<1
		Total Platyhelminthes	1	1.3 (1.3)	<1	<1	6	54.7 (38.8)	<1	1.3	4	63.7 (57.8)	<1	<1	11	48.4 (27.0)	<1
Gastropoda	Bithyniidae	*Bithynia tentaculata*					2	5.4 (5.1)	<1	<1	1	20.9 (20.9)	<1	<1	3	8.4 (5.9)	<1
	Hydrobiidae	*Amnicola limosa*	2	16.2 (14.7)	<1	<1	2	6.5 (6.1)	<1	<1	5	19.7 (10.1)	<1	<1	9	11.3 (5.0)	<1
		Marstonia decepta									1	52.4 (52.4)	<1	<1	1	12.9 (12.9)	<1
	Physidae	*Physa*									1	0.9 (0.9)	<1	<1	1	0.2 (0.2)	<1
	Pleuroceridae	*Elimia livescens*					1	0.4 (0.4)	<1	<1					1	0.2 (0.2)	<1
		Pleurocera acuta									2	16.9 (12.6)	<1	<1	2	4.2 (3.2)	<1
	Valvatidae	*Valvata perdepressa*					1	0.4 (0.4)	<1	<1					1	0.2 (0.2)	<1
		Valvata piscinalis					1	0.7 (0.7)	<1	<1					1	0.4 (0.4)	<1
		Valvata sincera					3	3.6 (2.9)	<1	<1					3	2.1 (1.7)	<1
	Gastropoda	Total Gastropoda	2	16.2 (14.7)	<1	<1	10	17.0 (8.2)	<1	<1	7	110.7 (74.1)	<1	<1	19	39.9 (19.3)	<1
Bivalvia	Dreissenidae	*Dreissena bugensis*	6	45.1 (17.5)	<1	1.5	17	614.6 (199.8)	5.7	14.4	17	8379.1 (1909.3)	32.1	60.7	40	2436.8 (629.0)	37.9
		Dreissena polymorpha	4	25.6 (17.3)	<1	<1	11	20.6 (10.2)	<1	<1					15	16.3 (6.7)	<1
		Total Dreissena	6	70.7 (31.8)	<1	2.3	17	635.2 (201.9)	5.9	14.9	17	8379.1 (1909.3)	32.1	60.7	40	2453.1 (628.5)	38.2
	Sphaeriidae	Unident Sphaeriidae	2	44.4 (37.6)	<1	1.5	5	55.3 (35.9)	<1	1.3					7	39.9 (22.2)	<1
		Pisidium	6	162.9 (67.7)	<1	5.4	9	121.4 (45.3)	1.1	2.8					15	98.1 (29.5)	1.5
		Sphaerium	3	56.6 (35.6)	<1	1.9	4	24.9 (17.1)	<1	<1					7	23.8 (11.7)	<1
		Sphaerium corneum					2	6.1 (5.1)	<1	<1					2	3.6 (3.1)	<1
		Sphaerium rhombiodium	1	9.4 (9.4)	<1	<1	1	7.6 (7.6)	<1	<1	1	0.9 (0.9)	<1	<1	3	6.2 (4.7)	<1
		Total *Sphaerium*	4	66.0 (35.3)	<1	2.2	6	38.7 (20.9)	<1	<1	1	0.9 (0.9)	<1	<1	11	33.7 (13.7)	<1
		Total Sphaeriidae	6	273.4 (103.4)	<1	9.0	12	215.3 (81.5)	2.0	5.0	1	0.9 (0.9)	<1	<1	19	171.7 (52.2)	2.7
Hydracarina	Hydracarina	*Hydracarina*	3	6.7 (4.2)	<1	<1	9	12.6 (5.8)	<1	<1	7	126.8 (92.5)	<1	<1	19	39.8 (23.3)	<1
Amphipoda	Gammaridae	*Echinogammarus ischnus*					2	10.8 (8.2)	<1	<1	9	108.7 (60.3)	<1	<1	11	33.2 (16.2)	<1
		Gammarus fasciatus					4	8.1 (5.5)	<1	<1	7	443.9 (277.1)	1.7	3.2	11	114.2 (70.6)	1.8
		Gammarus pseudolimneas					1	0.4 (0.4)	<1	<1					1	0.2 (0.2)	<1
		Total Amphipoda					6	19.3 (9.9)	<1	<1	11	552.5 (319.0)	2.1	4.0	17	147.6 (82.0)	2.3
Isopoda		*Caecidotea*					5	60.0 (36.7)	<1	1.4					5	35.6 (22.0)	<1
		Caecidotea intermedius					1	0.4 (0.4)	<1	<1					1	0.2 (0.2)	<1
		Caecidotea racovitzai					3	30.3 (25.3)	<1	<1					3	18.0 (15.1)	<1
		Lirceus									1	12.5 (12.5)	<1	<1	1	3.1 (3.1)	<1
		Total Isopoda					7	90.7 (59.8)	<1	2.1	1	12.5 (12.5)	<1	<1	8	57.0 (35.8)	<1

(Continued)

Table 5. (Continued).

			Basin														
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density
Ephemeroptera	Caenidae	*Caenis*					2	1.4 (1.1)	<1	<1	1	10.0 (10.0)	<1	<1	3	3.3 (2.5)	<1
	Ephemeridae	*Hexagenia*	4	266.6 (169.2)	<1	8.8									4	42.5 (28.5)	<1
		Total Ephemeroptera	4	266.6 (169.2)	<1	8.8	2	1.4 (1.1)	<1	<1	1	10.0 (10.0)	<1	<1	7	45.8 (28.5)	<1
Trichoptera	Hydroptilidae	*Hydroptila*									4	32.1 (16.4)	<1	<1	4	7.9 (4.3)	<1
	Leptoceridae	*Oecetis*					1	0.4 (0.4)	<1	<1	2	3.7 (3.1)	<1	<1	3	1.1 (0.8)	<1
	Trichoptera	Total Trichoptera					1	0.4 (0.4)	<1	<1	5	35.9 (18.4)	<1	<1	6	9.1 (4.8)	<1
Coleoptera	Elmidae	*Optioservus*	1	2.7 (2.7)	<1	<1									1	0.4 (0.4)	<1
		Stenelmis	1	1.3 (1.3)	<1	<1									1	0.2 (0.2)	<1
	Coleoptera	Total Coleoptera	1	4.0 (4.0)	<1	<1									1	0.6 (0.6)	<1
Diptera	Ceratopogonidae	Ceratopogonidae					1	1.1 (1.1)	<1	<1					1	0.6 (0.6)	<1
	Chironomidae	Unident Chironomidae					1	0.4 (0.4)	<1	<1					1	0.2 (0.2)	<1
	Diamesinae	*Monodiamesa*									2	7.0 (5.0)	<1	<1	2	1.7 (1.3)	<1
		Potthastia									2	1.2 (0.9)	<1	<1	2	0.3 (0.2)	<1
		Total Diamesinae									3	8.2 (5.3)	<1	<1	3	2.0 (1.3)	<1
	Chironomini	*Chironomus*	8	315.1 (141.3)	<1	10.4	27	320.1 (84.0)	3.0	7.5	12	199.1 (59.4)	<1	1.4	47	289.5 (56.4)	4.5
		Crytpochironomus	10	191.2 (46.5)	<1	6.3	25	79.5 (24.7)	<1	1.9	5	24.4 (14.9)	<1	<1	40	83.7 (17.8)	1.3
		Cyphomella					3	4.0 (2.8)	<1	<1					3	2.4 (1.7)	<1
		Dicrotendipes					2	3.6 (3.0)	<1	<1	5	92.4 (62.8)	<1	<1	7	24.9 (15.9)	<1
		Dicrotendipes lt									5	44.6 (31.6)	<1	<1	5	11.0 (7.9)	<1
		Total *Dicrotendipes*					2	3.6 (3.0)	<1	<1	7	137.0 (94.0)	<1	<1	9	35.9 (23.8)	<1
		Hamischia grp					2	6.5 (4.8)	<1	<1	1	0.9 (0.9)	<1	<1	3	4.1 (2.9)	<1
		Microtendipes					1	2.2 (2.2)	<1	<1	6	31.1 (13.4)	<1	<1	7	8.9 (3.8)	<1
		Microtendipes dk									3	12.2 (7.9)	<1	<1	3	3.0 (2.0)	<1
		Parachironomus									1	0.6 (0.6)	<1	<1	1	0.2 (0.2)	<1
		Paracladopelma					1	0.4 (0.4)	<1	<1	1	0.6 (0.6)	<1	<1	2	0.4 (0.3)	<1
		Paratendipes									3	22.5 (19.3)	<1	<1	3	5.5 (4.8)	<1
		Phaenopsectra									3	5.6 (3.5)	<1	<1	3	1.4 (0.9)	<1
		Polypedilum	2	22.9 (20.1)	<1	<1	5	120.5 (117.4)	1.1	2.8	9	73.0 (25.5)	<1	<1	16	93.2 (69.9)	1.5
		Pseudochirnomus	4	114.5 (89.0)	<1	3.8	4	4.5 (2.7)	<1	<1	4	24.3 (15.5)	<1	<1	12	26.9 (15.0)	<1
		Saetheria					1	2.9 (2.9)	<1	<1					1	1.7 (1.7)	<1
		Stictochironomus	2	20.2 (14.4)	<1	<1	6	9.0 (4.1)	<1	<1					8	8.6 (3.4)	<1
		Total Chironomini	11	663.9 (132.8)	1.6	21.9	40	553.2 (140.9)	5.1	12.9	15	531.2 (131.1)	2.0	3.8	66	565.4 (91.5)	8.8
	Tanytarsini	Unident Tanytarsini									8	137.9 (99.6)	<1	<1	8	34.0 (25.0)	<1
		Cladotanytarsus					1	0.5 (0.5)	<1	<1					1	0.3 (0.3)	<1
		Microspectra	1	2.7 (2.7)	<1	<1	1	0.4 (0.4)	<1	<1					2	0.6 (0.5)	<1
		Paratanytarsus					1	0.5 (0.5)	<1	<1					1	0.3 (0.3)	<1
		Rheotanytarsus					2	3.3 (2.3)	<1	<1					2	1.9 (1.4)	<1
		Tanytarsus	8	57.9 (18.0)	<1	1.9	20	561.5 (255.0)	5.2	13.1	6	73.4 (50.7)	<1	<1	34	360.9 (154.1)	5.6
		Total Tanytarsini	8	60.6 (20.1)	<1	2.0	22	566.2 (254.8)	5.2	13.2	12	211.3 (110.7)	<1	1.5	42	398.1 (155.1)	6.2
		Unident Chironominae									3	135.4 (125.7)	<1	<1	3	33.4 (31.1)	<1
		Total Chironominae	11	724.5 (134.9)	1.8	23.9	41	1119.3 (305.1)	10.3	26.2	15	878.0 (311.1)	3.4	6.4	67	996.9 (197.3)	15.5

(Continued)

Table 5. (Continued).

			Basin															
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density
	Orthocladiinae	*Cricotopus*					1	1.1 (1.1)	<1	<1	3	15.6 (10.2)	<1	<1	4	4.5 (2.7)	<1
		Epoicocladius	1	2.7 (2.7)	<1	<1									1	0.4 (0.4)	<1
		Heterotrissocladius									1	7.0 (7.0)	<1	<1	1	1.7 (1.7)	<1
		Psectrocladius									6	45.2 (32.6)	<1	<1	6	11.1 (8.2)	<1
		Tvetenia	1	1.3 (1.3)	<1	<1									1	0.2 (0.2)	<1
		Total Orthocladiinae	2	4.0 (2.9)	<1	<1	1	1.1 (1.1)	<1	<1	7	67.8 (33.8)	<1	<1	10	18.0 (8.9)	<1
	Tanypodinae	*Ablabesmyia*	3	31.0 (20.1)	<1	1.0					1	3.1 (3.1)	<1	<1	4	5.7 (3.4)	<1
		Apsectrotanypus					1	0.4 (0.4)	<1	<1					1	0.2 (0.2)	<1
		Coelotanypus	6	325.9 (176.4)	<1	10.7	1	0.4 (0.4)	<1	<1					7	52.2 (30.6)	<1
		Conchapelopia									2	18.1 (17.4)	<1	<1	2	4.5 (4.3)	<1
		Paramerina	6	39.1 (21.1)	<1	1.3					1	3.5 (3.5)	<1	<1	7	7.1 (3.7)	<1
		Procladius	5	35.0 (23.7)	<1	1.2	16	44.8 (16.6)	<1	1.0	10	44.8 (16.0)	<1	<1	31	43.2 (11.2)	<1
		Tanypus	1	4.0 (4.0)	<1	<1									1	0.6 (0.6)	<1
		Total Tanypodinae	8	435.0 (212.0)	1.1	14.3	16	45.5 (16.6)	<1	1.1	10	69.5 (26.1)	<1	<1	34	113.5 (38.5)	1.8
		Total Chironomidae	11	1163.5 (248.2)	2.9	38.3	41	1166.3 (309.9)	10.8	27.3	15	1023.6 (339.8)	3.9	7.4	67	1130.7 (204.3)	17.6
Oligochaeta	Lumbriculidae	Unident Lumbriculidae					3	24.1 (14.2)	<1	<1	3	15.9 (12.5)	<1	<1	6	18.2 (9.0)	<1
		Stylodrilus herringianus									2	59.3 (54.8)	<1	<1	2	14.6 (13.6)	<1
		Total Lumbriculidae					3	24.1 (14.2)	<1	<1	5	75.2 (55.2)	<1	<1	8	32.8 (16.0)	<1
	Naididae	Unident Naididae									8	290.8 (129.3)	1.1	2.1	8	71.6 (34.6)	1.1
		Arcteonais lomondi	1	1.3 (1.3)	<1	<1									1	0.2 (0.2)	<1
		Dero digitata	2	28.3 (24.2)	<1	<1									2	4.5 (3.9)	<1
		Nais bretscheri					2	14.8 (12.8)	<1	<1					2	8.8 (7.6)	<1
		Nais communis	1	5.4 (5.4)	<1	<1									1	0.9 (0.9)	<1
		Nais simplex	2	2.7 (1.8)	<1	<1	5	30.0 (16.0)	<1	<1					7	18.2 (9.6)	<1
		Nais variabilis					9	32.1 (16.3)	<1	<1					9	19.1 (9.8)	<1
		Total *Nais*	3	8.1 (5.4)	<1	<1	12	76.9 (27.5)	<1	1.8					15	47.0 (16.8)	<1
		Ophidonais serpentina					2	3.6 (3.3)	<1	<1					2	2.1 (1.9)	<1
		Piguetiella michiganensis	7	261.3 (107.2)	<1	8.6	17	87.4 (30.8)	<1	2.0					24	93.6 (26.4)	1.5
		Specaria josinae	1	4.0 (4.0)	<1	<1									1	0.6 (0.6)	<1
		Stylaria lacustris					3	8.7 (5.2)	<1	<1					3	5.2 (3.1)	<1
		Uncinais uncinata	4	114.5 (70.5)	<1	3.8	9	32.9 (13.9)	<1	<1					13	37.8 (14.2)	<1
		Vejdovskyella									2	37.3 (36.0)	<1	<1	2	9.2 (8.9)	<1
		Vejdovskyella intermedia					3	6.7 (5.3)	<1	<1					3	4.0 (3.2)	<1
		Total *Vejdovskyella*					3	6.7 (5.3)	<1	<1	2	37.3 (36.0)	<1	<1	5	13.1 (9.4)	<1
		Total Naididae	9	417.5 (136.3)	1.0	13.7	25	216.2 (42.3)	2.0	5.1	9	328.1 (129.4)	1.3	2.4	43	275.8 (46.0)	4.3

(Continued)

Table 5. (Continued).

			Basin															
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density	Percent Basin Density	f	Mean Density ±SEM	Percent Total Density
	Tubificidae	*Aulodrilus americanus*					1	2.9 (2.9)	<1	<1	1	0.9 (0.9)	<1	<1	2	1.9 (1.7)	<1
		Aulodrilus piqueti	1	35.0 (35.0)	<1	1.2									1	5.6 (5.6)	<1
		Aulodrilus pluriseta	5	37.7 (27.7)	<1	1.2	5	4.7 (3.0)	<1	<1					10	8.8 (4.8)	<1
		Total *Aulodrilus*	6	72.7 (41.6)	<1	2.4	6	7.6 (4.1)	<1	<1	1	0.9 (0.9)	<1	<1	13	16.3 (7.4)	<1
		Branchiura sowerbyi	2	5.4 (3.6)	<1	<1	2	22.0 (15.4)	<1	<1					4	14.0 (9.2)	<1
		Ilyodrilus templetoni	1	1.3 (1.3)	<1	<1	1	0.4 (0.4)	<1	<1					2	0.4 (0.3)	<1
		Imm Tubificid with hair	6	26.9 (14.7)	<1	<1	17	141.8 (93.1)	1.3	3.3	11	136.1 (54.4)	<1	<1	34	122.1 (56.8)	1.9
		Imm Tubificid no hair	11	584.5 (129.5)	1.4	19.2	35	1049.7 (255.9)	9.7	24.6	17	2822.6 (792.0)	10.8	20.4	63	1412.3 (263.8)	22.0
		Potamothrix vejdovskyi					13	173.8 (107.9)	1.6	4.1	3	41.0 (22.8)	<1	<1	16	113.4 (64.7)	1.8
		Potamothrix moldaviensis	3	22.9 (14.5)	<1	<1	15	49.5 (16.6)	<1	1.2	6	33.5 (18.8)	<1	<1	24	41.3 (11.1)	<1
		Total *Potamothrix*	3	22.9 (14.5)	<1	<1	21	223.3 (110.6)	2.1	5.2	6	74.4 (40.4)	<1	<1	30	154.7 (66.9)	2.4
		Limnodrilus cervix	3	24.2 (18.8)	<1	<1	3	13.0 (11.2)	<1	<1					6	11.6 (7.3)	<1
		Limnodrilus claparedianus					1	1.2 (1.2)	<1	<1					1	0.7 (0.7)	<1
		Limnodrilus hoffmeisteri	7	45.8 (15.0)	<1	1.5	11	10.8 (3.6)	<1	<1	5	30.5 (15.6)	<1	<1	23	21.3 (5.2)	<1
		Total *Limnodrilus*	7	70.0 (28.6)	<1	2.3	14	25.1 (11.6)	<1	<1	5	30.5 (15.6)	<1	<1	26	33.6 (9.2)	<1
		Spirosperma ferox					7	103.7 (39.4)	<1	2.4	2	6.5 (4.5)	<1	<1	9	63.2 (24.1)	<1
		Tubifex tubifex									2	1.7 (1.2)	<1	<1	2	0.4 (0.3)	<1
		Total Tubificidae	11	783.8 (181.5)	1.9	25.8	37	1573.6 (433.8)	14.5	36.8	17	3072.8 (834.7)	11.8	22.2	65	1817.0 (340.1)	28.3
		Total Oligochaeta	11	1201.2 (95.1)	3.0	39.5	38	1813.8 (443.9)	16.8	42.4	17	3476.0 (832.7)	13.3	25.2	66	2125.7 (344.6)	33.1
Hirudinea	Erpobdellidae	*Erpobdella punctata*									1	0.6 (0.6)	<1	<1	1	0.2 (0.2)	<1
	Glossiphoniidae	*Helobdella*	3	8.1 (5.4)	<1	<1	2	2.5 (2.2)	<1	<1					5	2.8 (1.6)	<1
		Helobdella stagnalis	2	25.6 (17.4)	<1	<1	6	13.0 (6.5)	<1	<1					8	11.8 (4.8)	<1
		Total *Helobdella*	3	33.7 (22.3)	<1	1.1	7	15.5 (6.7)	<1	<1					10	14.6 (5.4)	<1
		Total Hirudinea	3	33.7 (22.3)	<1	1.1	7	15.5 (6.7)	<1	<1	1	0.6 (0.6)	<1	<1	11	14.8 (5.4)	<1
		Total Invertebrates		3037.4 (415.8)	7.5			4273.5 (765.8)	39.5			13811.7 (2615.4)	53			6426.5 (933.1)	
		Total No. Taxa		44				69				56				107	

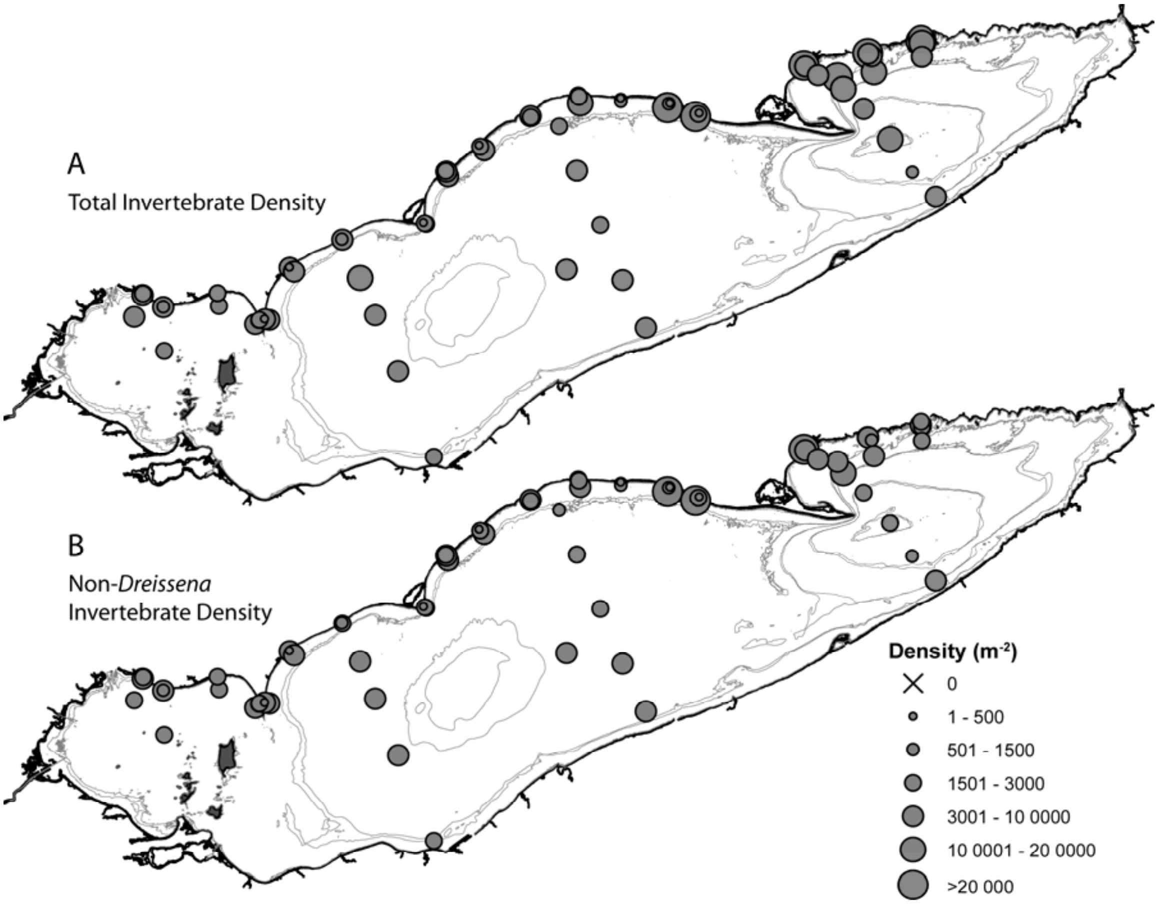

Figure 10. Distribution of A) total invertebrate and B) non-*Dreissena* invertebrate density (individuals m^{-2}) in Lake Erie, 2002.

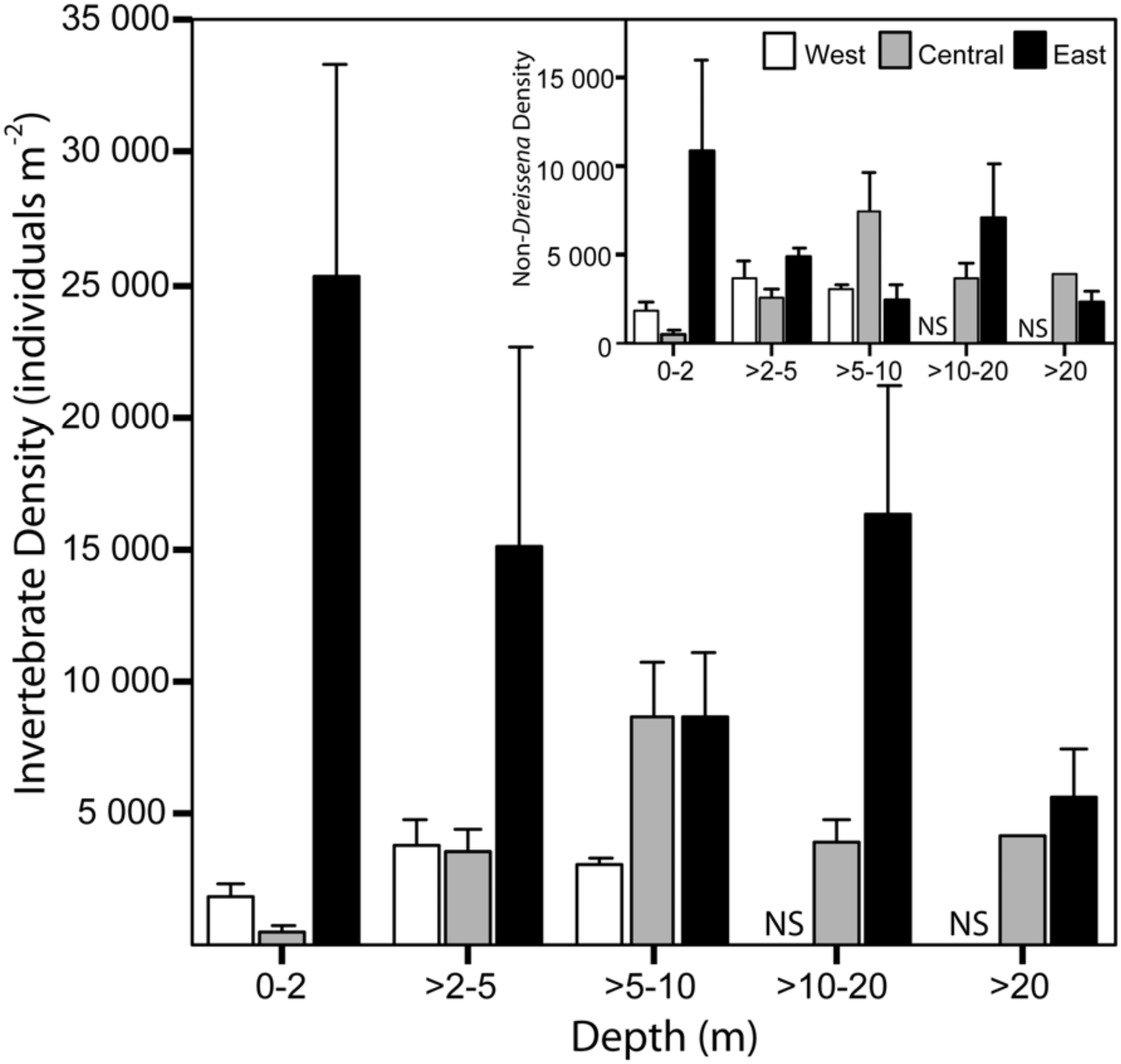

Figure 11. Mean invertebrate density (individuals m^{-2}) by basin and depth class for Lake Erie 2002 zoobenthic surveys. Inset graph shows non-*Dreissena* invertebrate density (note change in scale). Error bars indicate 1 SE. NS indicates not sampled.

Table 6. Results of non-parametric Kruskal-Wallis one-way analysis of variance on rank differences in median invertebrate density (individuals m^{-2}) by basin (west, central, east), whole-lake depth class (2m, >2-5, >5-10, >10-20, >20m), and within basin depth class for Lake Erie 2002, including Dunn's multiple comparison test. NS = not significant, *p<0.05, **p<0.01, ***p<0.001.

Taxa	Kruskal-Wallis *H*	df	*p*		Dunn's Post Test
Gastropoda					
Basin	3.17	2	0.2054	NS	
Depth Class	4.30	4	0.3670	NS	
West x Depth Class	3.85	2	0.1459	NS	
Central x Depth Class	4.50	4	0.3423	NS	
East x Depth Class	2.47	4	0.6496	NS	
Dreissena					
Basin	31.15	2	0.0000	***	East > West, Central
Depth Class	7.55	4	0.1094	NS	
West x Depth Class	1.98	2	0.3710	NS	
Central x Depth Class	9.70	4	0.0458	*	2m < 5-10m
East x Depth Class	4.39	4	0.3559	NS	
Sphaeriidae					
Basin	8.30	2	0.0157	*	West > East
Depth Class	13.24	4	0.0102	*	2m, 2-5m < 10-20m
West x Depth Class	5.83	2	0.0543	NS	
Central x Depth Class	22.80	4	0.0001	***	2m, 2-5m, 5-10m < 10-20m
East x Depth Class	3.25	4	0.5169	NS	
Amphipoda					
Basin	20.14	2	0.0000	***	East > West, Central
Depth Class	2.76	4	0.5995	NS	
West x Depth Class	0.00	2	1.0000	NS	
Central x Depth Class	3.25	4	0.5162	NS	
East x Depth Class	6.08	4	0.1930	NS	
Isopoda					
Basin	3.09	2	0.2131	NS	
Depth Class	8.14	4	0.0865	NS	
West x Depth Class	0.00	2	1.0000	NS	
Central x Depth Class	8.79	4	0.0666	NS	
East x Depth Class	4.67	4	0.3232	NS	
Ephemeroptera					
Basin	10.40	2	0.0055	**	West > Central, East
Depth Class	8.31	4	0.0809	NS	
West x Depth Class	3.54	2	0.1706	NS	
Central x Depth Class	5.59	4	0.2319	NS	
East x Depth Class	4.67	4	0.3232	NS	
Chironomidae					
Basin	4.03	2	0.1331	NS	
Depth Class	12.75	4	0.0126	*	NS
West x Depth Class	1.91	2	0.3850	NS	
Central x Depth Class	18.03	4	0.0012	**	2m < 5-10, 10-20 m
East x Depth Class	8.13	4	0.0870	NS	

(*continued*)

Table 6. Continued.

Taxa	Kruskal-Wallis *H*	df	*p*		Dunn's Post Test
Oligochaeta					
Basin	14.50	2	0.0007	***	East > West, Central
Depth Class	8.07	4	0.0891	NS	
West x Depth Class	0.33	2	0.8497	NS	
Central x Depth Class	15.06	4	0.0046	**	2m < 5-10m
East x Depth Class	5.24	4	0.2637	NS	
Total Density					
Basin	18.29	2	0.0001	***	East > West, Central
Depth Class	12.71	4	0.0128	**	2m < 5-10
West x Depth Class	4.21	2	0.1217	NS	
Central x Depth Class	21.23	4	0.0003	***	2m < 2-5, 5-10, 10-20
East x Depth Class	6.85	4	0.1440	NS	
Non-*Dreissena* Density					
Basin	3.90	2	0.1423	NS	
Depth Class	15.19	4	0.0043	**	2m < 5-10, 10-20
West x Depth Class	4.21	2	0.1217	NS	
Central x Depth Class	21.39	4	0.0003	***	2m < 5-10, 10-20
East x Depth Class	6.51	4	0.1644	NS	

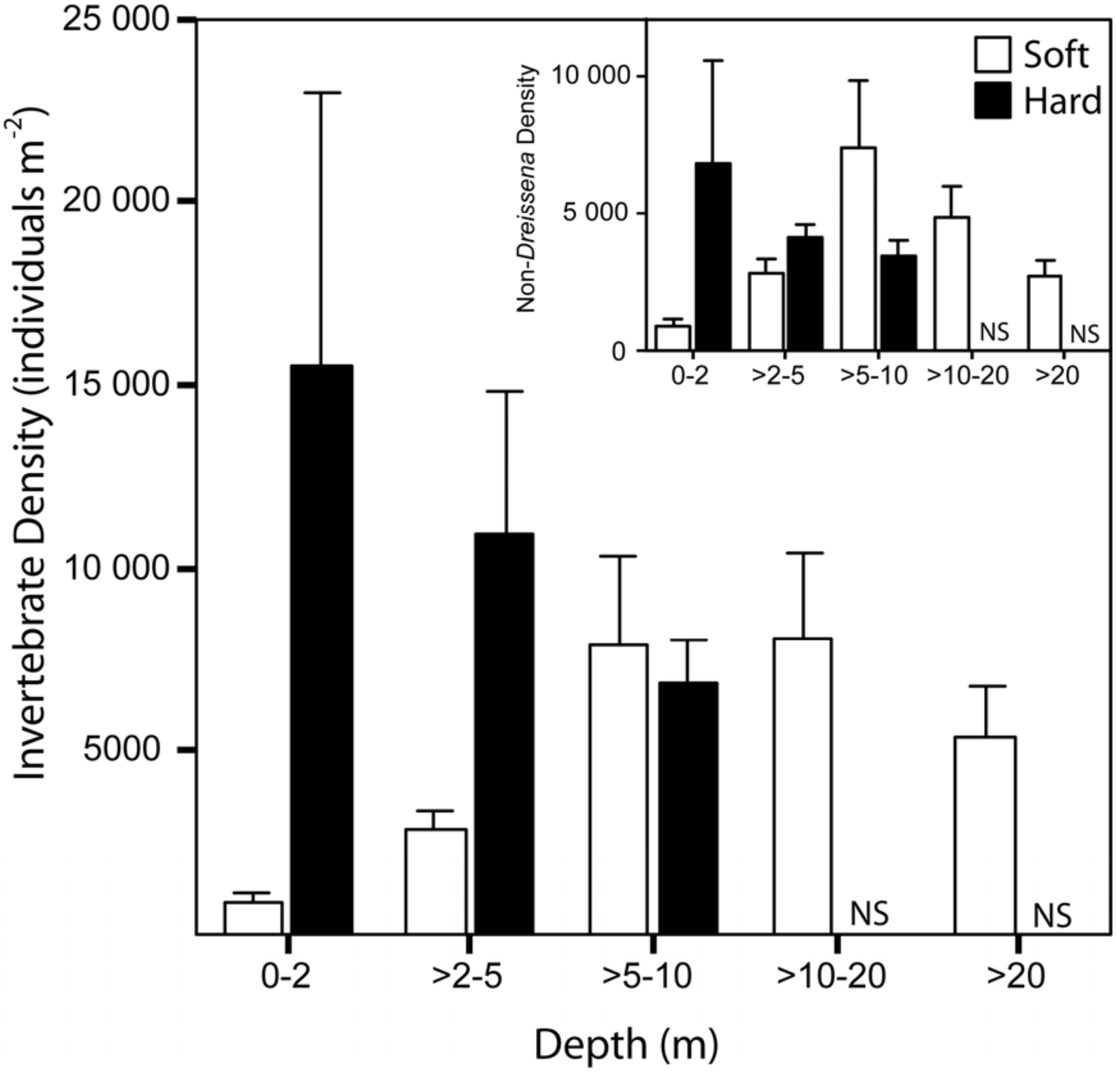

Figure 12. Mean invertebrate density (individuals m^{-2}) by depth class and substrate type for Lake Erie 2002 zoobenthic surveys. Inset graph shows non-*Dreissena* invertebrate density (note change in scale). Error bars indicate 1 SE. NS indicates not sampled.

Table 7. Non-*Dreissena* benthic invertebrate density (individuals $m^{-2} \pm SE$) for Lake Erie 2002 for *Dreissena* colonized and non-colonized sites on hard and soft substrates.

		Basin											
		West			Central			East			Total		
		N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE
No *Dreissena*	Soft	5	3173.0	682.5	22	3559.8	1280.8	·	·	·	27	3488.2	1045.9
	Hard				2	1381.3	1359.1	·	·	·	2	1381.3	1359.1
	Total	5	3173.0	682.5	24	3378.3	1181.3	·	·	·	29	3342.9	980.0
With *Dreissena*	Soft	5	3036.7	656.8	10	4080.9	873.2	8	4741.3	1666.5	23	4083.6	691.2
	Hard	1	1585.0	.	7	3898.0	514.1	9	6047.1	1962.1	17	4899.7	1081.5
	Total	6	2794.8	588.3	17	4005.6	541.9	17	5432.6	1271.8	40	4430.4	602.6
Total	Soft	10	3104.9	447.1	32	3722.6	913.8	8	4741.3	1666.5	50	3762.1	643.3
	Hard	1	1585.0	.	9	3338.8	585.1	9	6047.1	1962.1	19	4529.4	1002.9
	Total	11	2966.7	427.4	41	3638.4	721.7	17	5432.6	1271.8	69	3973.4	539.6

Table 8. Individual-based rarefaction for Lake Erie 2002 zoobenthic surveys by basin., based on mean number of individuals (n=3037) collected from west basin sites, including 95% confidence limits.

			Rarefied		
Basin	n	Number of Taxa Observed	Number of Taxa	Lower 95% Confidence Interval	Upper 95% Confidence Interval
West	11	44	42.52	40.38	44.66
Central	41	69	55.788	51.43	60.15
East	17	56	44.79	41.06	48.52

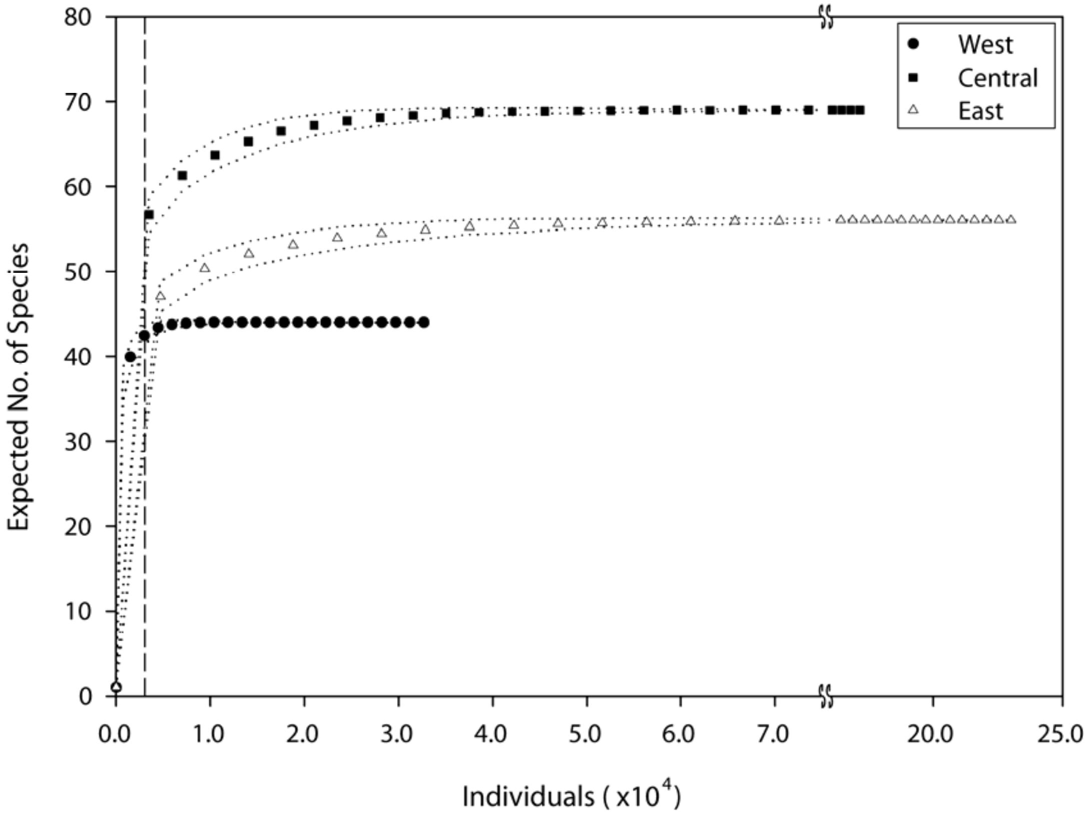

Figure 13. Individual-based rarefaction curves for Lake Erie 2002 zoobenthic surveys by basin (same data as used to generate Table 2). Symbol lines indicate expected number of species for a given sample size. Fine-dotted lines indicate 95% confidence limits. Note break in x-axis. Vertical reference line indicates sample of 3037 individuals.

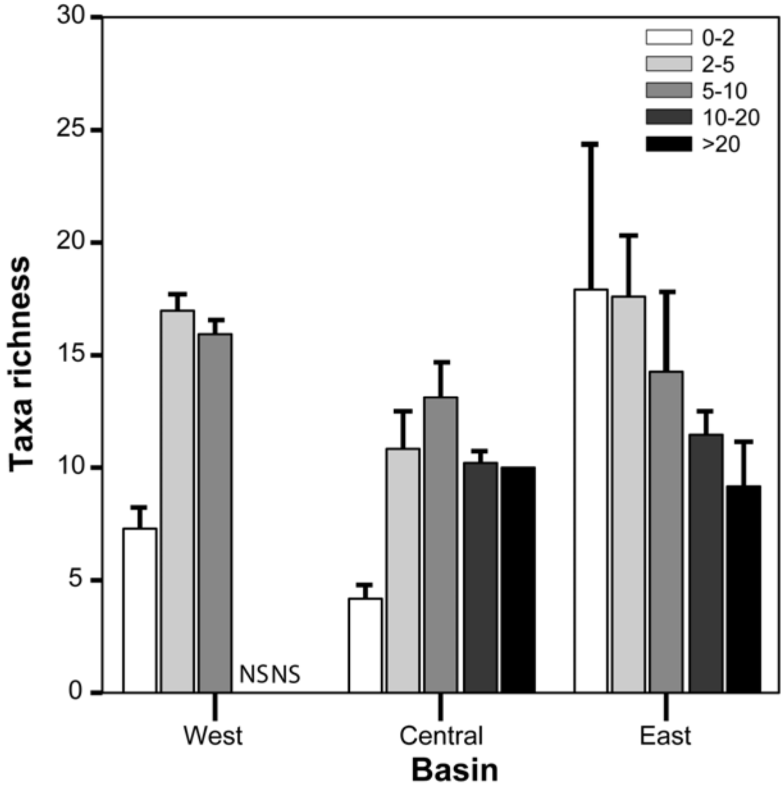

Figure 14. Taxa richness for Lake Erie depths by basin. Error bars indicate standard error of the mean. NS indicates not sampled.

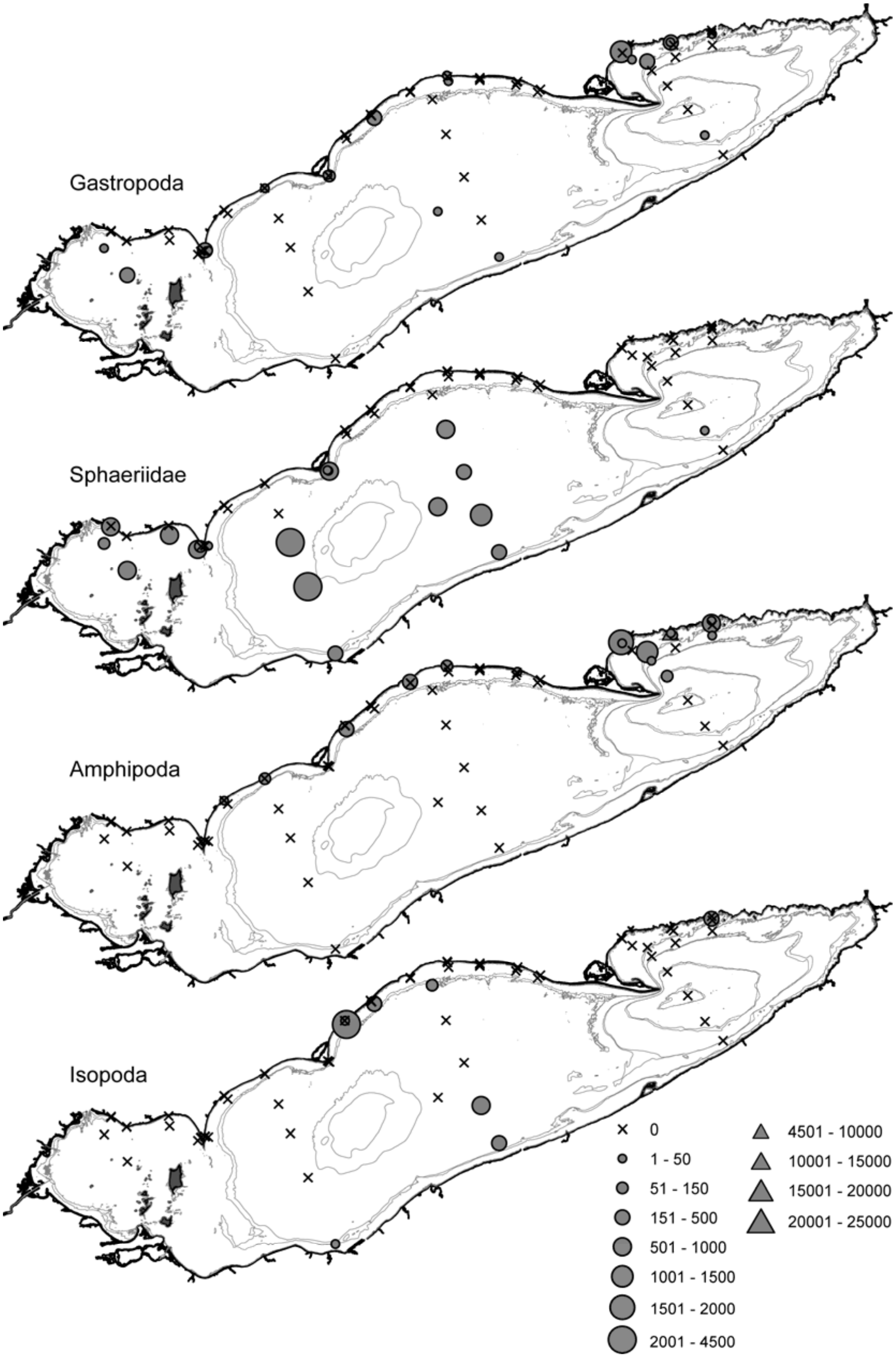

Figure 15a. Density distribution (individuals m^{-2}) of common taxa in Lake Erie, 2002.

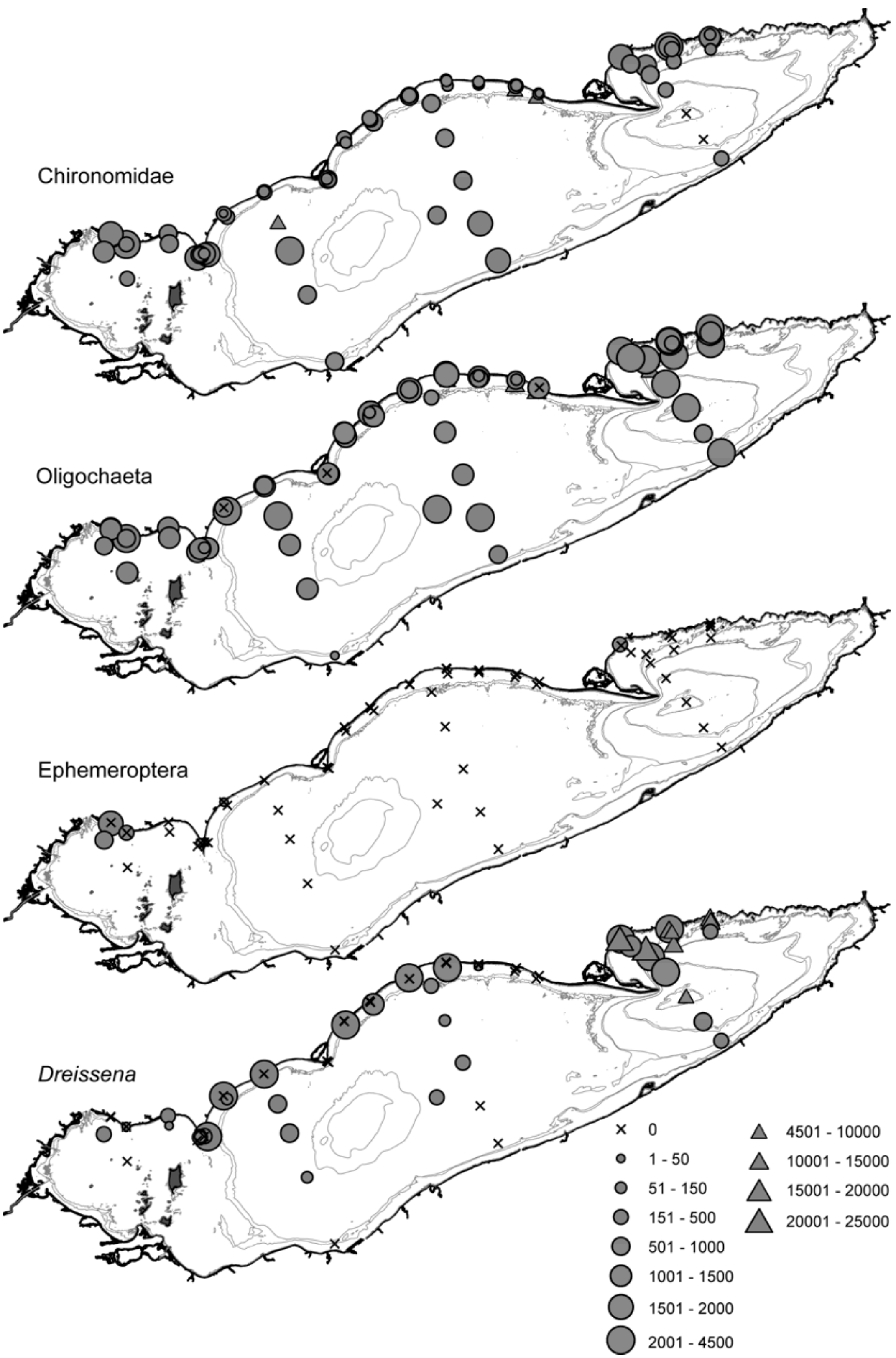

Figure 15b. Density distribution (individuals m^{-2}) of common taxa in Lake Erie, 2002.

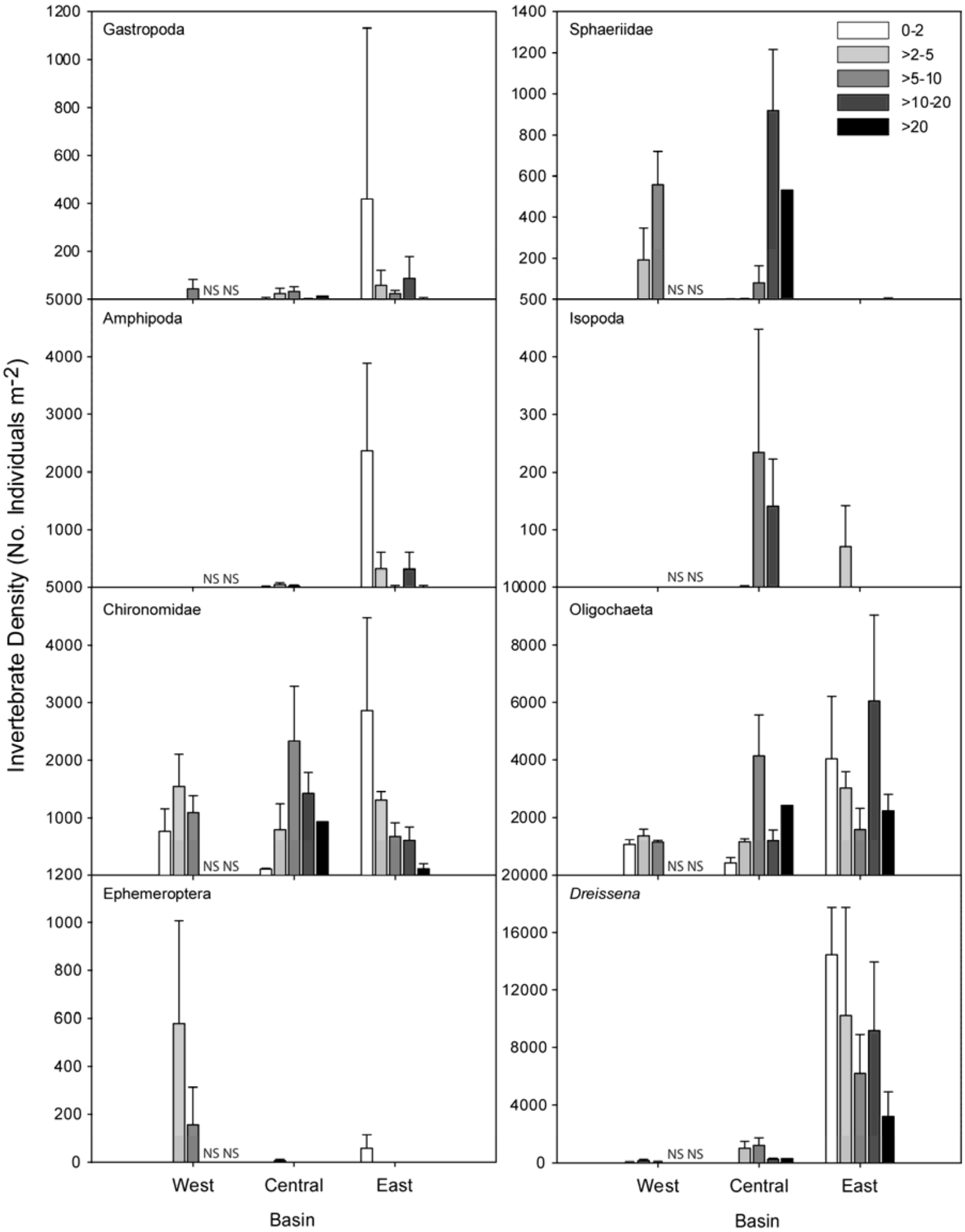

Figure 16. Lake Erie 2002 invertebrate density (individuals m^{-2}) for five depth classes by basin. No samples were collected from >10-20 m and >20 m depths in the west basin and only a single >20 m site in the central basin. Error bars indicate one SEM. NS indicates not sampled.

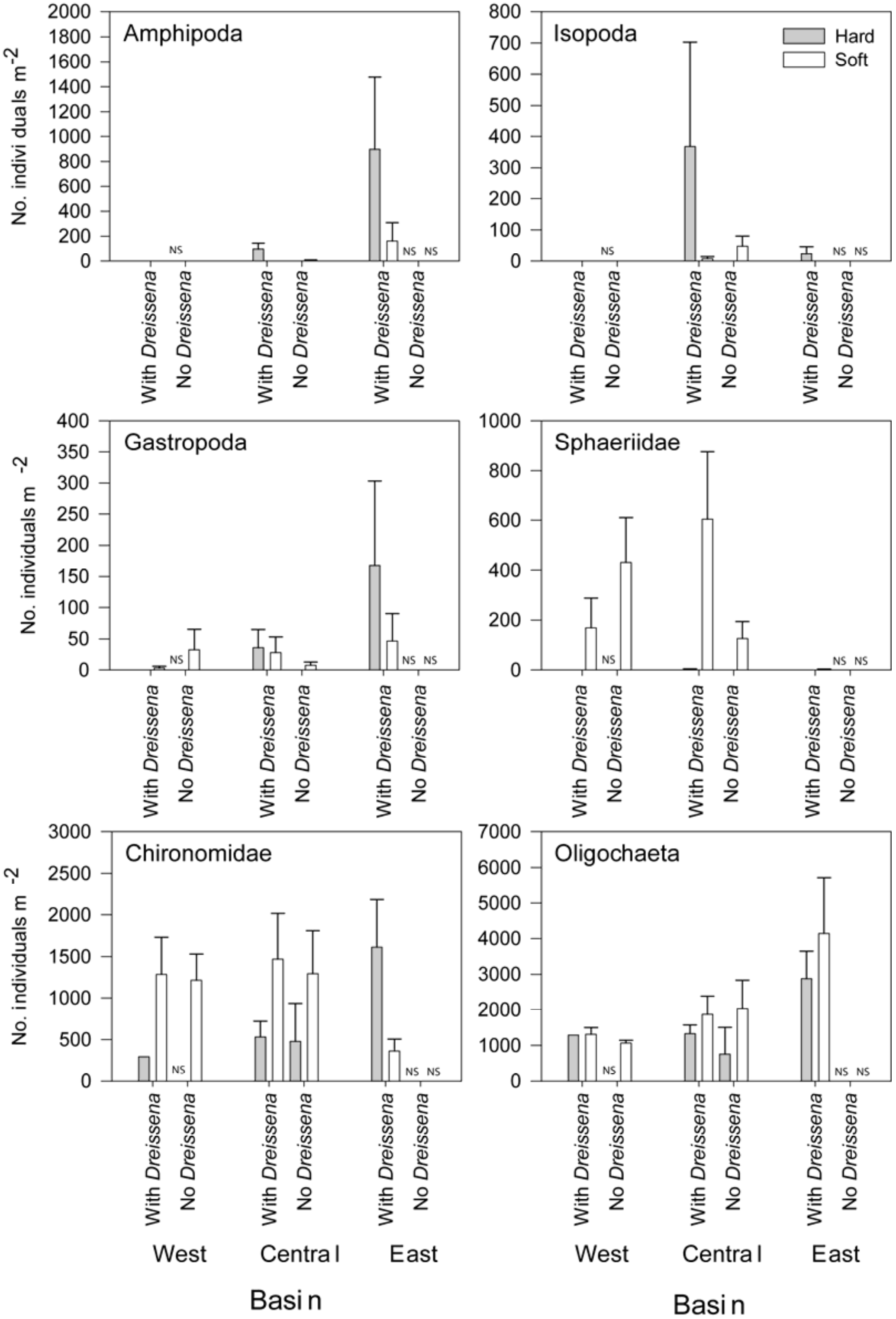

Figure 17. Mean invertebrate density for sites with and without *Dreissena* on hard (shaded bars) and soft (open bars) substrates by basin. ns indicates no sample of that description available. Error bars indicate one standard error.
NS indicates not sampled

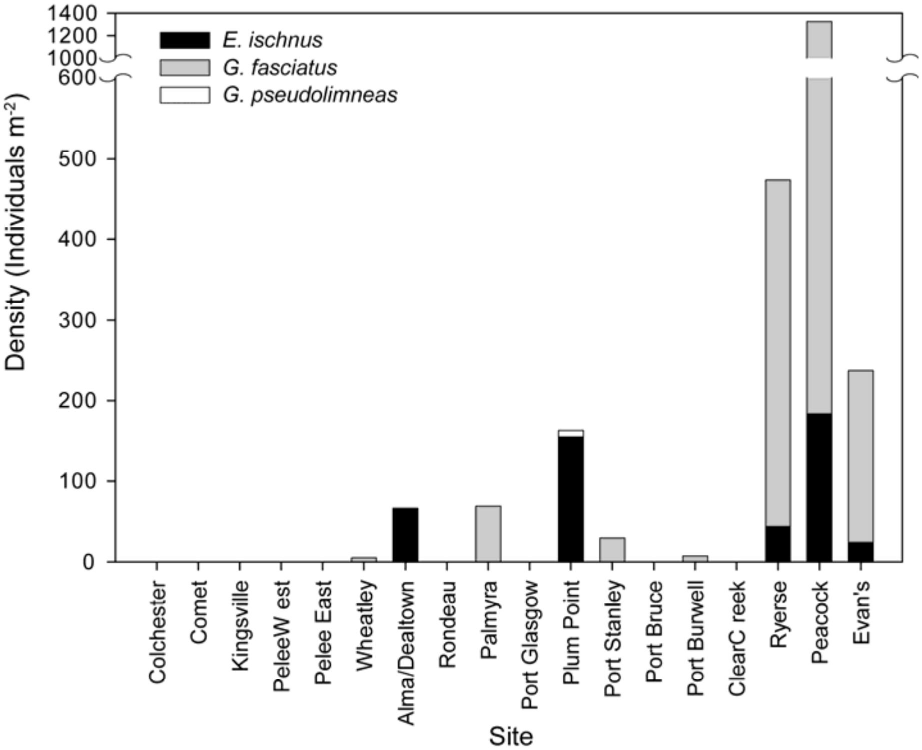

Figure 18. Density of Amphipod taxa (individuals m^{-2}) from Lake Erie 2002 Northshore transects arranged West to East.

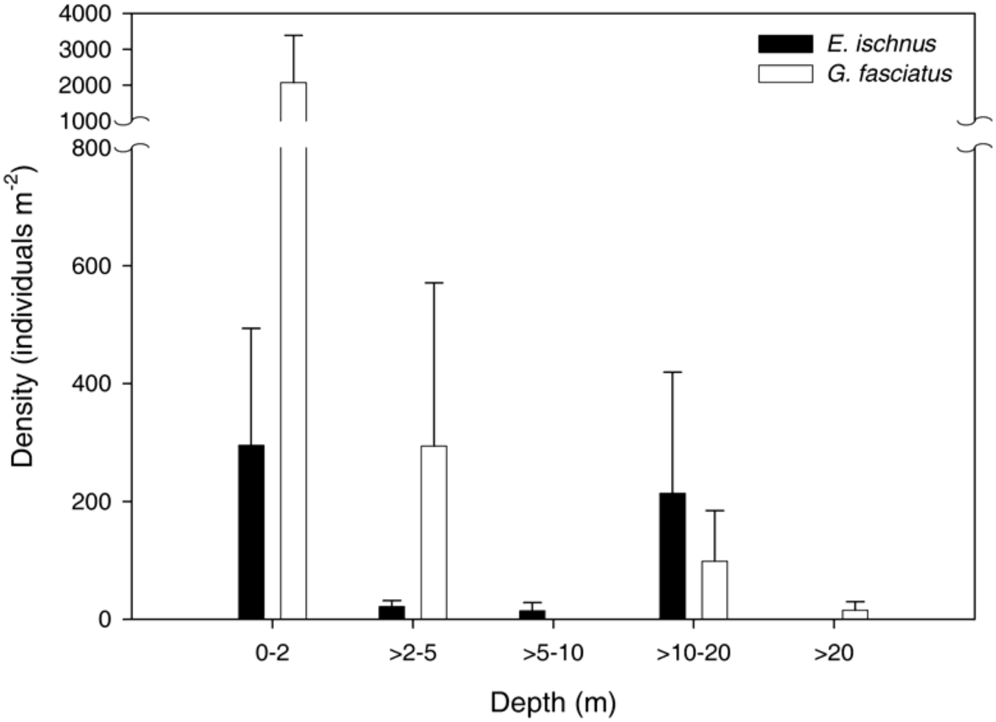

Figure 19. Density (individuals m^{-2}) of *E. ischnus* and *G. fasciatus* in the eastern basin of Lake Erie 2002, by depth. Error bars indicate 1 SE.

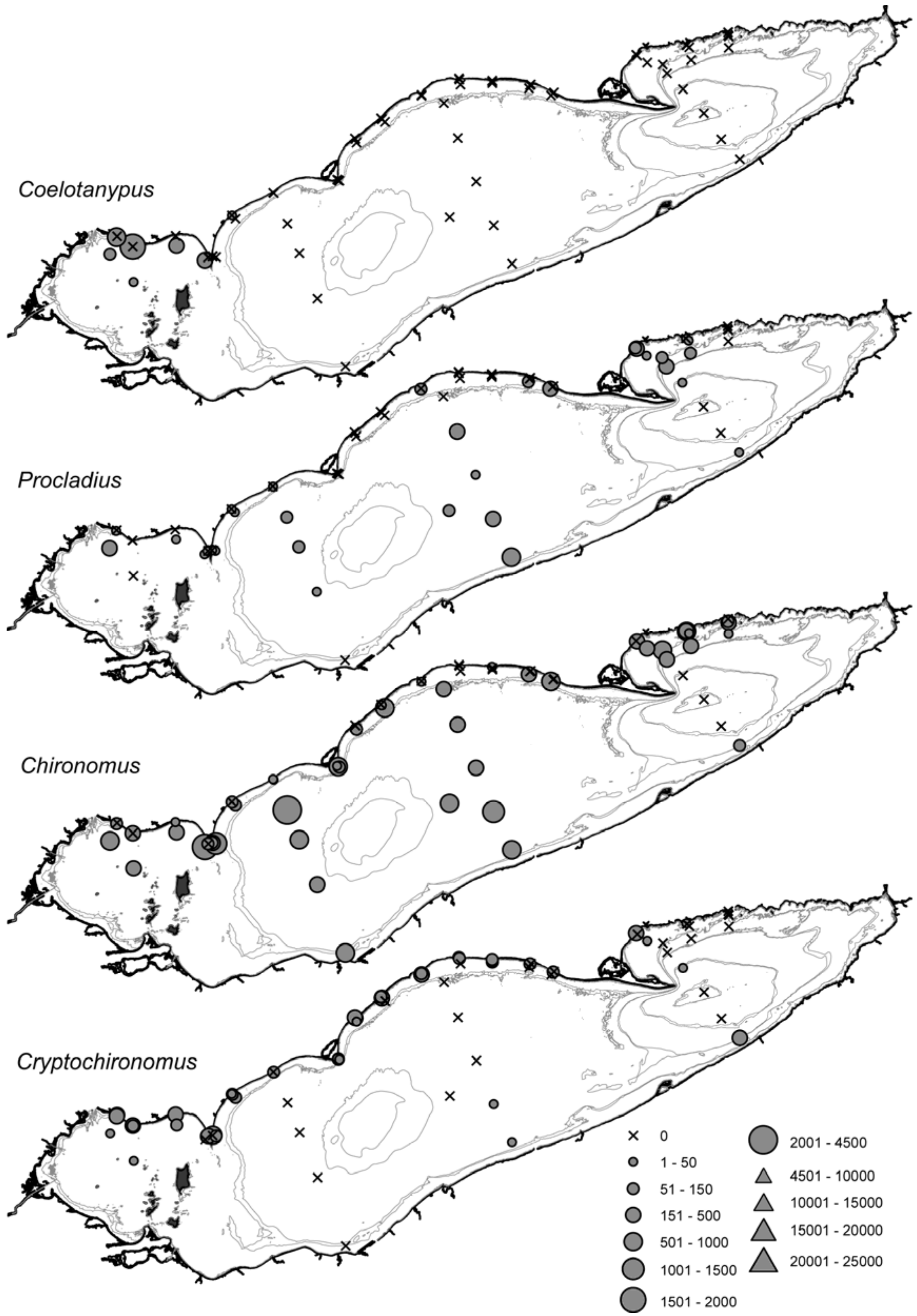

Figure 20a. Distribution of common chironomids (individuals m^{-2}) in Lake Erie, 2002.

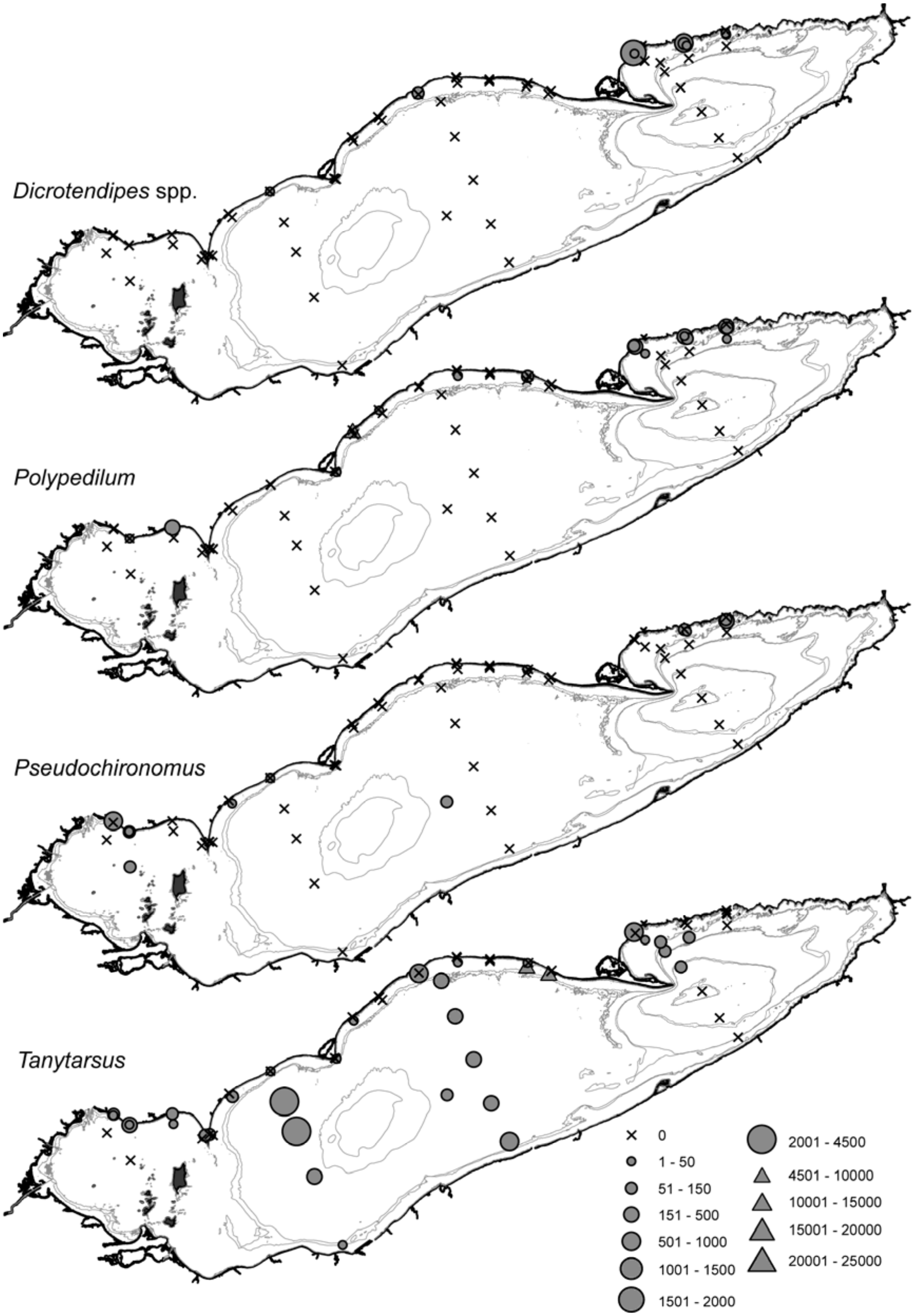

Figure 20b. Distribution of common chironomids (individuals m^{-2}) in Lake Erie, 2002.

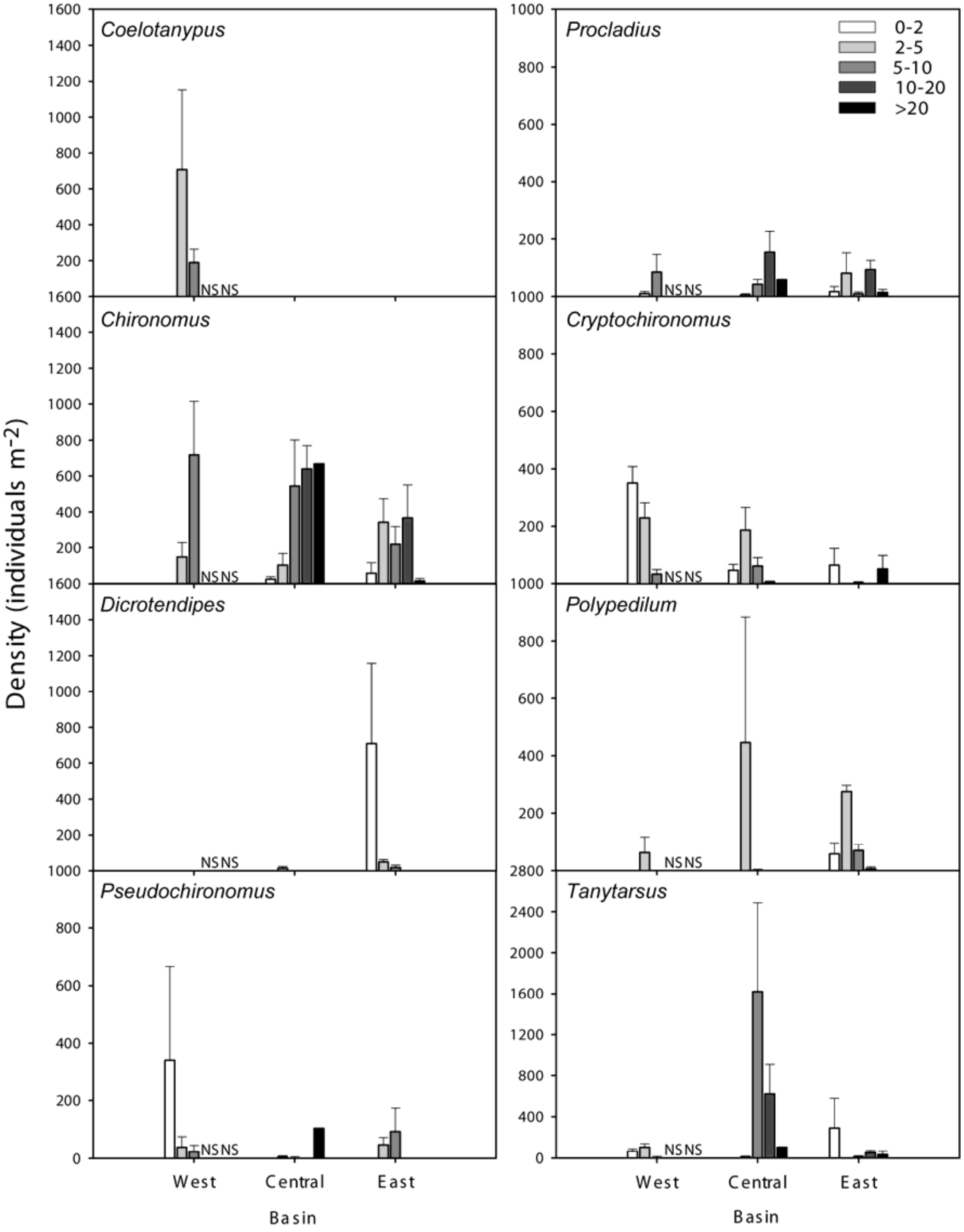

Figure 21. Chironomid density (individuals m^{-2}) for eight taxa with highest mean density for five depth classes (m) by basin in Lake Erie, 2002. No samples collected from >10-20 m and >20 m depths in the west basin and only a single >20m site in the central basin. Error bars indicate one SEM. Note different scales used. NS indicates not sampled.

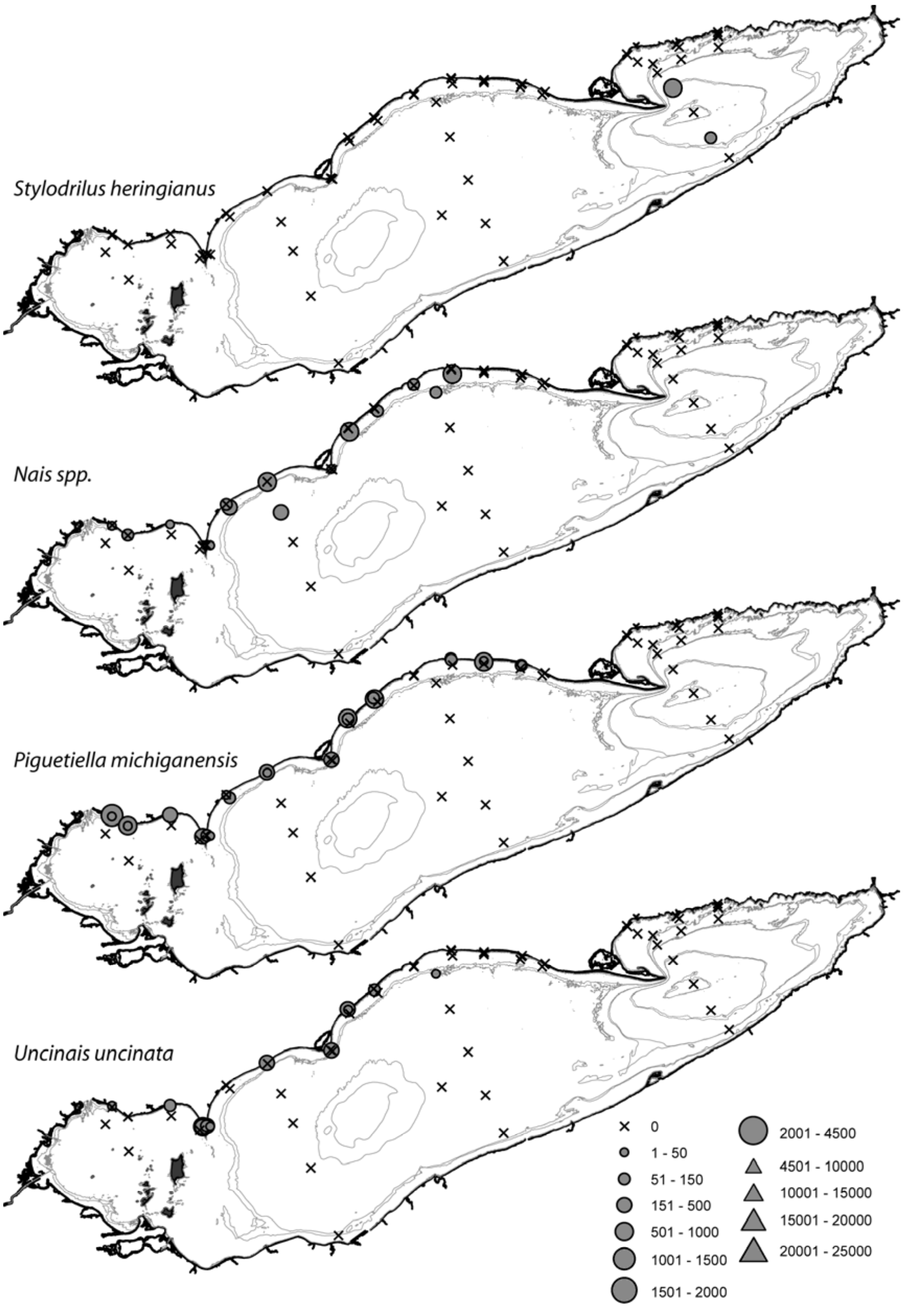

Figure 22a. Distribution of common oligochaetes (individuals m^{-2}) in Lake Erie, 2002.

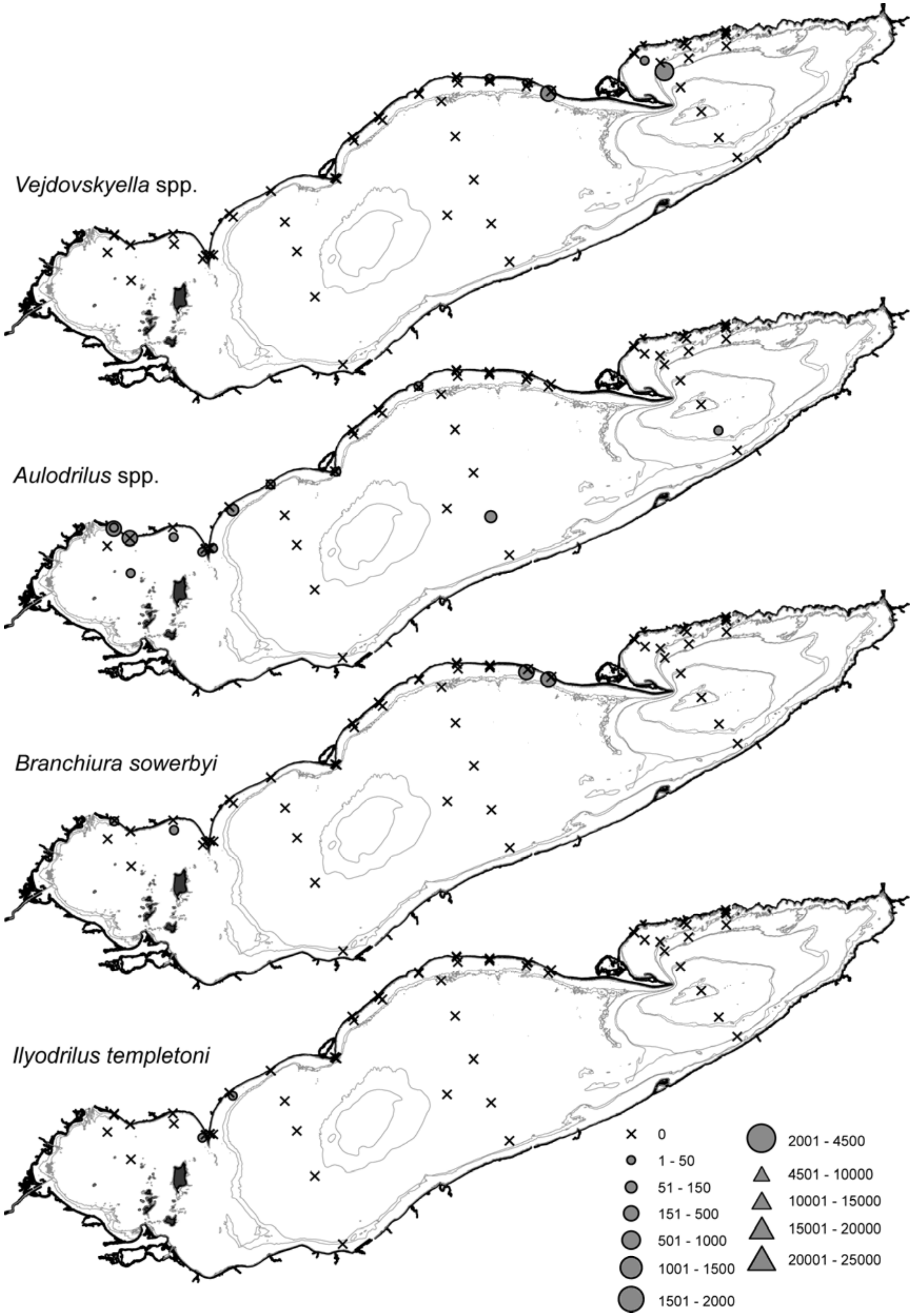

Figure 22b. Distribution of common oligochaetes (individuals m^{-2}) in Lake Erie, 2002.

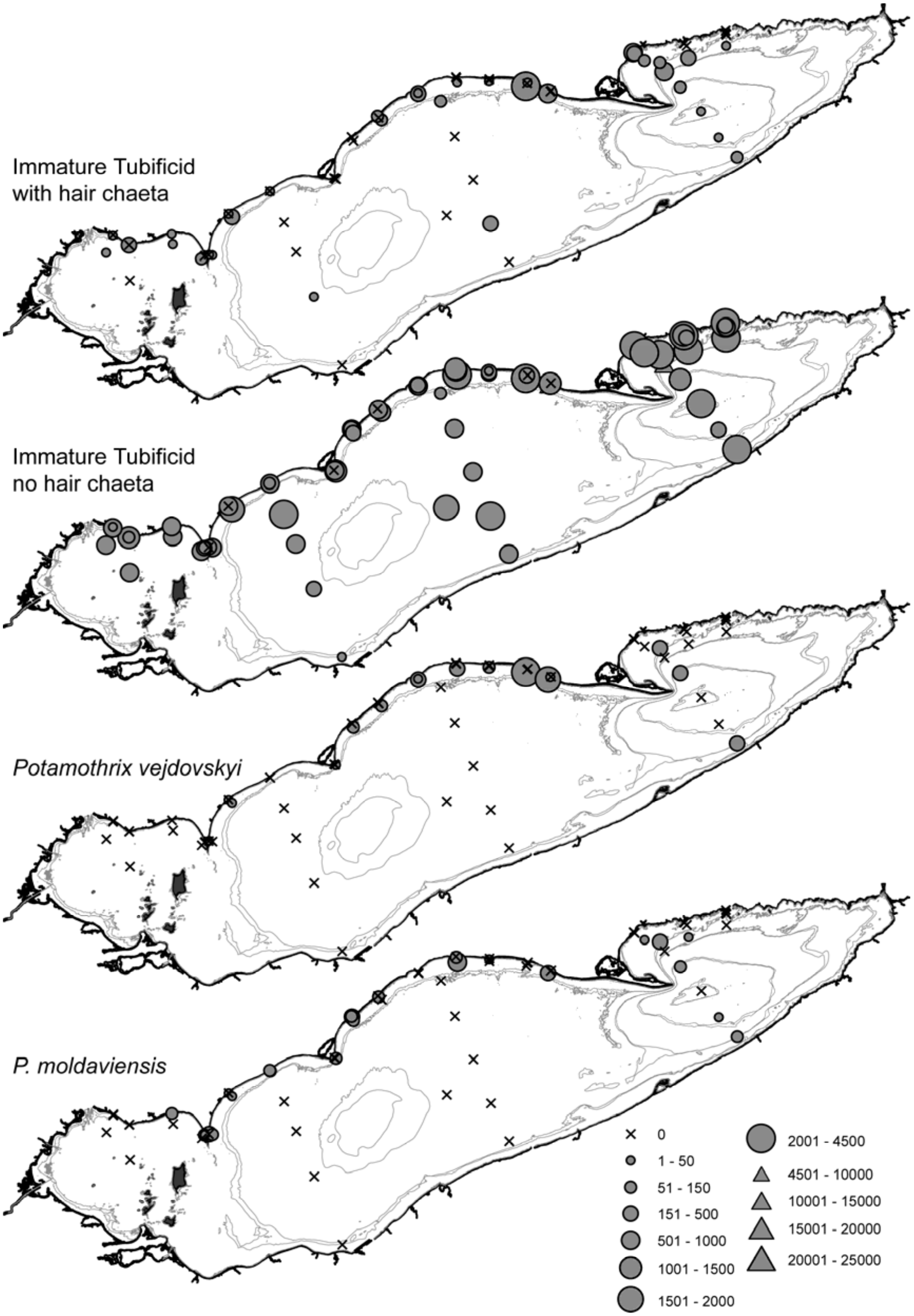

Figure 22c. Distribution of common oligochaete (individuals m^{-2}) in Lake Erie, 2002.

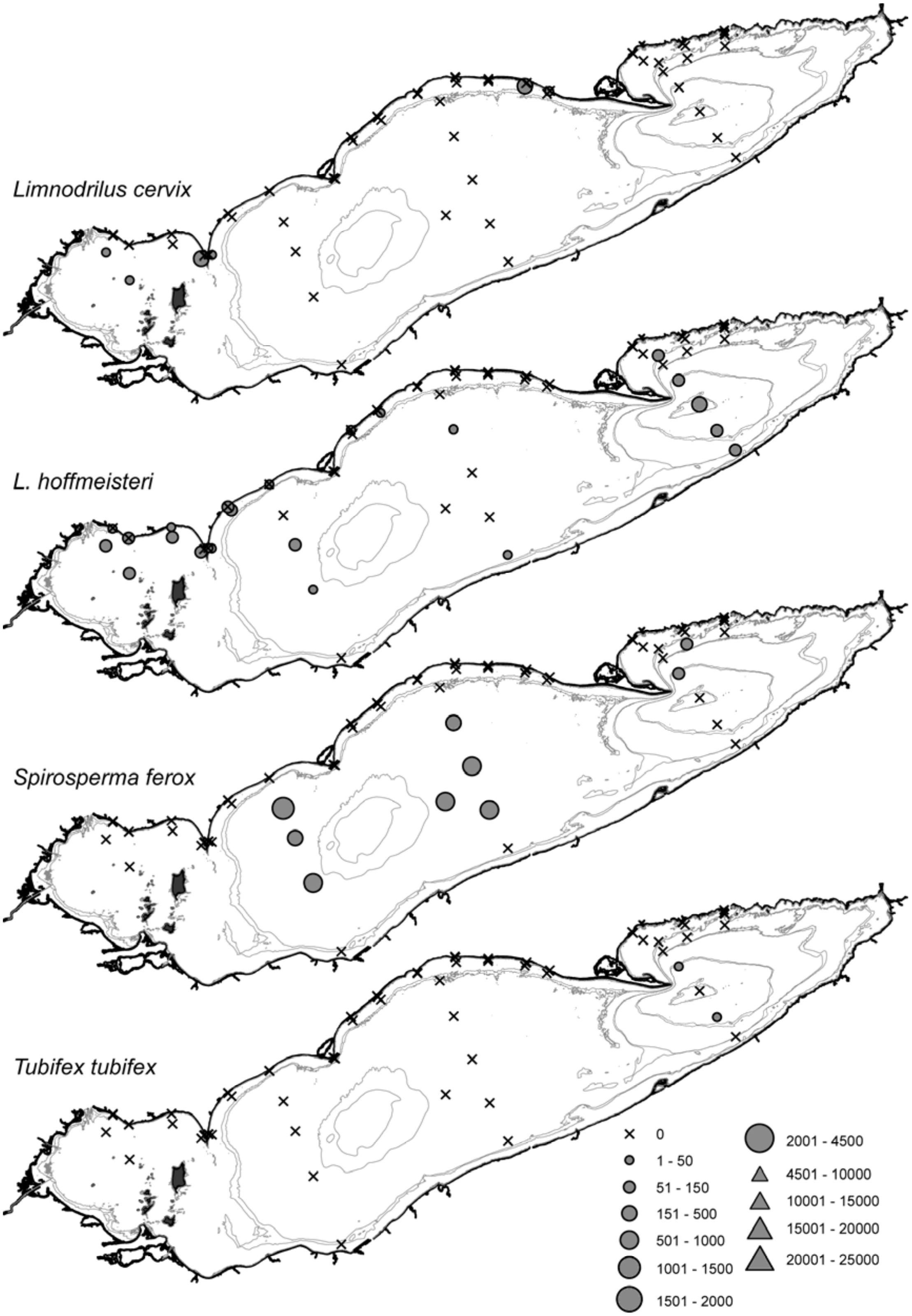

Figure 22d. Distribution of common oligochaete (individuals m^{-2}) in Lake Erie, 2002.

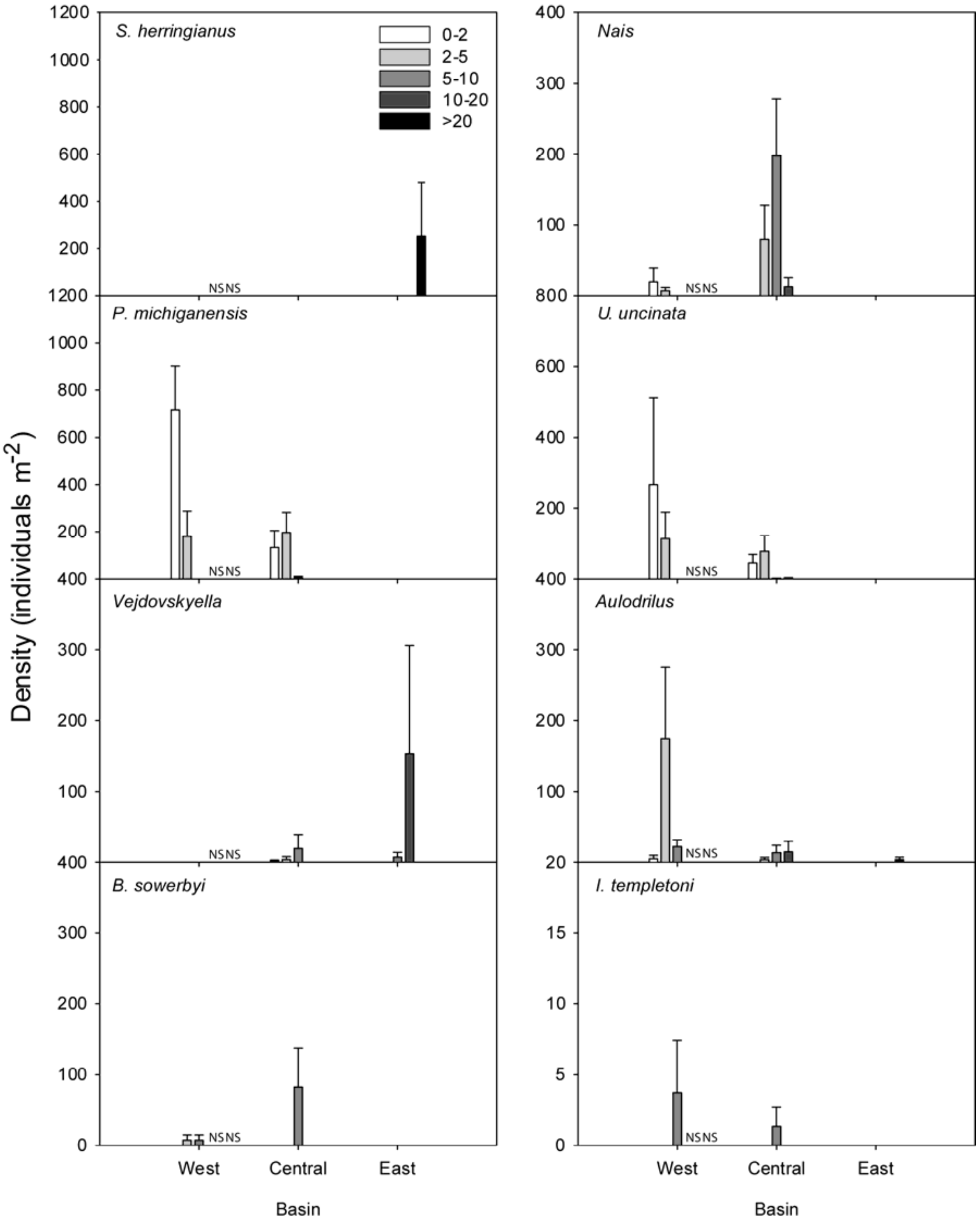

Figure 23a. Oligochaete density (individuals m^{-2}) for five depth classes (m) by basin in Lake Erie, 2002. No samples were collected from >10-20 m and >20 m depths in the west basin and only a single >20m site in the central basin. Error bars indicate one SEM. Note different scales used. NS indicates not sampled.

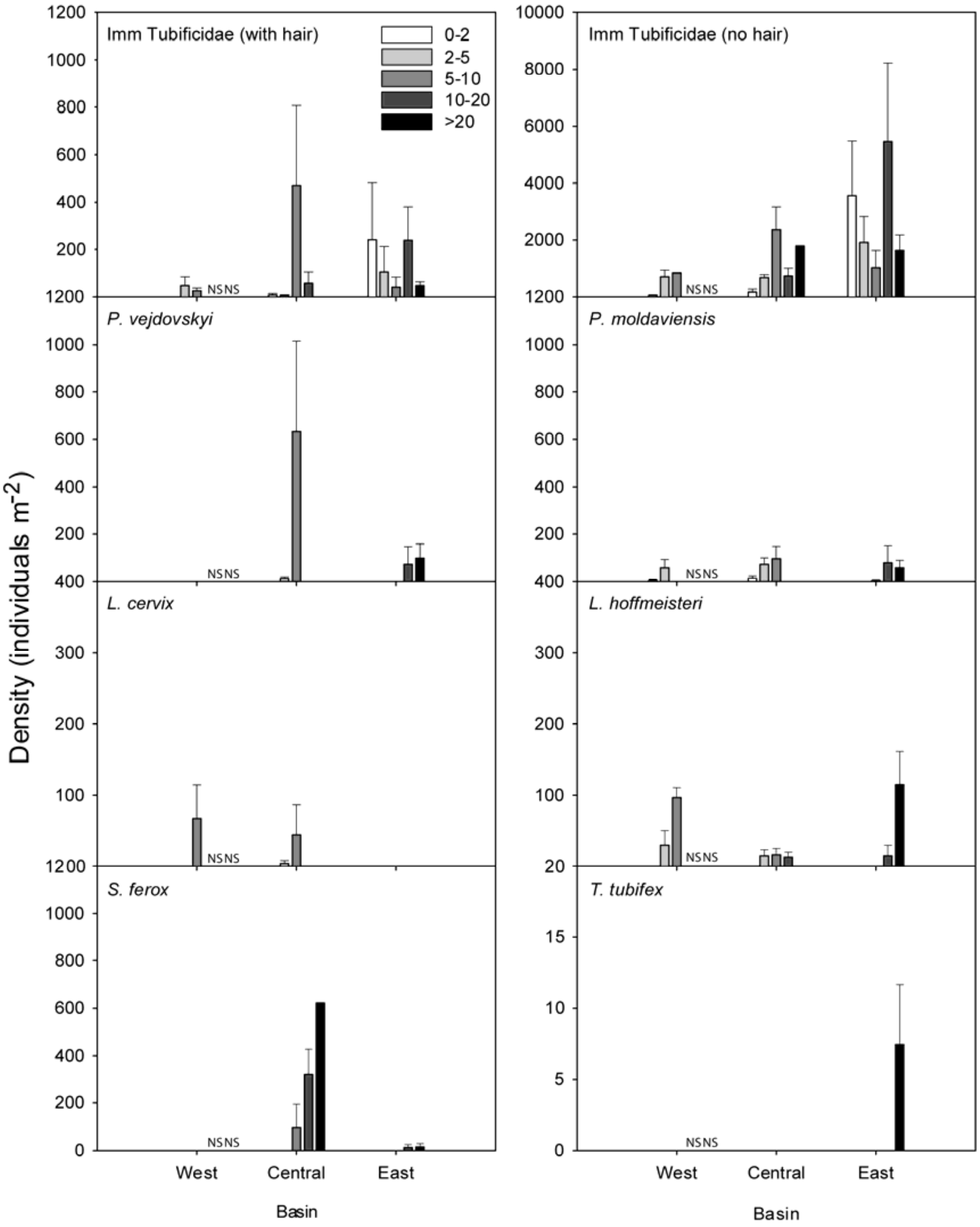

Figure 23b. Oligochaete density (individuals m^{-2}) for five depth classes (m) by basin in Lake Erie, 2002. No samples were collected from >10-20 m and >20 m depths in the west basin and only a single >20m site in the central basin. Error bars indicate one SEM. Note different scales used. NS indicates not sampled.

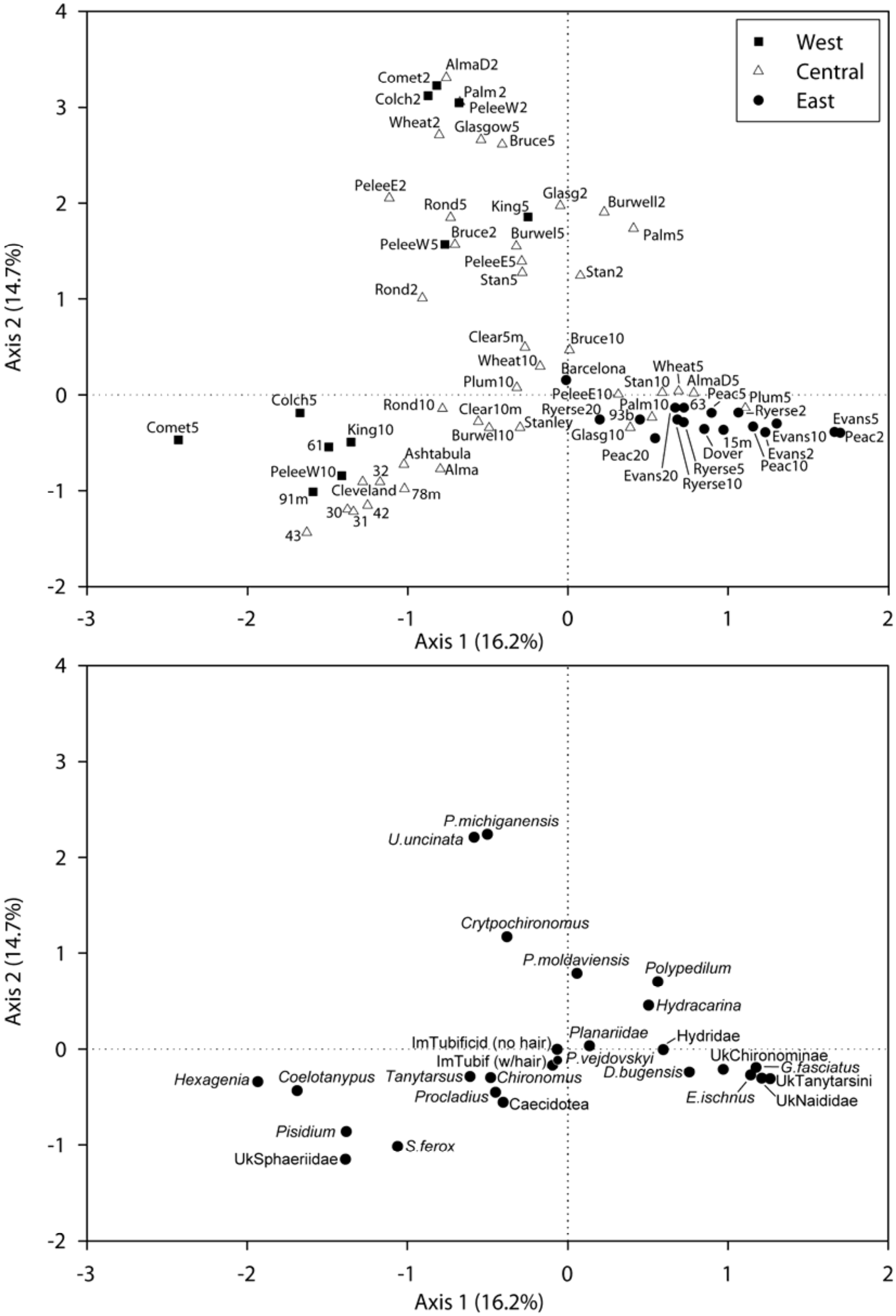

Figure 24. CA scatterplots for site- (A) and species-scores (B) based on square-root transformed, benthic invertebrate adundance for taxa comprising >0.5% total lake abundance, from Lake Erie 2002 Northshore and Guardian surveys. Percent variation accounted for by each axis in parentheses.

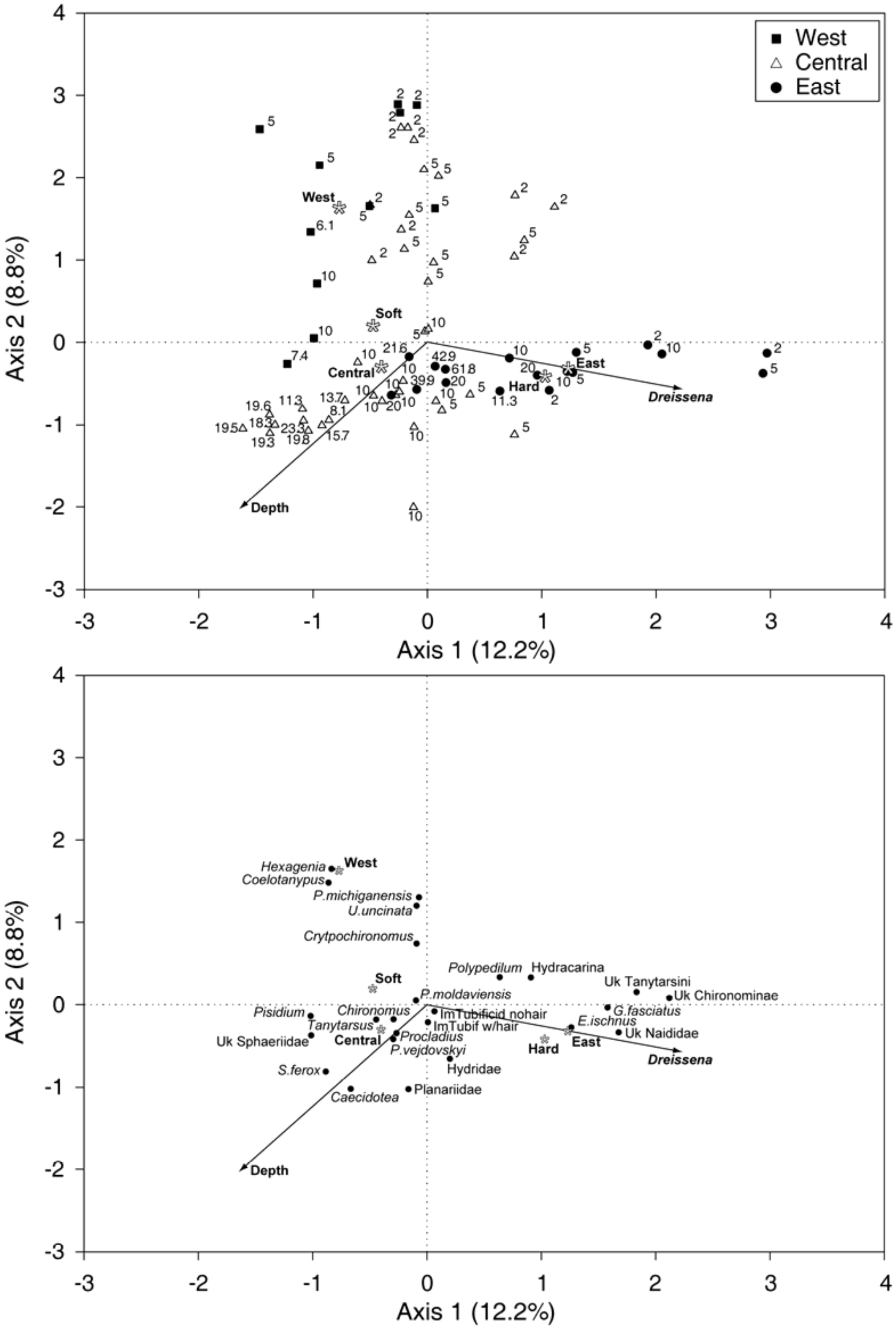

Figure 25. CCA scatterplots for weighted average site scores (A), and species scores (B) based on square-root transformed benthic invertebrate sample means for taxa comprising >0.5% total lake abundance, from Lake Erie 2002 Northshore and Guardian surveys. Percent variation accounted for by each axis in parentheses. Asterisks indicate centroids (weighted average) for nominal variables. Environmental vector scaling x3.

Table 9. Environmental variables, canonical coefficients and interset correlations of standardized variables from the first two axes of CCA. Central basin and soft substrate were used as the reference classes for CCA.

Environmental variable	Canonical coefficients		Interset correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
West	-0.229	0.425	-0.31	0.61
Central	0	0	-0.424	-0.293
East	0.574	0.303	0.717	-0.17
Depth	-0.511	-0.841	-0.506	-0.579
Hard Substrate	0.165	-0.526	0.645	-0.242
Soft Substrate	0	0	-0.645	0.242
Dreissena	0.112	-0.251	0.683	-0.167

Table 10. Statistics from canonical correspondence analysis (CCA) for eigenvalues, species-environment correlations and cumulative percent of variation explained from unconstrained and constrained axes.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.392	0.283	0.137	0.115
Species-environment correlations	0.924	0.863	0.701	0.598
Cumulative percentage variance species data (unconstrained)	12.234	21.073	25.346	28.94
Cumulative percentage variance species-environment relation (constrained)	40.335	69.478	83.568	95.417

Table 11. Mean total invertebrate and non-*Dreissena* invertebrate density (individuals m^{-2}±standard error) from Lake Erie 2002-1979 'matched' sites.

Year	Basin	Total Invertebrate Density		Non-*Dreissena* Density
		N	Mean ± Std. Error of Mean	Mean ± Std. Error of Mean
1979	West	7	1735.57 ± 251.24	·
	Central	19	5563.26 ± 681.66	·
	East	9	6996.78 ± 1035.65	·
	Total	**35**	**5166.34 ± 545.67**	·
2002	West	3	2896.00 ± 92.01	2839.21 ± 50.11
	Central	14	5723.34 ± 1386.76	5215.46 ± 1412.37
	East	11	10 280.07 ± 2338.91	4562.25 ± 1209.54
	Total	**28**	**7210.56 ± 1229.20**	**4704.24 ± 843.83**

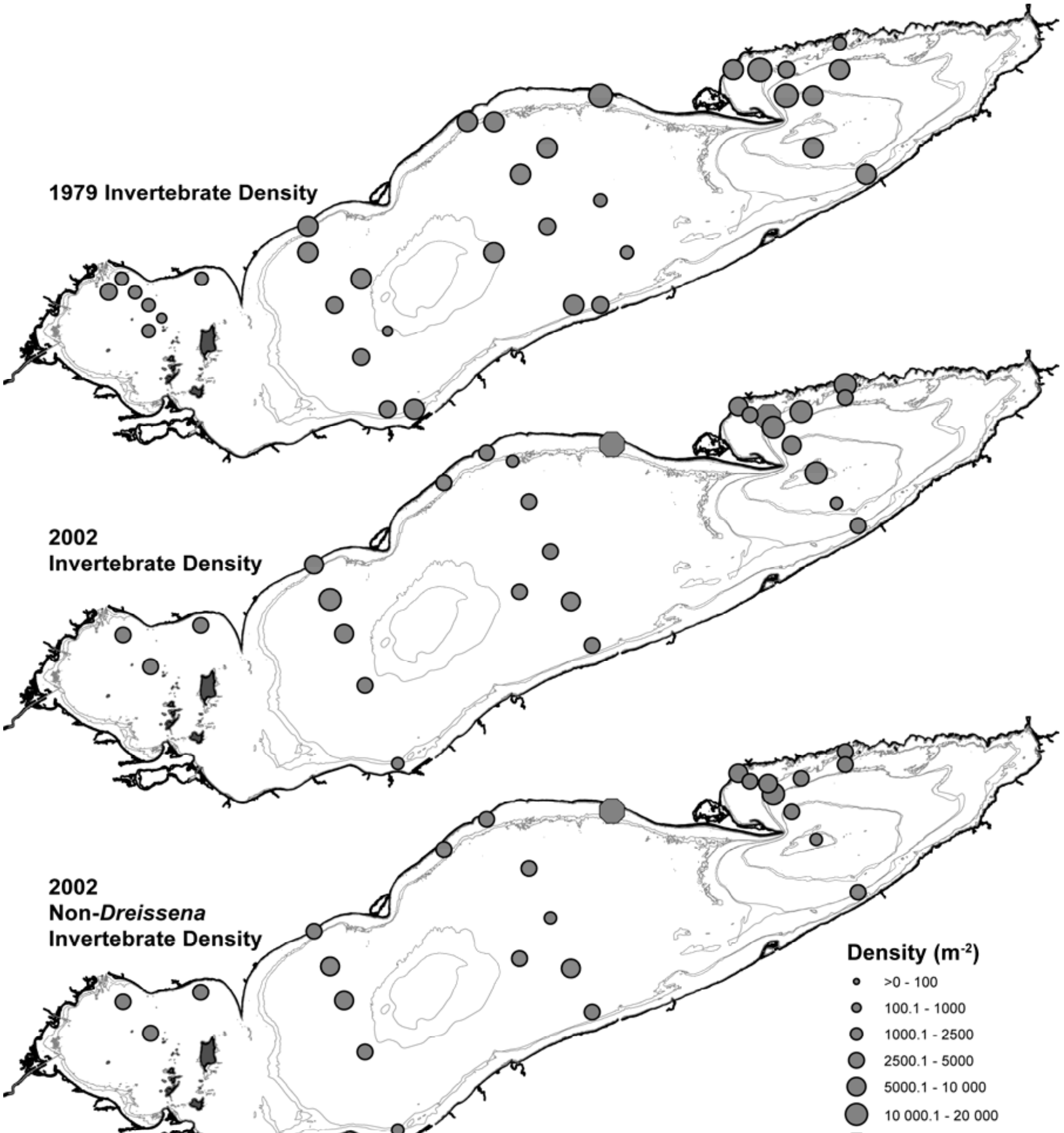

Figure 26. Distribution of bentic invertebrate density (individuals m^{-2}) in Lake Erie 1979-2002 "matched" sites. 2002 distributions are given both with *Dreissena* and excluding *Dreissena* from density calculations.

Table 12. 1979-2002 “Matched” sites benthic macroinvertebrate mean density (individuals m^{-2}±standard error) and percent contribution to total lake density. 2002 percent density given with and without *Dreissena*.

			1979 (N=35)			2002 (N=28)			
			n	Mean Density	Percent Density	n	Mean Density	Percent Density	
								w/o *Dreissena*	w *Dreissena*
Cnidaria	Hydridae	*Hydridae*				5	64.9 ± 36.2	1.4	<1
Platyhelminthes		*Platyhelminthes*	3	11.1 ± 8.0	<1	3	5.5 ± 3.0	<1	<1
Gastropoda	Bithyniidae	*Bithynia tentaculata*				2	20.1 ± 13.5	<1	<1
	Hydrobiidae	*Amnicola*	4	19.7 ± 12.2	<1	4	9.0 ± 5.6	<1	<1
	Lymnaeidae	*Stagnicola catascopium*	1	0.9 ± 0.9	<1				
	Physidae	*Physa*	1	12.9 ± 12.9	<1	1	0.5 ± 0.5	<1	<1
	Pleuroceridae	*Elimia livescens*				1	0.5 ± 0.5	<1	<1
	Valvatidae	*Valvata*	3	13.7 ± 9.2	<1	2	1.1 ± 0.7	<1	<1
	Viviparidae	*Viviparus georgianus*	1	0.9 ± 0.9	<1				
		Gastropods	6	48.0 ± 33.1	<1	10	31.2 ± 14.1	<1	<1
Bivalvia	Dreissenidae	*Dreissena bugensis*				22	2483.0 ± 854.5	52.5	34.3
		Dreissena polymorpha				8	23.3 ± 13.0	<1	<1
		Dreissena				22	2506.3 ± 852.8		34.7
Bivalvia	Sphaeriidae	Unident *Sphaeriidae*				5	95.2 ± 49.9	2.0	1.3
		Pisidium	31	715.7 ± 142.1	13.8	11	190.5 ± 59.2	4.0	2.6
		Sphaerium	19	157.7 ± 46.0	3.0	6	50.8 ± 23.7	1.1	<1
		Sphaeriidae	33	873.4 ± 151.3	16.8	12	336.5 ± 107.0	7.1	4.7
Acari	Acari	*Acari*	1	0.9 ± 0.9	<1	4	18.5 ± 12.0	<1	<1
Amphipoda	Gammaridae	*Diporiea*	10	333.4 ± 152.8	6.4				
		Echinogammarus ischnus				4	35.7 ± 27.9	<1	<1
		Total *Gammarus*	5	18.0 ± 13.8	<1	3	16.2 ± 12.0	<1	<1
		Amphipoda	13	351.4 ± 156.8	6.8	6	51.9 ± 39.6	1.1	<1
Isopoda		*Caecidotea*	11	172.3 ± 75.2	3.3	5	47.6 ± 24.4	1.0	<1
Ephemeroptera		*Hexagenia*	1	0.9 ± 0.9	<1	1	22.2 ± 20.8	<1	<1
Trichoptera		*Oecetis*	2	1.7 ± 1.2	<1	1	0.4 ± 0.4	<1	<1
Chironomidae	Diamesinae	*Monodiamesa*				2	4.3 ± 2.9	<1	<1
	Diamesinae	*Potthastia*	1	0.9 ± 0.9	<1	2	0.8 ± 0.5	<1	<1
	Chironominae Chironomini	*Chironomus*	20	141.4 ± 41.9	2.7	25	481.8 ± 99.1	10.2	6.7
		Cryptochironomus	7	36.9 ± 31.6	<1	10	27.4 ± 12.1	<1	<1
		Cryptotendipes	3	3.4 ± 2.0	<1				
		Demicryptochironomus	1	2.6 ± 2.6	<1				
		Dicrotendipes				3	3.7 ± 2.0	<1	<1
		Endochironomus	1	0.9 ± 0.9	<1				
		Hamischia grp				2	3.7 ± 3.0	<1	<1
		Microtendipes	2	4.3 ± 3.0	<1	4	9.5 ± 5.1	<1	<1
		Parachironomus				1	0.4 ± 0.4	<1	<1
		Paracladopelma	1	1.7 ± 1.7	<1	1	0.4 ± 0.4	<1	<1
		Paralauterborniella	1	0.9 ± 0.9	<1				
		Paratendipes				1	11.7 ± 11.0	<1	<1
		Phaenopsectra				1	0.4 ± 0.4	<1	<1
		Polypedilum				4	16.4 ± 10.9	<1	<1
		Pseudochirnomus				4	17.0 ± 9.4	<1	<1
		Stictochironomus				1	3.2 ± 3.0	<1	<1

(Continued)

Table 12. Continued.

			1979 (N=35)			2002 (N=28)			
			n	Mean Density	Percent Density	n	Mean Density	Percent Density	
								w/o Dreissena	w Dreissena
	Chironominae Tanytarsini	Unident Tanytarsini				4	10.2 ± 5.1	<1	<1
		Cladotanytarsus	1	16.3 ± 16.3	<1				
		Rheotanytarsus				1	2.1 ± 2.0	<1	<1
		Tanytarsus	12	22.3 ± 7.4	<1	19	574.8 ± 264.5	12.2	7.9
	Chironominae	Unident Chironominae				2	5.7 ± 4.3	<1	<1
	Orthocladiinae	*Epoicocladius*				1	1.1 ± 1.0	<1	<1
		Heterotrissocladius				1	4.2 ± 4.0	<1	<1
		Psectrocladius				2	4.9 ± 4.3	<1	<1
		Unident Orthocladiinae	1	1.7 ± 1.7	<1				
	Tanypodinae	*Ablabesmyia*				2	2.4 ± 1.8	<1	<1
		Coelotanypus	5	36.9 ± 17.9	<1	3	18.0 ± 12.5	<1	<1
		Paramerina				4	4.2 ± 2.2	<1	<1
		Procladius	16	126.9 ± 49.7	2.4	20	89.8 ± 22.8	1.9	1.2
		Unident Tanypodinae	2	6.0 ± 5.2	<1				
		Chironomidae	32	402.9 ± 101.6	7.7	26	1298.1 ± 304.3	27.5	18.0
Oligochaeta	Lumbriculidae	Unident Lumbriculidae				2	17.9 ± 15.4	<1	<1
		Lumbriculus	1	0.9 ± 0.9	<1				
		Stylodrilus herringianus	11	246.2 ± 93.1	4.7	2	36.0 ± 31.2	<1	<1
	Naididae	Unident Naididae				4	71.8 ± 38.0	1.5	<1
		Arcteonais lomondi	3	36.0 ± 24.0	<1				
		Chaetogaster diastrophus	1	6.0 ± 6.0	<1				
		Dero				1	9.5 ± 8.9	<1	<1
		Nais	2	9.4 ± 6.8	<1	4	39.1 ± 21.2	<1	<1
		Ophidonais serpentina	2	8.6 ± 7.7	<1	1	0.5 ± 0.5	<1	<1
		Piguetiella michiganensis				1	0.5 ± 0.5	<1	<1
		Pristina	1	1.5 ± 1.5	<1				
		Slavina nikalsky	1	3.4 ± 3.4	<1				
		Stylaria lacustris	2	6.9 ± 4.9	<1	2	10.6 ± 6.9	<1	<1
		Uncinais uncinata				1	0.5 ± 0.5	<1	<1
		Vejdovskyella	2	15.4 ± 12.4	<1	2	22.6 ± 20.4	<1	<1
	Tubificidae	*Aulodrilus*	15	116.4 ± 36.1	2.2	5	7.4 ± 4.2	<1	<1
		Branchiura sowerbyi	3	6.2 ± 3.9	<1	2	17.5 ± 15.3	<1	<1
		Ilyodrilus templetoni	1	3.4 ± 3.4	<1				
		Imm Tubificid with hair	20	386.0 ± 110.7	7.4	19	228.4 ± 126.1	4.8	3.2
		Imm Tubificid no hair	34	1550.7 ± 250.2	29.8	28	1930.0 ± 453.5	40.8	26.7
		Isochaetides freyi	1	6.0 ± 6.0	<1				
		Potamothrix vejdovskyi	11	125.2 ± 41.8	2.4	6	180.6 ± 135.8	3.8	2.5
		Potamothrix moldaviensis	9	86.2 ± 40.7	1.7	7	23.0 ± 11.1	<1	<1
		Quistadrilus	5	37.6 ± 19.1	<1				
		Limnodrilus	23	164.0 ± 40.2	3.2	15	53.4 ± 17.6	1.1	<1
		Spirosperma ferox	17	275.6 ± 106.8	5.3	9	155.8 ± 51.8	3.3	2.2
		Tubifex tubifex	6	51.0 ± 24.7	<1	2	1.1 ± 0.7	<1	<1
		Oligochaeta	34	3142.6 ± 408.7	60.4	28	2806.3 ± 608.5	59.4	38.8
Polychaeta	Sabellidae	*Manyunkia speciosa*	7	126.9 ± 70.4	2.4				
Hirudinea	Erpobdellidae	*Erpobdella punctata*	1	0.9 ± 0.9	<1				
Hirudinea	Glossiphoniidae	*Helobdella*	13	33.4 ± 11.1	<1	6	21.2 ± 9.4	<1	<1
		Invertebrate Density		5166.3 ± 545.7			7210.6 ± 1229.2		
		Total No. Taxa		54			63		

Table 13. Individual-based rarefaction for Lake Erie "matched" zoobenthic surveys of Lake Erie in 1979 and 2002, based on mean number of non-*Dreissena* individuals (n=4704) collected in 2002, including 95% confidence intervals.

			Rarefied		
Year	n	Number of Taxa Observed	Estimated Number of Taxa	Lower 95% Confidence Limit	Upper 95% Confidence Limit
1979	35	54	48.8	45.2	52.4
2002	28	63	53.2	49.4	57.0
2002 (*Dreissena* Omitted)	28	61	53.4	49.7	57.0

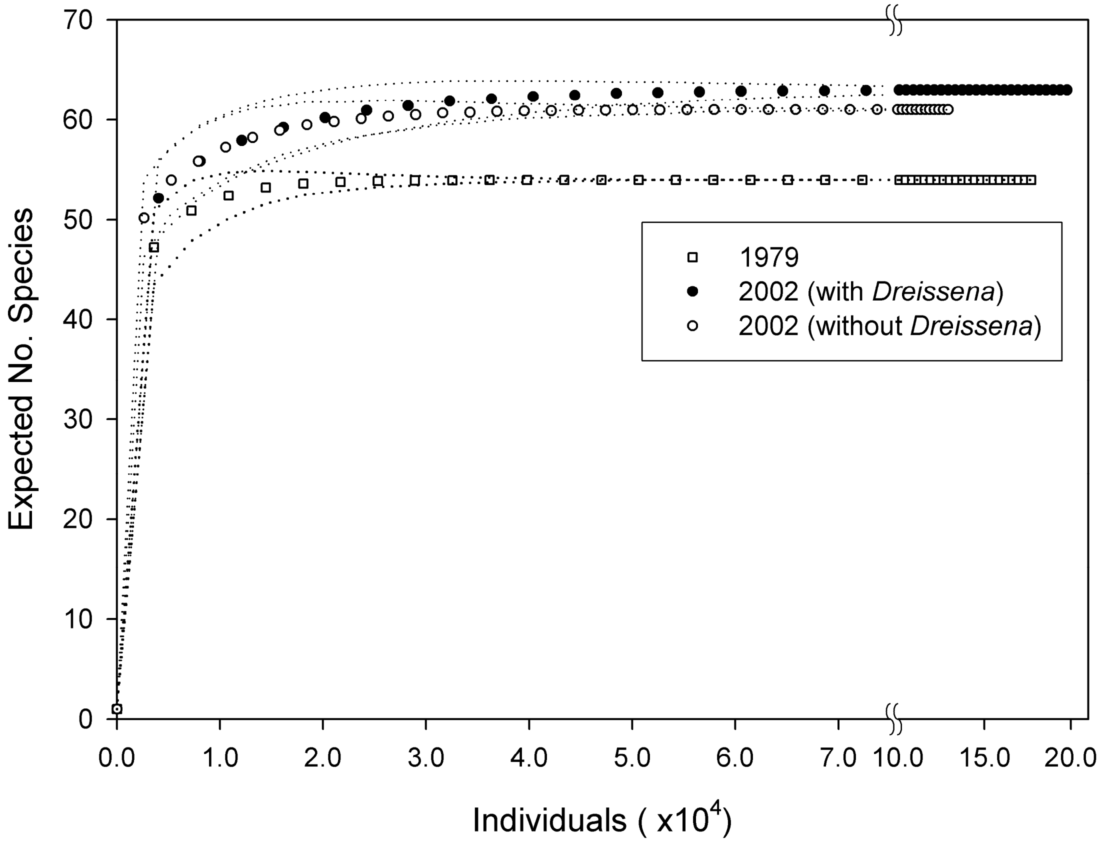

Figure 27. Individual-based rarefaction curves for Lake Erie in 1979 and 2002 based on "matched" zoobenthic data. Symbol lines indicate expected number of species for a given sample size. 2002 data presented with-*Dreissena* (solid circle) and *Dreissena*-omitted (open circle). Fine-dotted lines indicate 95% confidence limits.

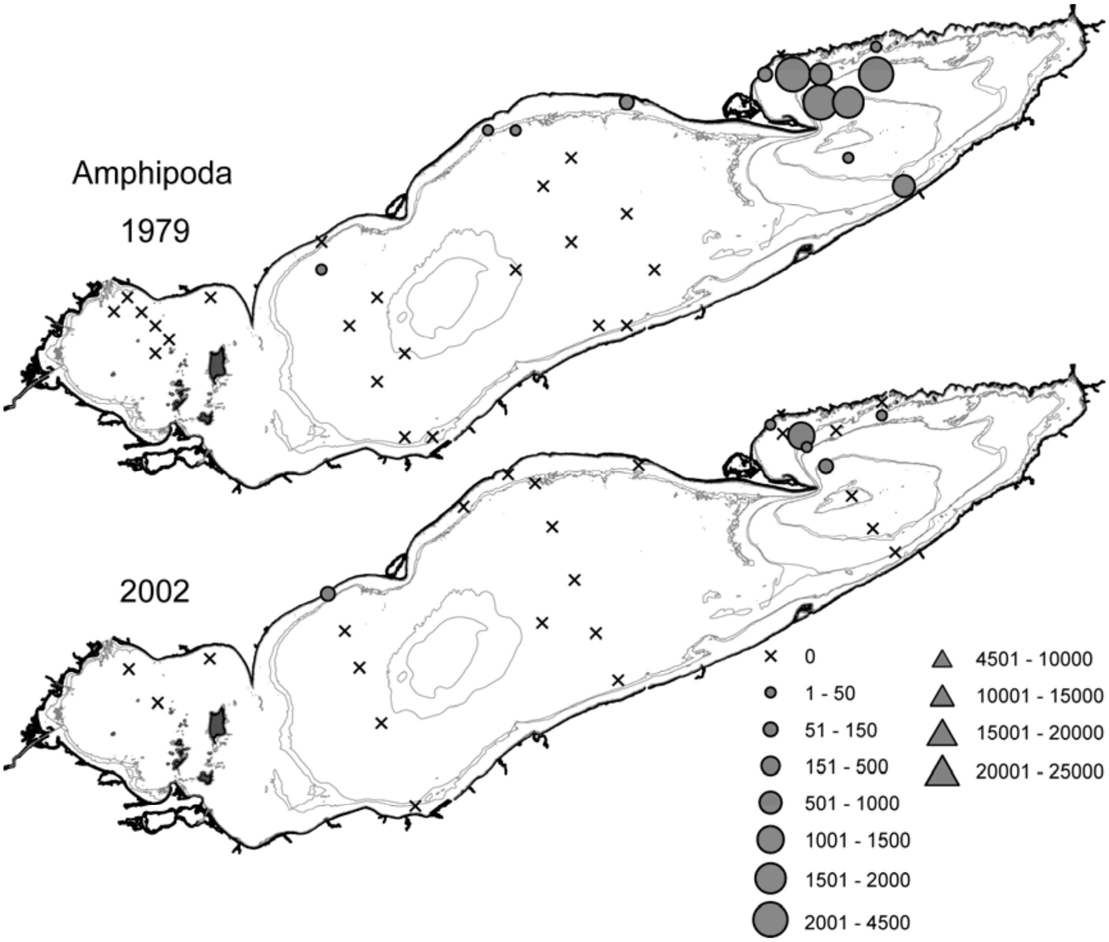

Figure 28. Distribution (individuals m^{-2}) of Amphipoda for Lake Erie 1979-2002 “matched” sites.

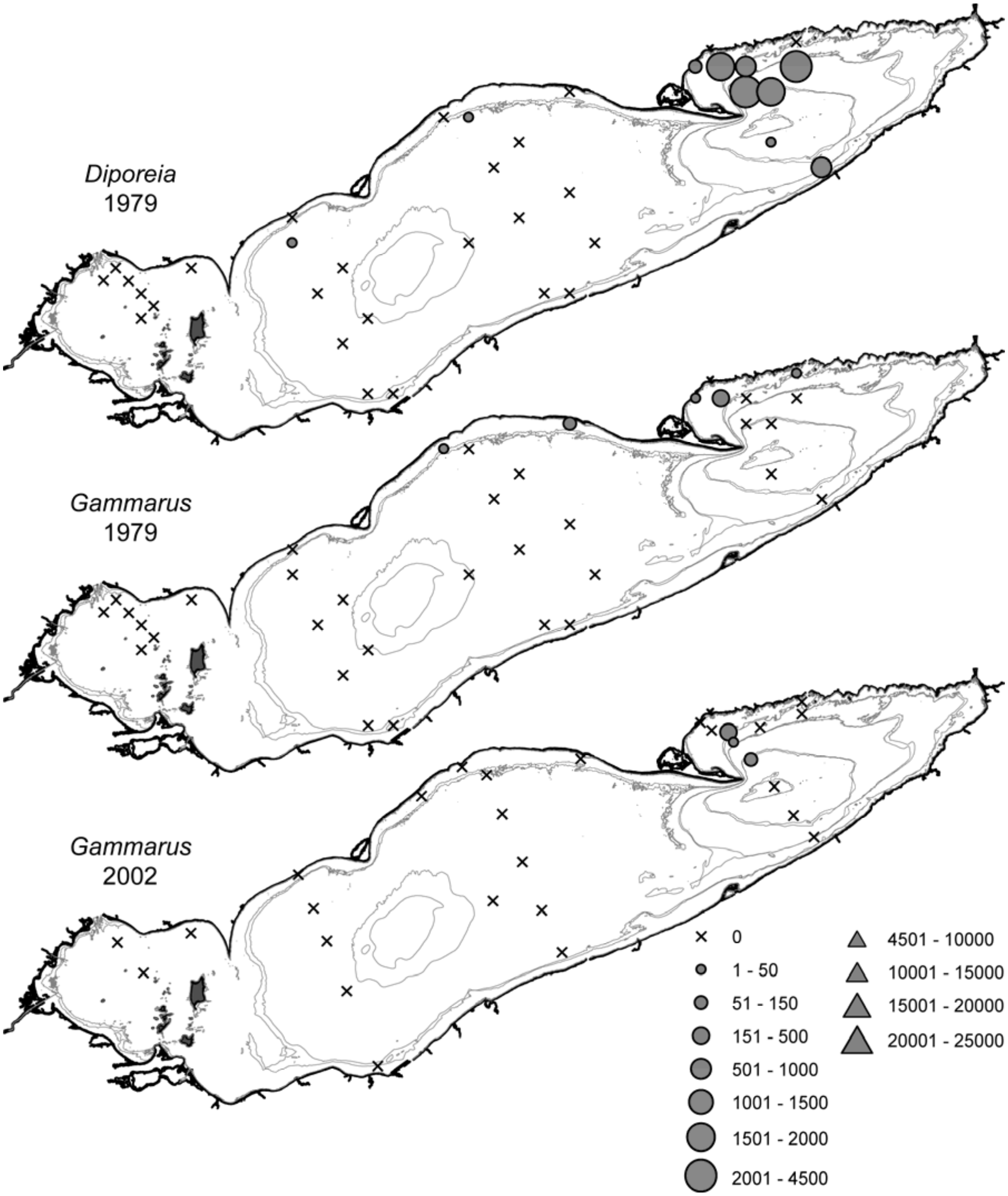

Figure 29. Distribution (individuals m^{-2}) of *Diporeia* and *Gammarus* amphipods for Lake Erie 1979-2002 "matched" sites. No *Diporeia* were found in 2002.

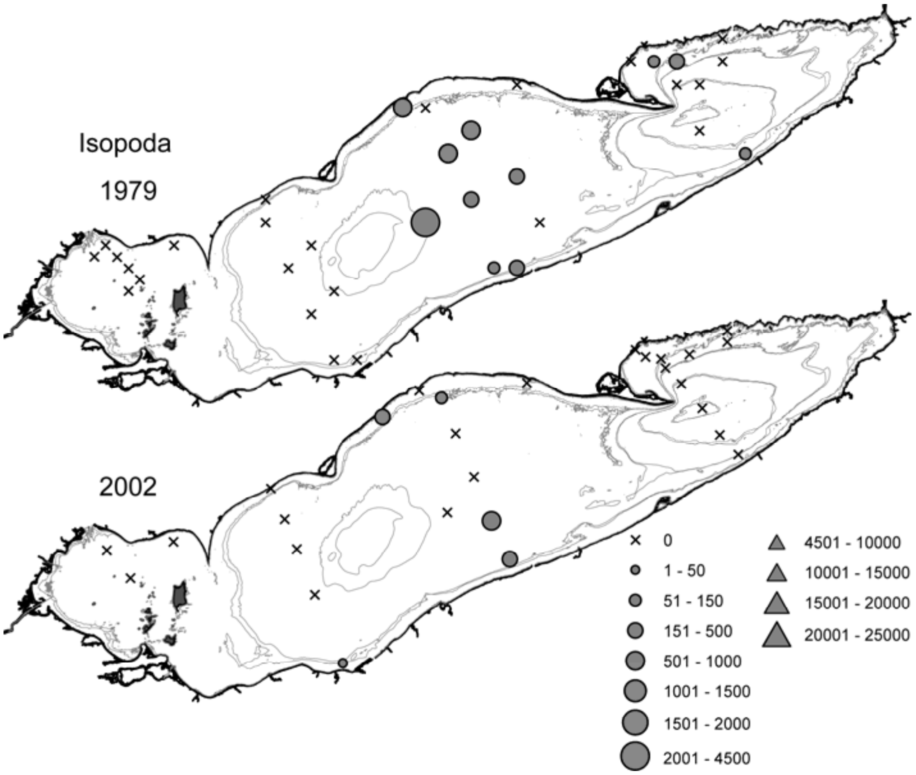

Figure 30. Distribution of Caecidotea (Isopoda) (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

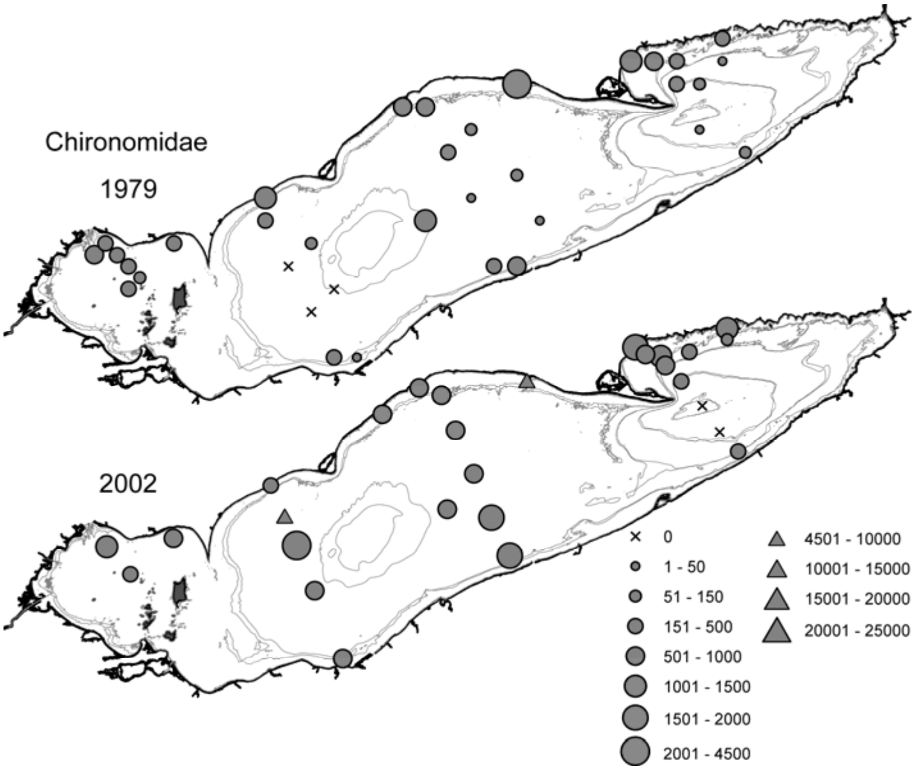

Figure 31. Distribution of Chironomidae (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

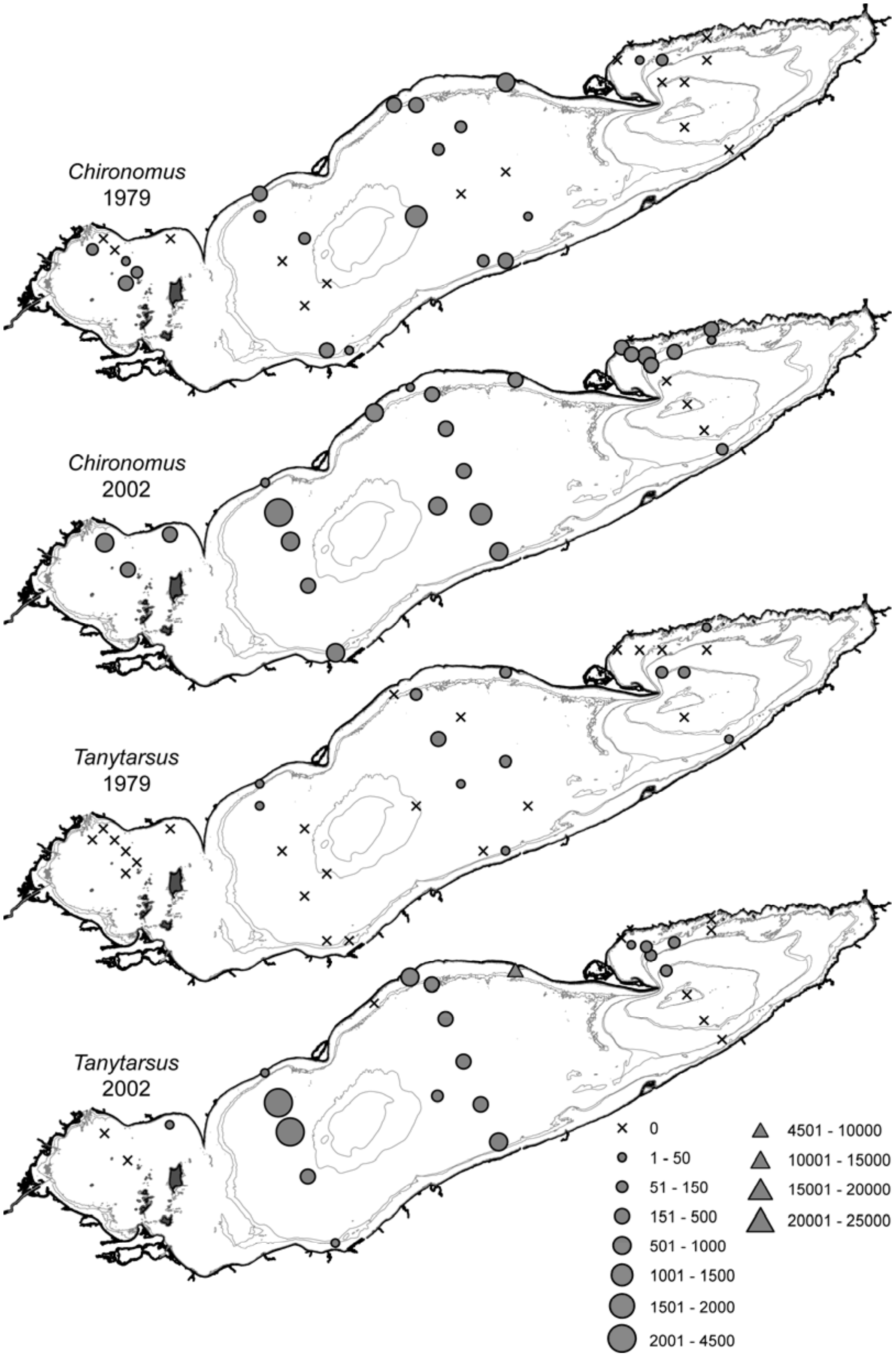

Figure 32. Distribution of *Chironomus* and *Tanytarsus* chironomids (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

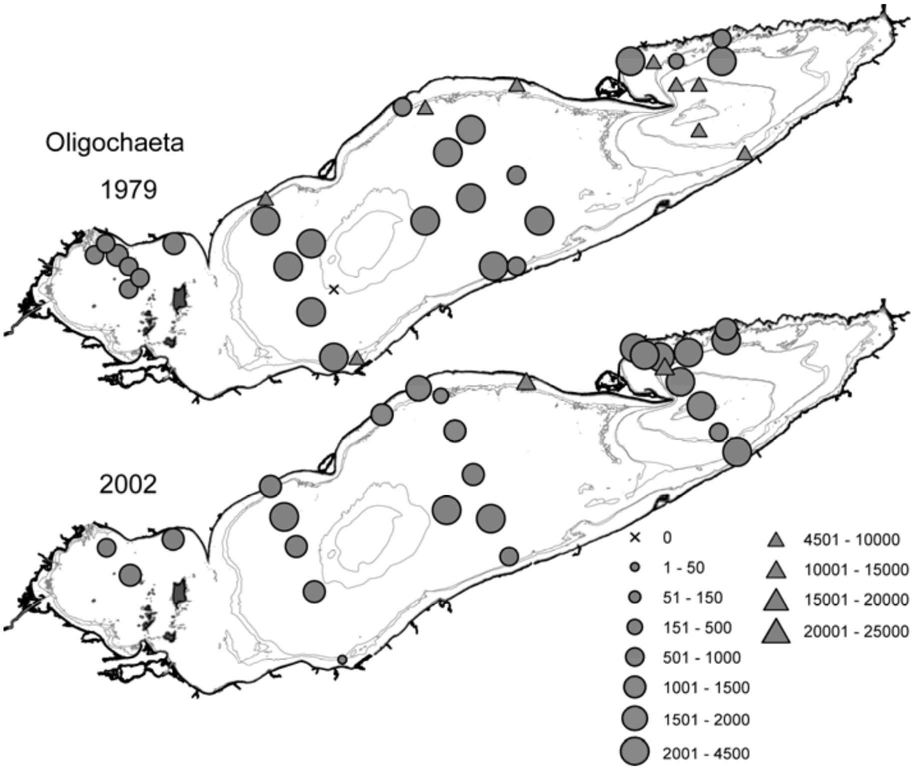

Figure 33. Distribution of Oligochaeta (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

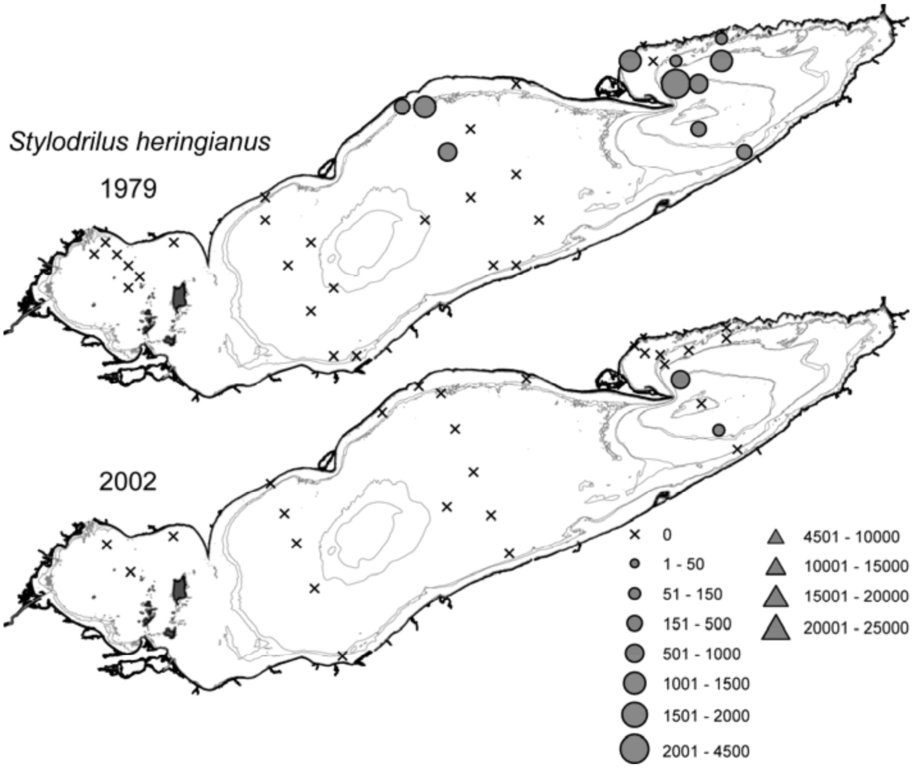

Figure 34. Distribution of *S. heringianus* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

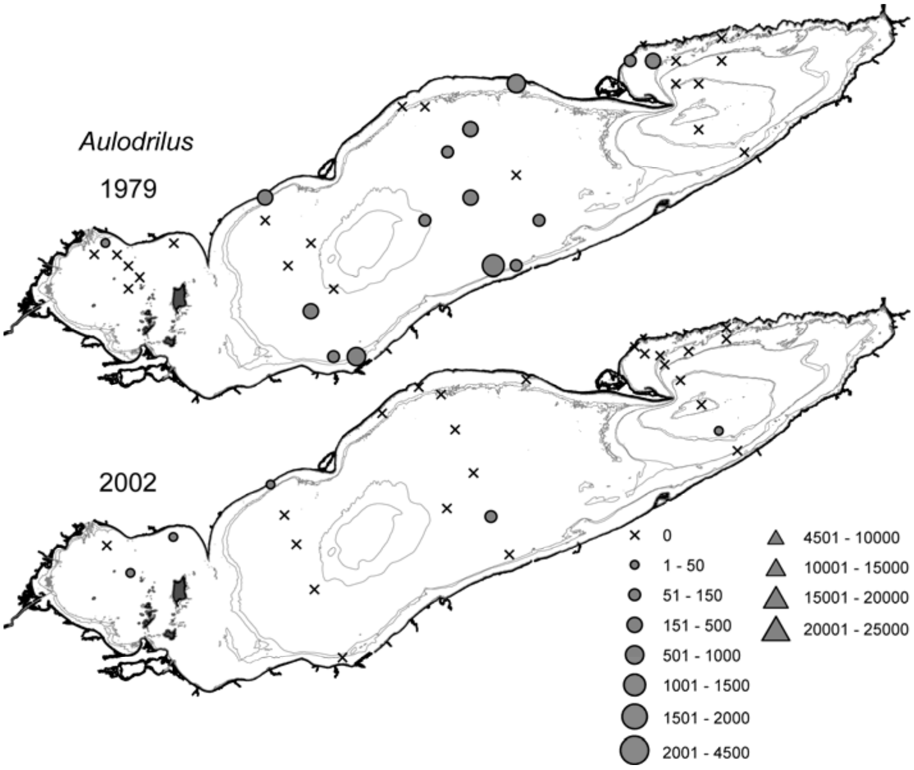

Figure 35. Distribution of *Aulodrilus* (individuals m^{-2}) for Lake Erie 1979-2002 “matched” sites.

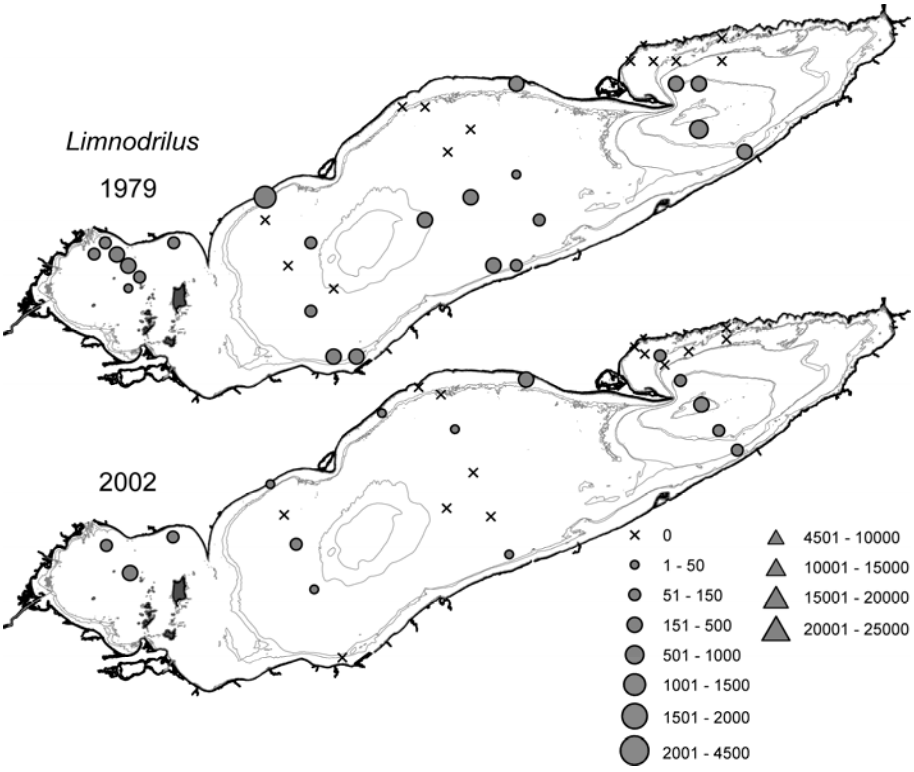

Figure 36. Distribution of *Limnodrilus* (individuals m^{-2}) for Lake Erie 1979-2002 “matched” sites.

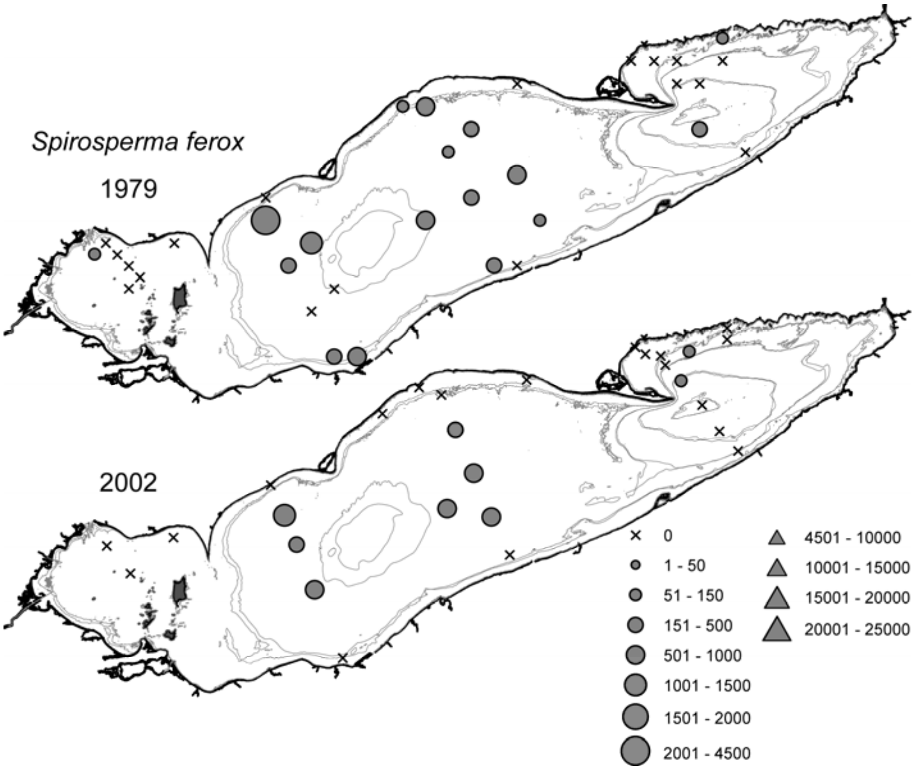

Figure 37. Distribution of *S. ferox* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

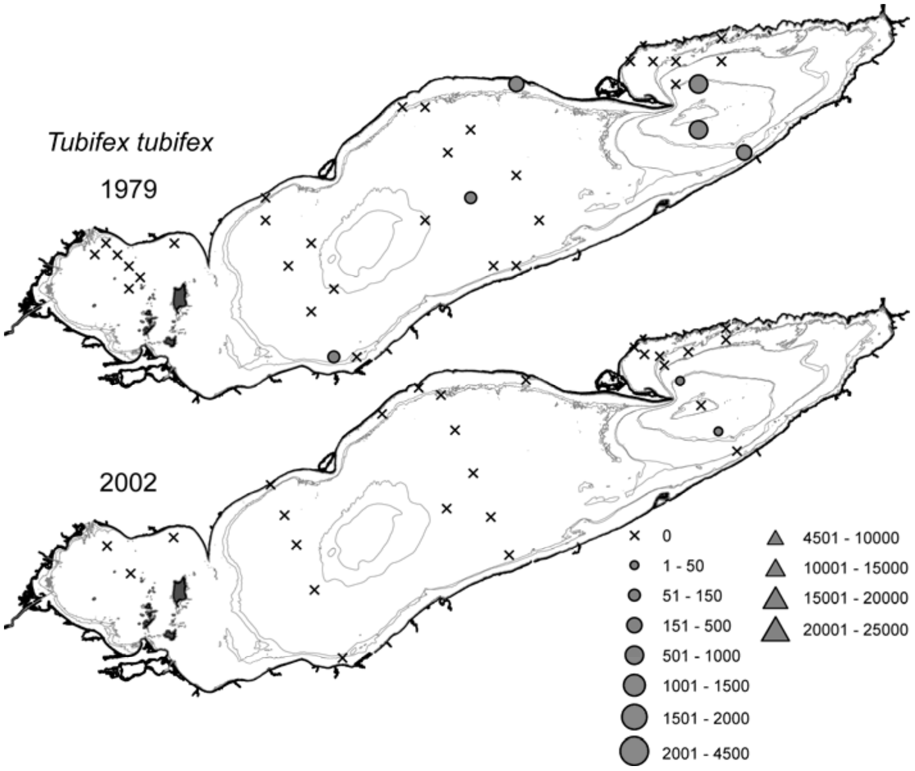

Figure 38. Distribution of *T. tubifex* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

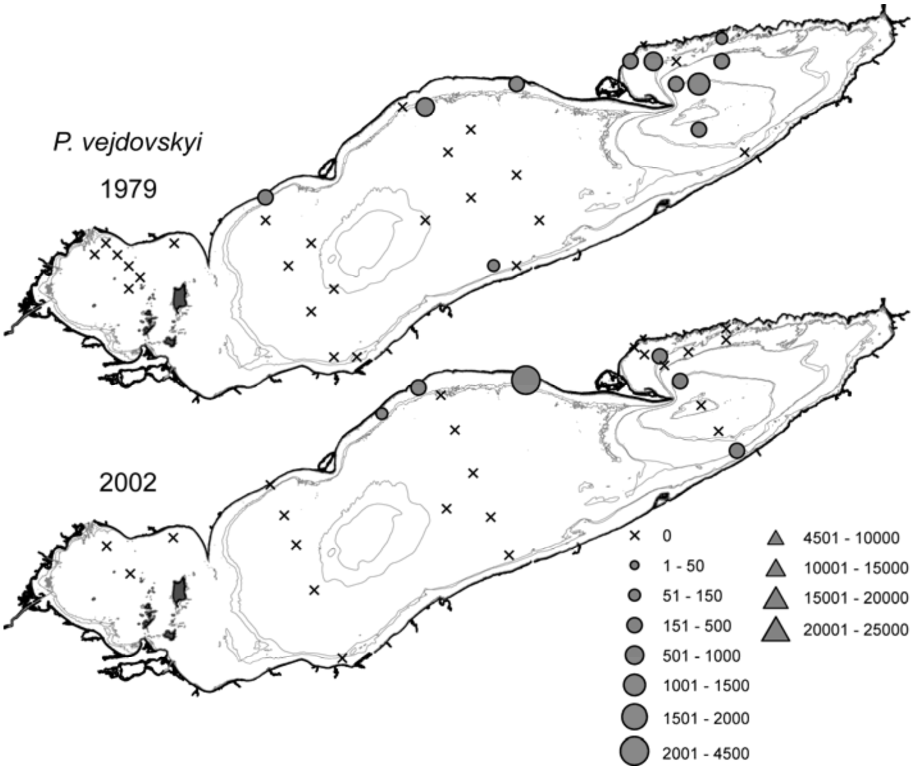

Figure 39. Distribution of *P. vejdovskyi* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

Table 14. Percent contribution of major oligochaete taxa to total oligochaete density for 1979-2002 “matched” sites. f= number of sites with taxa present.

		1979				2002			
Basin		f	Mean	±	SE	f	Mean	±	SE
West	*Stylodrilus heringianus*		0.0	±	0.0		0.0	±	0.0
	Dero spp		0.0	±	0.0	1	**7.1**	**±**	**7.1**
	Nais spp		0.0	±	0.0		0.0	±	0.0
	Vejdovskyella spp		0.0	±	0.0		0.0	±	0.0
	Aulodrilus spp	1	0.9	±	0.9	2	**1.7**	**±**	**1.2**
	Branchiura sowerbyi	3	**3.4**	**±**	**1.6**	1	0.8	±	0.8
	Ilyodrilus templetoni		0.0	±	0.0		0.0	±	0.0
	Imm Tubificid with hair		0.0	±	0.0	2	**1.3**	**±**	**0.7**
	Imm Tubificid no hair	7	76.1	±	3.4	3	**78.1**	**±**	**5.0**
	Potamothrix vejdovskyi		0.0	±	0.0		0.0	±	0.0
	Potamothrix moldaviensis	1	**1.2**	**±**	**1.2**		0.0	±	0.0
	Limnodrilus cervix		0.0	±	0.0	2	**1.8**	**±**	**1.1**
	Limnodrilus hoffmeisteri	6	**13.1**	**±**	**2.9**	3	9.2	±	2.3
	Limnodrilus profundicola	1	**0.8**	**±**	**0.8**		0.0	±	0.0
	Spirosperma ferox	1	**1.8**	**±**	**1.8**		0.0	±	0.0
	Tubifex tubifex		0.0	±	0.0		0.0	±	0.0
	Mean Oligochaete Density		801.3	±	103.0		1115.9	±	85.7
Central	*Stylodrilus heringianus*	3	**4.1**	**±**	**2.6**		0.0	±	0.0
	Dero spp	1	0.0	±	0.0	4	0.0	±	0.0
	Nais spp		0.7	±	0.7	1	**6.0**	**±**	**3.4**
	Vejdovskyella spp	2	**0.6**	**±**	**0.4**		0.0	±	0.0
	Aulodrilus spp	12	**5.6**	**±**	**1.9**	2	0.3	±	0.2
	Branchiura sowerbyi		0.0	±	0.0	1	**0.2**	**±**	**0.2**
	Ilyodrilus templetoni	1	**0.2**	**±**	**0.2**		0.0	±	0.0
	Imm Tubificid with hair	14	**11.2**	**±**	**3.3**	7	6.4	±	2.6
	Imm Tubificid no hair	18	44.8	±	5.9	14	**60.8**	**±**	**6.1**
	Potamothrix vejdovskyi	4	1.0	±	0.6	3	**3.6**	**±**	**2.2**
	Potamothrix moldaviensis	2	**0.5**	**±**	**0.4**	1	0.4	±	0.4
	Limnodrilus cervix	3	**0.4**	**±**	**0.2**	1	0.2	±	0.2
	Limnodrilus hoffmeisteri	10	**4.6**	**±**	**1.4**	6	1.0	±	0.4
	Limnodrilus profundicola	1	**0.2**	**±**	**0.2**		0.0	±	0.0
	Spirosperma ferox	14	15.2	±	5.8	7	**16.8**	**±**	**5.5**
	Tubifex tubifex	3	**0.7**	**±**	**0.4**		0.0	±	0.0
	Mean Oligochaete Density		3513.8	**±**	530.5		2397.7	±	912.9
East	*Stylodrilus heringianus*	8	**19.9**	**±**	**5.9**	2	4.3	±	3.3
	Dero spp	1	0.0	±	0.0		0.0	±	0.0
	Nais spp		**0.3**	**±**	**0.3**		0.0	±	0.0
	Vejdovskyella spp		0.0	±	0.0	2	**0.4**	**±**	**0.4**
	Aulodrilus spp	2	**1.0**	**±**	**0.7**	1	0.2	±	0.2
	Branchiura sowerbyi		0.0	±	0.0		0.0	±	0.0
	Ilyodrilus templetoni		0.0	±	0.0		0.0	±	0.0
	Imm Tubificid with hair	6	**10.0**	**±**	**3.6**	10	3.3	±	0.7
	Imm Tubificid no hair	9	43.1	±	6.9	11	**75.5**	**±**	**6.2**
	Potamothrix vejdovskyi	7	**8.9**	**±**	**2.6**	3	2.0	±	1.1
	Potamothrix moldaviensis	6	**8.4**	**±**	**3.1**	6	2.0	±	0.9
	Limnodrilus cervix		0.0	±	0.0		0.0	±	0.0
	Limnodrilus hoffmeisteri	4	2.6	±	1.3	5	**2.8**	**±**	**1.5**
	Limnodrilus profundicola		0.0	±	0.0		0.0	±	0.0
	Spirosperma ferox	2	**2.2**	**±**	**1.6**	2	0.3	±	0.2
	Tubifex tubifex	3	**2.5**	**±**	**1.4**	2	0.3	±	0.2
	Mean Oligochaete Density		4180.1	**±**	844.8		3787.3	±	1154.9

Table 15. Mean trophic index values (±SE) for Lake Erie 1979-2002 "Matched" sites, after Milbrink (1983).

Year	West				Central				East			
	N	Mean	±	SE	N	Mean	±	SE	N	Mean	±	SE
1979	7	0.93	±	0.15	18	1.05	±	0.11	9	0.92	±	0.22
2002	3	1.14	±	0.11	11	1.09	±	0.21	6	1.07	±	0.19

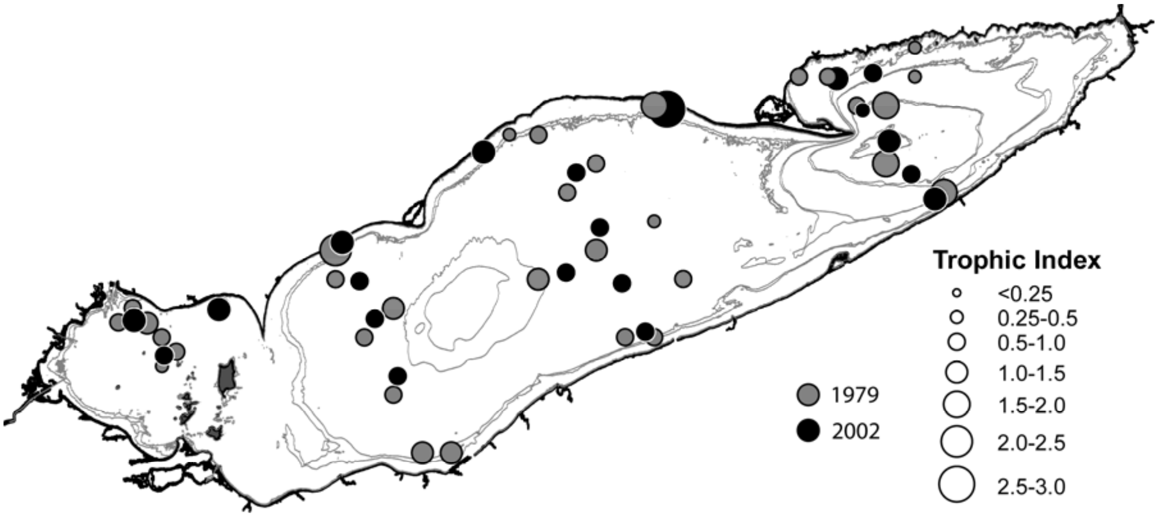

Figure 40. Lake Erie 1979-2002 "Matched" sites trophic index values based on number, identity and indicator status of oligochaetes.

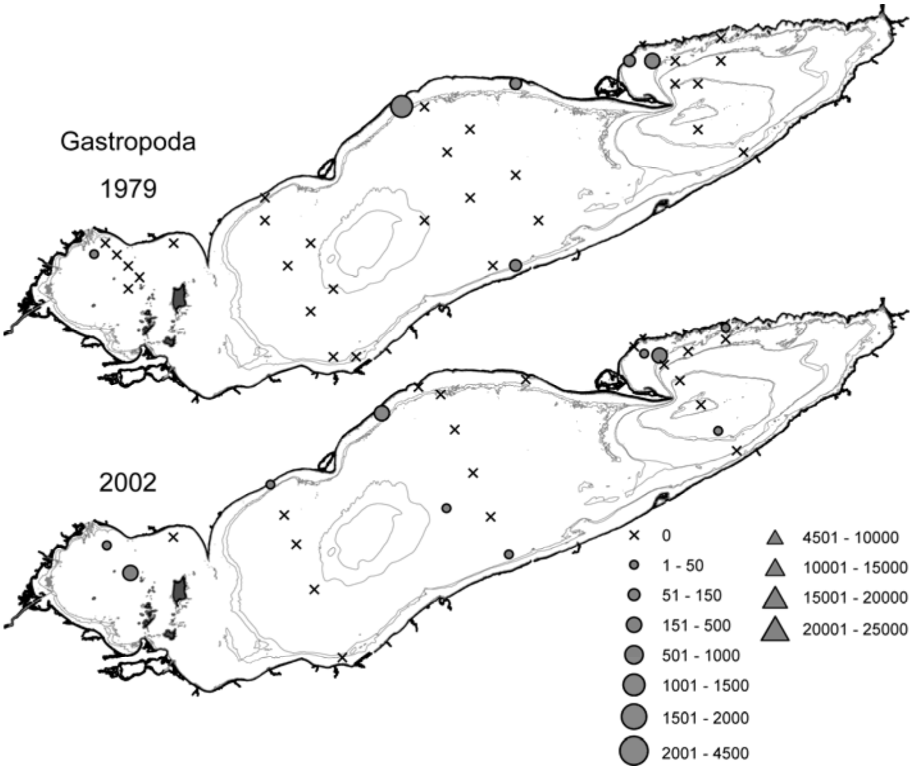

Figure 41. Distribution of Gastropoda (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

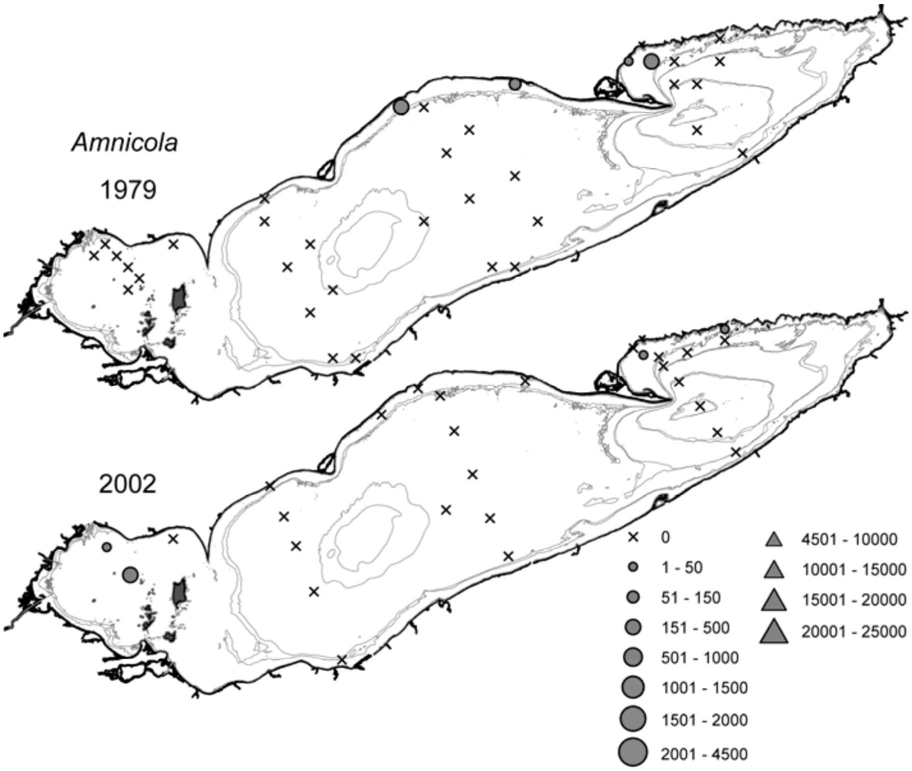

Figure 42. Distribution of *Amnicola* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

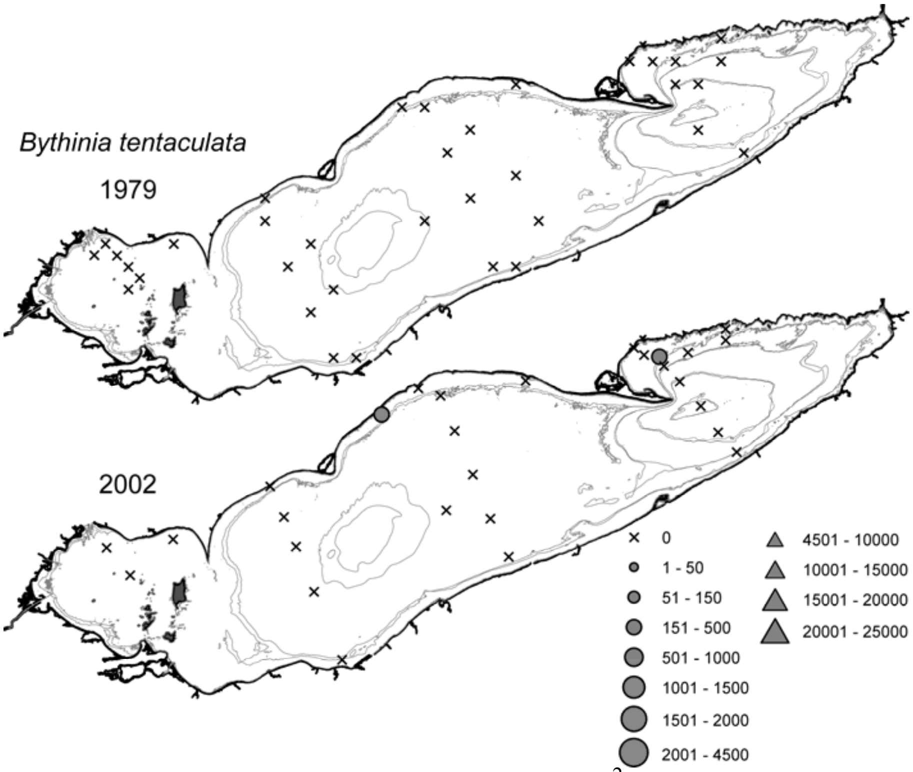

Figure 43. Distribution of *B. tentaculata* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

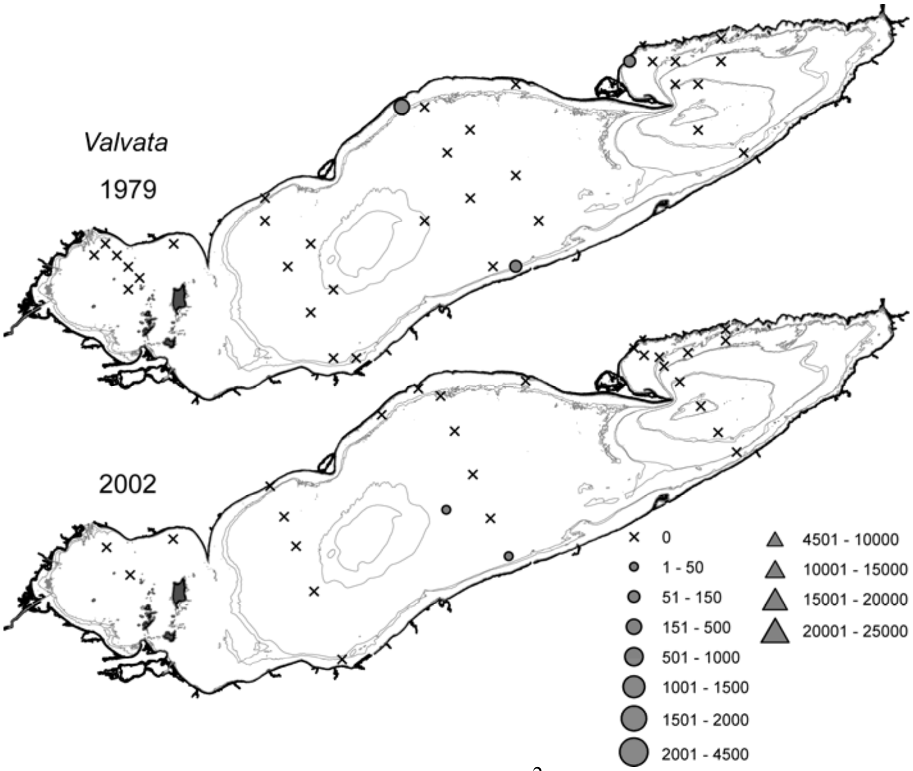

Figure 44. Distribution of *Valvata* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

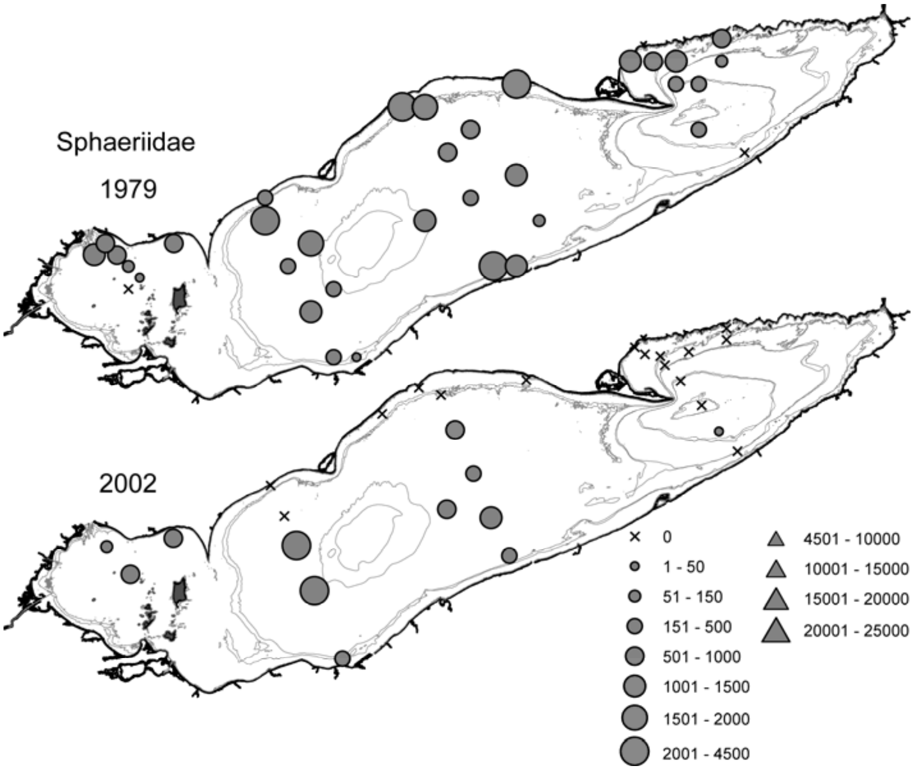

Figure 45. Distribution of Sphaeriidae (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

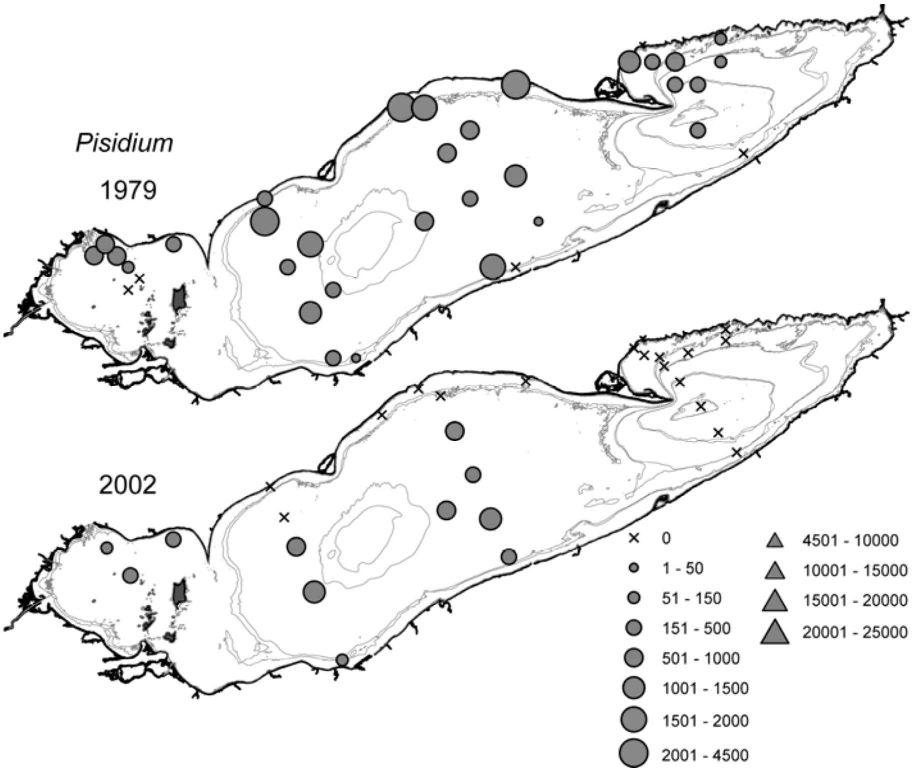

Figure 46. Distribution of *Pisidium* (individuals m^{-2}) for Lake Erie 1979-2002 "matched" sites.

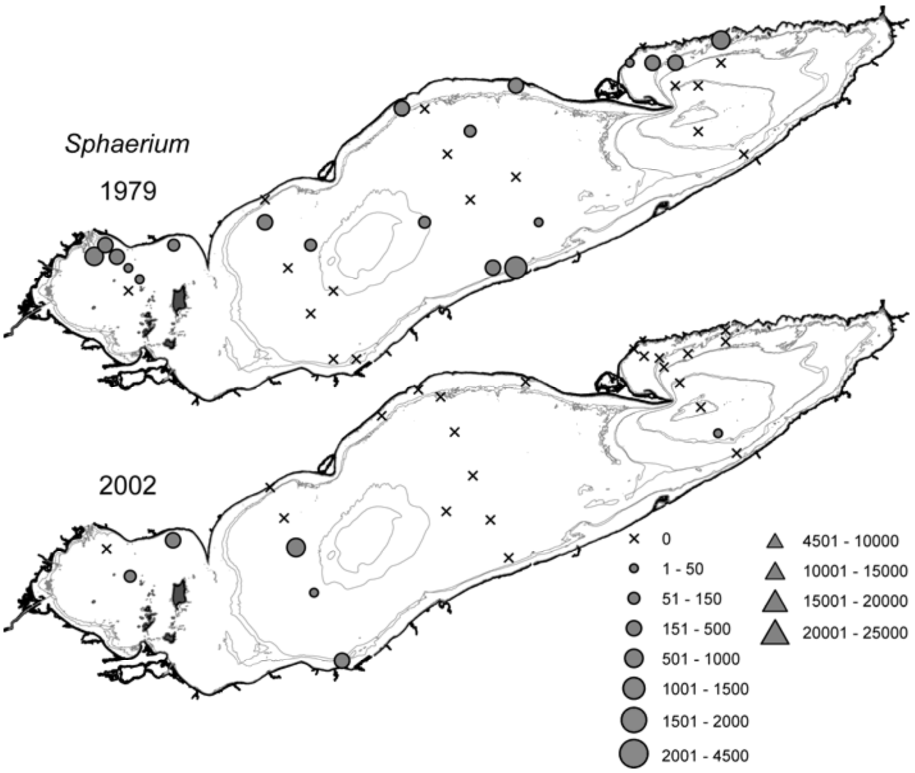

Figure 47. Distribution of *Sphaerium* (individuals m^{-2}) for Lake Erie 1979-2002 “matched” sites.

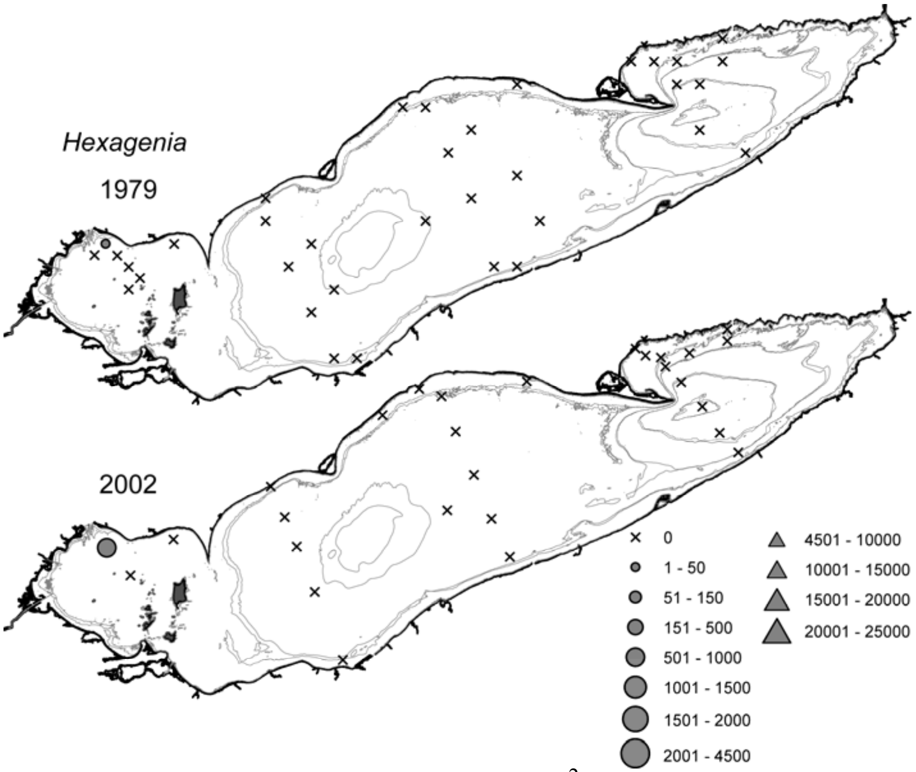

Figure 48. Distribution of *Hexagenia* (individuals m^{-2}) for Lake Erie 1979-2002 “matched” sites.

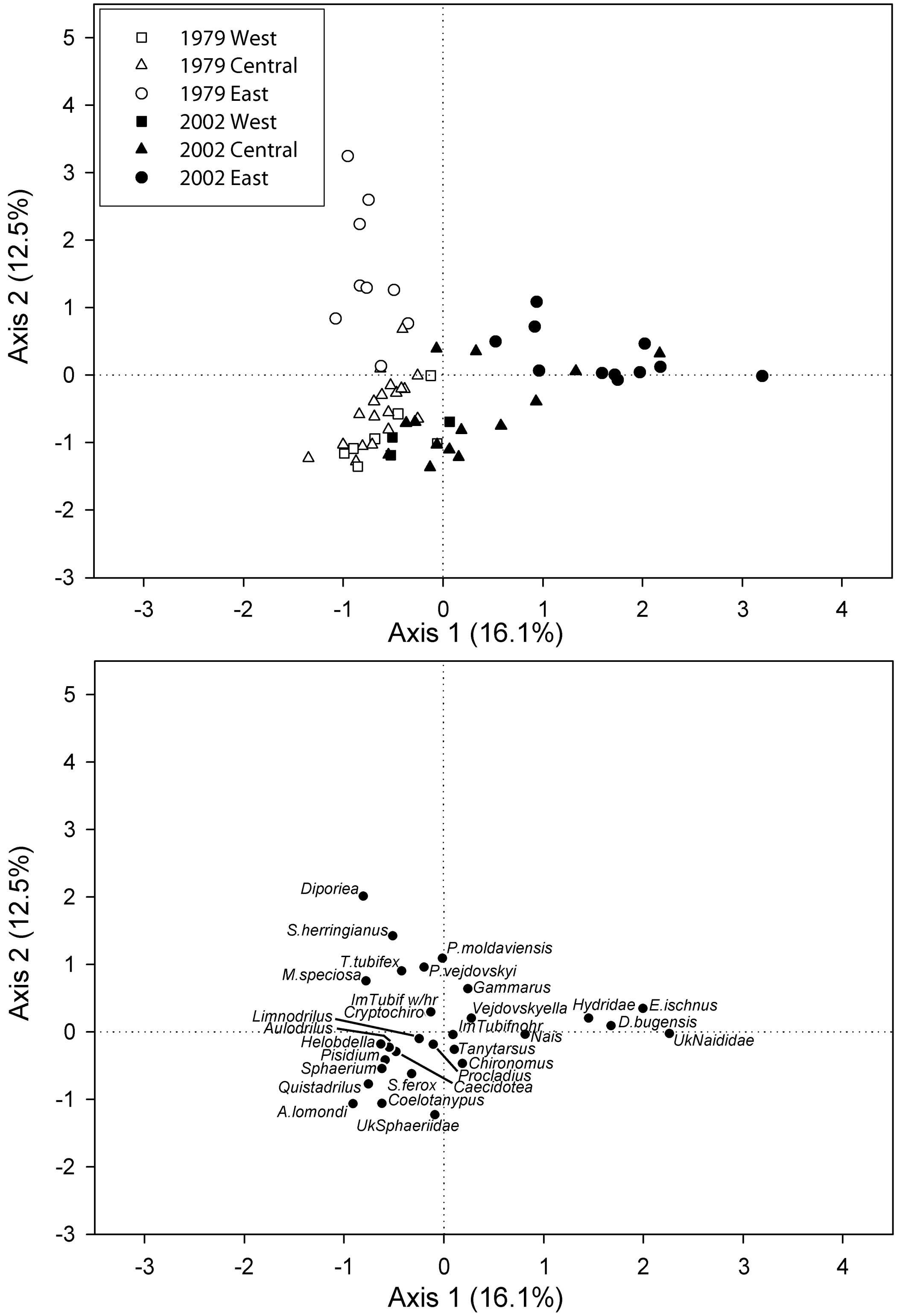

Figure 49a. 1979-2002 Lake Erie correspondence analysis site- and species-score scatterlpots based on square-root transformed species abundance of benthic macroinvertebrates accounting for >0.25% of lake-wide total abundance. Proportion of variance explained by each axis given in parenthesis.

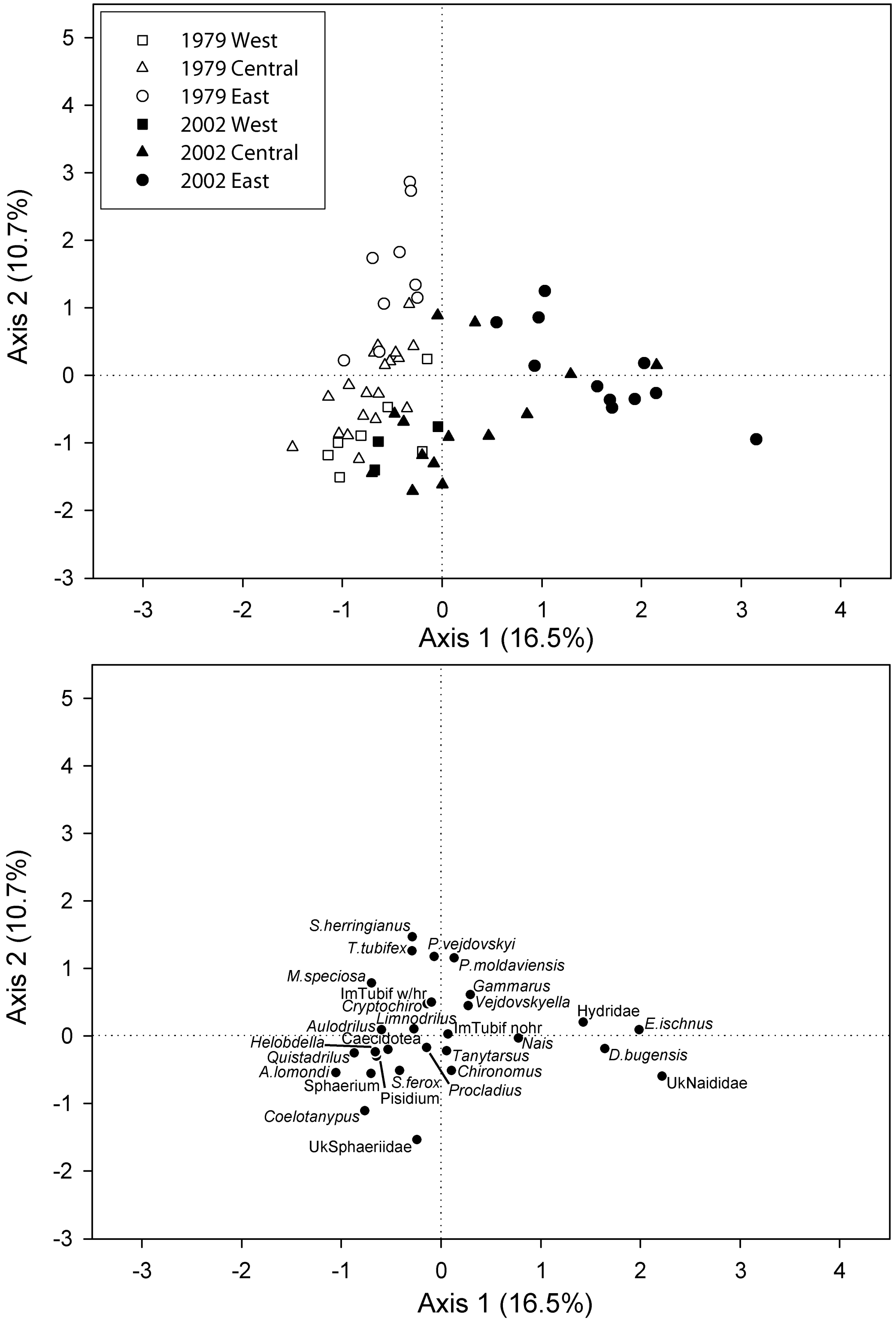

Figure 49b. 1979-2002 Lake Erie Erie correspondence analysis site- and species-score scatterlpots based on square-root transformed species abundance of benthic macroinvertebrates accounting for >0.25% of lake-wide total abundance. Proportion of variance explained by each axis given in parenthesis. *Diporeia* removed prior to CA.

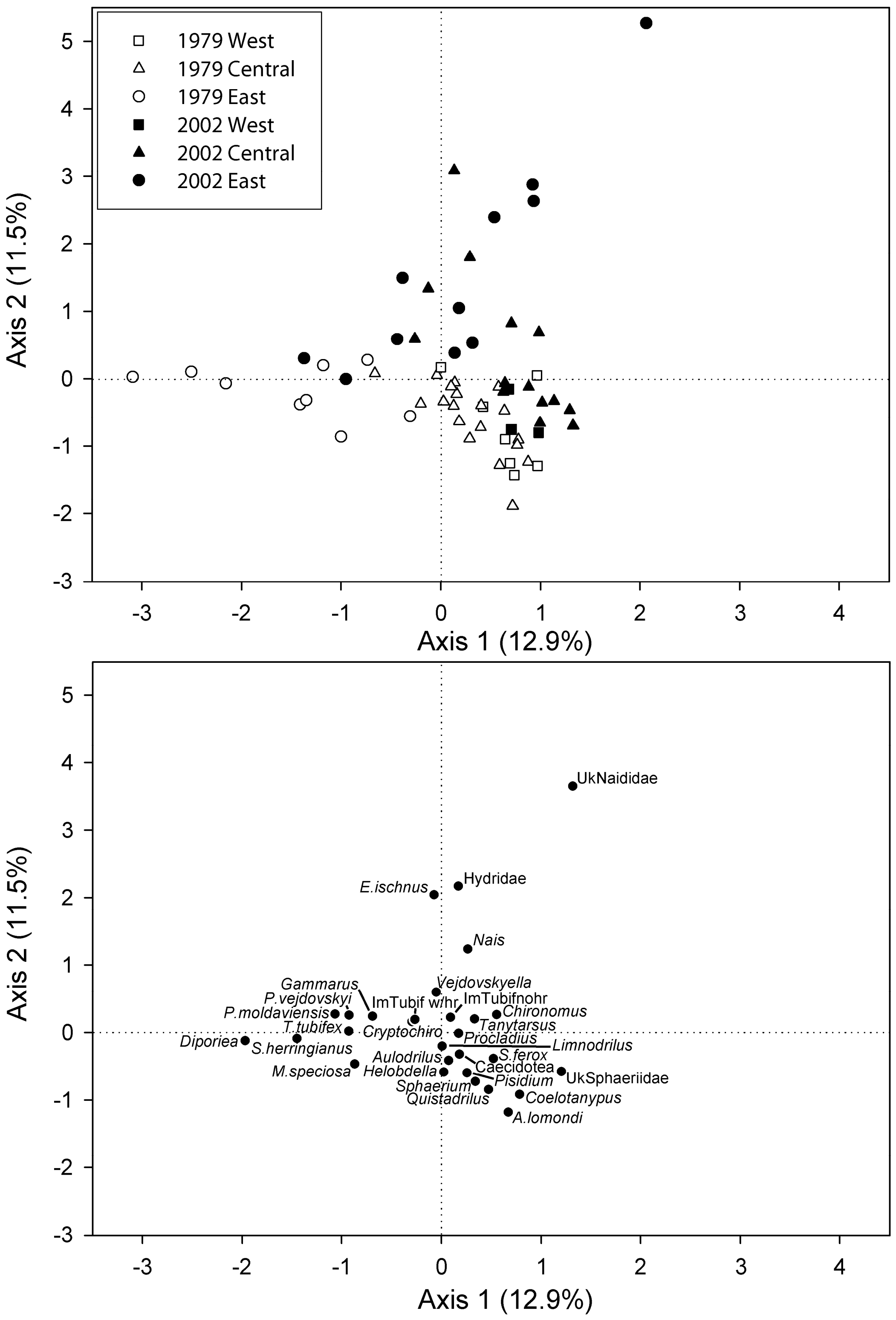

Figure 49c. 1979-2002 Lake Erie Erie correspondence alanysis site- and species-score scatterlpots based on square-root transformed species abundance of benthic macroinvertebrates accounting for >0.25% of lake-wide total abundance. Proportion of variance explained by each axis given in parenthesis. *Dreissena* removed prior to CA.

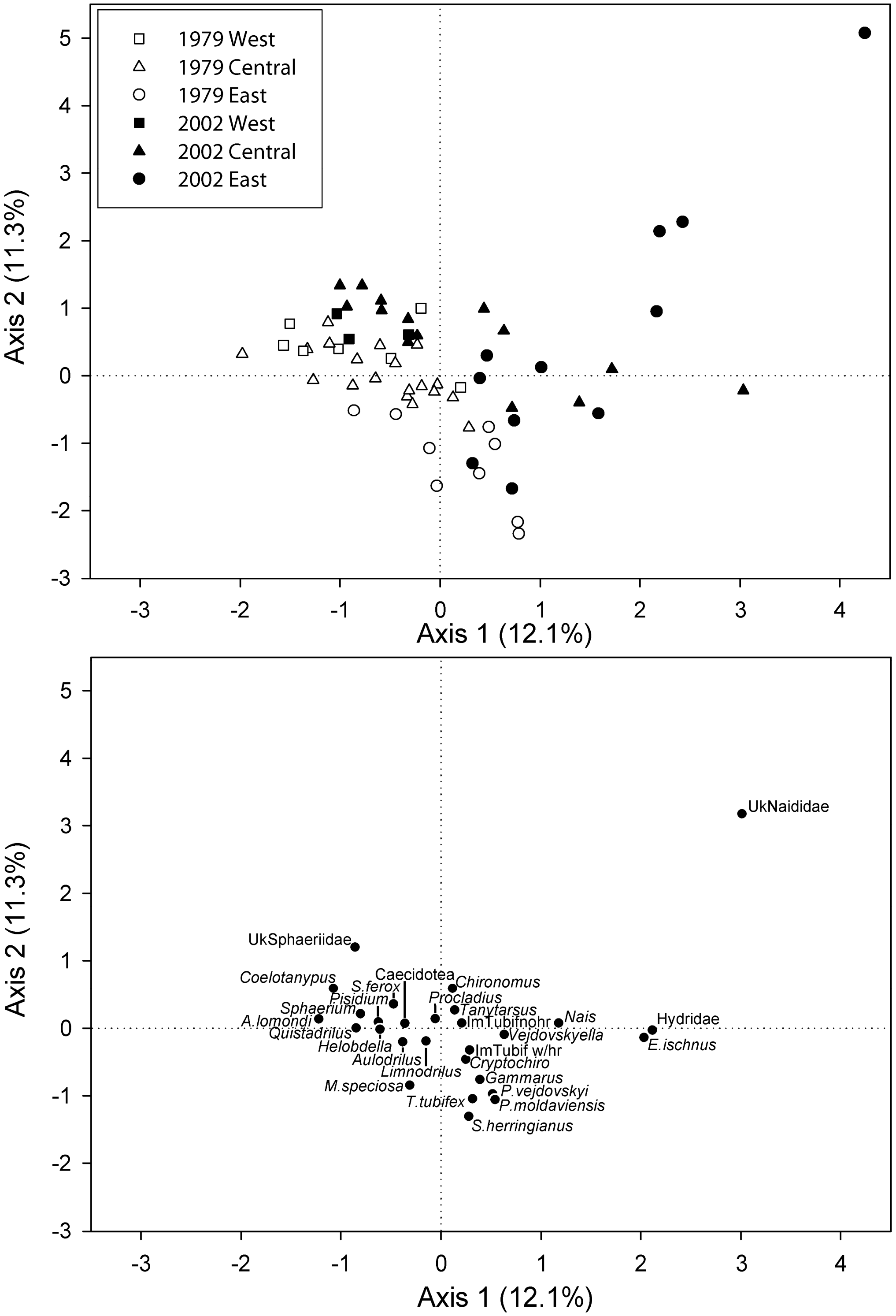

Figure 49d. 1979-2002 Lake Erie Erie correspondence analysis site- and species-score scatterlpots based on square-root transformed species abundance of benthic macroinvertebrates accounting for >0.25% of lake-wide total abundance. Proportion of variance explained by each axis given in parenthesis. *Dreissena* and *Diporeia* removed prior to CA.

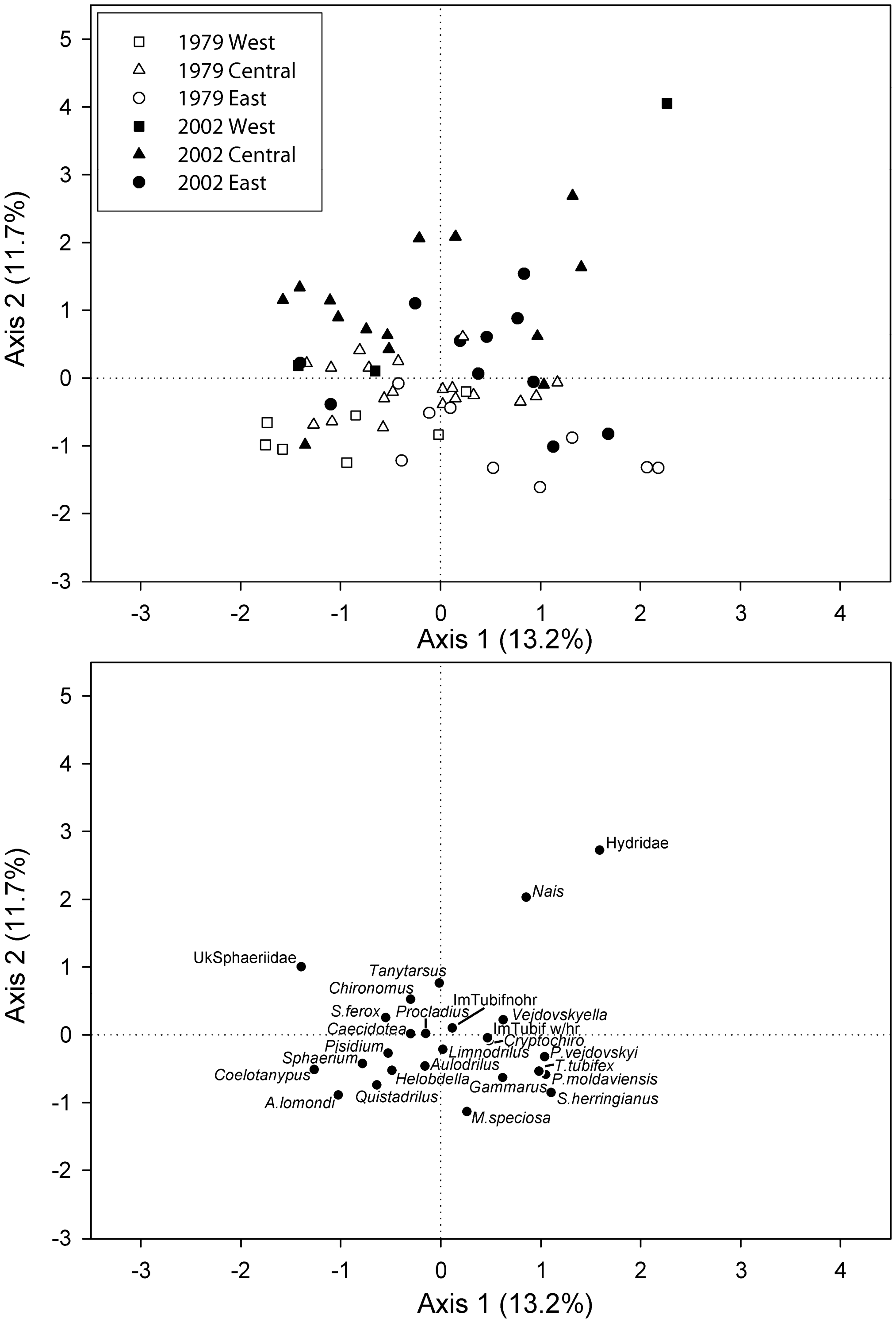

Figure 49e. 1979-2002 Lake Erie Erie correspondence analysis site- and species-score scatterlpots based on square-root transformed species abundance of benthic macroinvertebrates accounting for >0.25% of lake-wide total abundance. Proportion of variance explained by each axis given in parenthesis. *Dreissena*, *Diporeia*, *E. ischnus* and UkNaididae removed prior to CA.

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Appendices

Appendix 1a. Lake Erie 2002 sample site descriptions, including dominant substrate observed.

Date Sampled	Site	Depth (m)	Depth Category	Basin	Location (Nearshore/Offshore)	Survey	Substrate	Latitude	Longitude
19-Aug-02	Clear Creek 10m	10	5-10	Central	Nearshore	Nearshore	silt/clay	42° 35' 41.50"	80° 42' 25.30"
19-Aug-02	Clear Creek 5m	5	2-5	Central	Nearshore	Nearshore	fine sand	42° 36' 12.90"	80° 41' 41.50"
19-Aug-02	Clear Creek 2m	2	0-2	Central	Nearshore	Nearshore	hard clay	42° 36' 23.10"	80° 41' 29.30"
19-Aug-02	Port Burwell 10m	10	5-10	Central	Nearshore	Nearshore	mud/clay	42° 37' 25.00"	80° 49' 29.30"
19-Aug-02	Port Burwell 5m	5	2-5	Central	Nearshore	Nearshore	fine sand	42° 38' 08.70"	80° 49' 09.10"
19-Aug-02	Port Burwell 2m	2	0-2	Central	Nearshore	Nearshore	fine sand	42° 38' 16.60"	80° 48' 55.70"
29-Aug-02	Port Stanley 10m	10	5-10	Central	Nearshore	Nearshore	sand/silt	42° 38' 16.60"	81° 11' 30.10"
29-Aug-02	Port Stanley 5m	5	2-5	Central	Nearshore	Nearshore	sand/silt	42° 39' 26.90"	81° 11' 51.90"
29-Aug-02	Port Stanley 2m	2	0-2	Central	Nearshore	Nearshore	sand	42° 39' 42.20"	81° 12' 00.20"
29-Aug-02	Port Bruce 10m	10	5-10	Central	Nearshore	Nearshore	sand	42° 38' 36.10"	81° 01' 16.50"
29-Aug-02	Port Bruce 5m	5	2-5	Central	Nearshore	Nearshore	sand	42° 38' 57.50"	81° 01' 16.20"
29-Aug-02	Port Bruce 2m	2	0-2	Central	Nearshore	Nearshore	sand	42° 39' 12.30"	81° 01' 18.90"
4-Sep-02	Plum Point 10m	10	5-10	Central	Nearshore	Nearshore	coarse	42° 35' 36.70"	81° 23' 57.70"
4-Sep-02	Plum Point 5m	5	2-5	Central	Nearshore	Nearshore	hard	42° 35' 48.30"	81° 24' 01.10"
4-Sep-02	Plum Point 2m	2	0-2	Central	Nearshore	Nearshore	hard	42° 36' 11.40"	81° 24' 15.50"
4-Sep-02	Port Glasgow 10m	10	5-10	Central	Nearshore	Nearshore	hard	42° 29' 19.70"	81° 35' 38.50"
4-Sep-02	Port Glasgow 5m	5	2-5	Central	Nearshore	Nearshore	sand	42° 29' 56.60"	81° 36' 38.20"
4-Sep-02	Port Glasgow 2m	2	0-2	Central	Nearshore	Nearshore	sand	42° 30' 12.90"	81° 36' 56.60"
4-Sep-02	Palmyra 10m	10	5-10	Central	Nearshore	Nearshore	hard	42° 24' 19.20"	81° 44' 40.70"
4-Sep-02	Palmyra 5m	5	2-5	Central	Nearshore	Nearshore	sand	42° 25' 11.80"	81° 45' 06.70"
4-Sep-02	Palmyra 2m	2	0-2	Central	Nearshore	Nearshore	sand	42° 25' 19.20"	81° 45' 15.40"
5-Sep-02	Alma/Dealtown 5m	5	2-5	Central	Nearshore	Nearshore	hard	42° 12' 07.40"	82° 10' 59.50"
5-Sep-02	Alma/Dealtown 2m	2	0-2	Central	Nearshore	Nearshore	sand	42° 12' 14.60"	82° 11' 09.40"
5-Sep-02	Rondeau 10m	10	5-10	Central	Nearshore	Nearshore	sand/mud	42° 15' 16.20"	81° 50' 04.70"
5-Sep-02	Rondeau 5m	5	2-5	Central	Nearshore	Nearshore	sand	42° 15' 23.00"	8° 15' 02.40"
5-Sep-02	Rondeau 2m	2	0-2	Central	Nearshore	Nearshore	sand	42° 15' 30.90"	81° 50' 45.40"
7-Sep-02	Wheatley 10m	10	5-10	Central	Nearshore	Nearshore	coarse	42° 05' 55.80"	82° 22' 59.70"
7-Sep-02	Wheatley 5m	5	2-5	Central	Nearshore	Nearshore	hard	42° 06' 41.50"	82° 24' 04.70"
7-Sep-02	Wheatley 2m	2	0-2	Central	Nearshore	Nearshore	sand	42° 06' 47.10"	82° 24' 12.20"

(continued)

Appendix 1a. (continued).

Date Sampled	Site	Depth (m)	Depth Category	Basin	Location (Nearshore/Offshore)	Survey	Substrate	Latitude	Longitude
7-Sep-02	Pelee East 10m	10	5-10	Central	Nearshore	Nearshore	coarse	41° 56’ 46.60”	82° 20’ 00.50”
7-Sep-02	Pelee East 5m	5	2-5	Central	Nearshore	Nearshore	sand/clay	41° 56’ 53.80”	82° 30’ 04.60”
7-Sep-02	Pelee East 2m	2	0-2	Central	Nearshore	Nearshore	sand	41° 56’ 55.10”	82° 30’ 12.10”
8-Sep-02	Pelee West 10m	10	5-10	West	Nearshore	Nearshore	silt	41° 55’ 53.70”	82° 32’ 26.90”
8-Sep-02	Pelee West 5m	5	2-5	West	Nearshore	Nearshore	sand	41° 56’ 38.80”	82° 31’ 32.10”
8-Sep-02	Pelee West 2m	2	0-2	West	Nearshore	Nearshore	coarse	41° 56’ 43.80”	82° 31’ 25.60”
8-Sep-02	Kingsville 10m	10	5-10	West	Nearshore	Nearshore	silt	41° 59’ 12.40”	82° 41’ 35.50”
8-Sep-02	Kingsville 5m	5	2-5	West	Nearshore	Nearshore	sand/silt	42° 01’ 37.40”	82° 42’ 00.70”
8-Sep-02	Comet 5m	5	2-5	West	Nearshore	Nearshore	sand/clay	41° 58’ 46.10”	83° 00’ 42.80”
9-Sep-02	Comet 2m	2	0-2	West	Nearshore	Nearshore	sand	41° 58’ 50.40”	83° 00’ 37.70”
8-Sep-02	Colchester 5m	5	2-5	West	Nearshore	Nearshore	sand/silt	42° 00’ 56.90”	82° 55’ 29.60”
8-Sep-02	Colchester 2m	2	0-2	West	Nearshore	Nearshore	sand	42° 01’ 12.60”	82° 55’ 30.20”
17-Aug-02	Port Dover	11.3	10-20	East	Nearshore	Guardian	fine sand/silt	42° 42’ 52.02”	80° 06’ 28.44”
17-Aug-02	93b	39.9	>20	East	Offshore	Guardian	sand/silt	42° 36’ 56.76”	80° 00’ 01.68”
17-Aug-02	15m	61.8	>20	East	Offshore	Guardian	sand/silt	42° 31’ 08.28”	79° 53’ 25.08”
17-Aug-02	63	42.9	>20	East	Offshore	Guardian	sand/silt	42° 24’ 51.06”	79° 47’ 58.32”
17-Aug-02	Barcelona	21.6	>20	East	Offshore	Guardian	sand/silt	42° 20’ 09.42”	79° 42’ 08.46”
18-Aug-02	Port Stanley	13.7	10-20	Central	Nearshore	Guardian	sand/silt	42° 33’ 53.40”	81° 16’ 47.82”
18-Aug-02	30	18.3	10-20	Central	Nearshore	Guardian	sand/silt	42° 25’ 31.74”	81° 12’ 16.74”
18-Aug-02	31	19.3	10-20	Central	Nearshore	Guardian	sand/silt	42° 15’ 15.30”	81° 06’ 21.90”
18-Aug-02	32	19.8	10-20	Central	Nearshore	Guardian	sand/silt	42° 04’ 51.84”	81° 00’ 46.74”
18-Aug-02	Ashtabula	15.7	10-20	Central	Nearshore	Guardian	sand/silt	41° 55’ 49.86”	80° 54’ 58.76”
18-Aug-02	78m	23.3	>20	Central	Offshore	Guardian	sand/silt	42° 06’ 51.42”	81° 14’ 49.26”
20-Aug-02	Port Alma	8.1	5-10	Central	Nearshore	Guardian	sand/silt	42° 04’ 55.86”	82° 06’ 28.26”
20-Aug-02	42	19.6	10-20	Central	Nearshore	Guardian	sand/silt	41° 57’ 56.94”	82° 02’ 32.40”
20-Aug-02	43	19.5	10-20	Central	Nearshore	Guardian	sand/silt	41° 47’ 18.90”	81° 56’ 40.08”
20-Aug-02	Cleveland	11.3	10-20	Central	Nearshore	Guardian	sand/silt	41° 31’ 14.64”	81° 47’ 35.40”
21-Aug-02	61	6.1	5-10	West	Nearshore	Guardian	sand/silt	41° 56’ 51.12”	83° 02’ 40.68”
21-Aug-02	91m	7.4	5-10	West	Nearshore	Guardian	sand/silt	41° 50’ 27.48”	82° 54’ 59.58”

(continued)

Appendix 1a. (continued).

Date Sampled	Site	Depth (m)	Depth Category	Basin	Location (Nearshore/Offshore)	Survey	Substrate	Latitude	Longitude
21-Aug-02	55	7.4	5-10	West	Nearshore	Guardian	sand/silt	41° 44' 17.22"	82° 44' 00.36"
21-Aug-02	Sandusky Basin	11	10-20	West	Nearshore	Guardian	sand/silt	41° 32' 01.44"	82° 27' 02.70"
21-Aug-02	Port Ryerse 20m	20	10-20	East	Nearshore	Nearshore	sand/silt	42° 40' 42.48"	80° 05' 03.78"
21-Aug-02	Port Ryerse 10m	10	5-10	East	Nearshore	Nearshore	hard	42° 43' 21.00"	80° 11' 24.78"
21-Aug-02	Port Ryerse 5m	5	2-5	East	Nearshore	Nearshore	hard	42° 45' 03.00"	80° 14' 37.20"
21-Aug-02	Port Ryerse 2m	2	0-2	East	Nearshore	Nearshore	hard	42° 45' 14.88"	80° 14' 58.02"
23-Aug-02	Evan's Pt. 20m	20	10-20	East	Nearshore	Nearshore	sand/silt	42° 46' 36.96"	79° 45' 07.86"
23-Aug-02	Evan's Pt. 10m	10	5-10	East	Nearshore	Nearshore	hard	42° 49' 15.12"	79° 45' 04.32"
23-Aug-02	Evan's Pt. 5m	5	2-5	East	Nearshore	Nearshore	hard	42° 49' 33.60"	79° 45' 17.40"
23-Aug-02	Evan's Pt. 2m	2	0-2	East	Nearshore	Nearshore	hard	42° 50' 13.26"	79° 45' 15.00"
19-Aug-02	Peacock Point 20m	20	10-20	East	Nearshore	Nearshore	sand/silt	42° 43' 51.00"	79° 57' 17.80"
19-Aug-02	Peacock Point 10m	10	5-10	East	Nearshore	Nearshore	hard	42° 46' 20.80"	79° 58' 11.70"
19-Aug-02	Peacock Point 5m	5	2-5	East	Nearshore	Nearshore	hard	42° 47' 20.80"	79° 58' 39.50"
19-Aug-02	Peacock Point 2m	2	0-2	East	Nearshore	Nearshore	hard	42° 47' 25.80"	79° 58' 46.20"

Appendix 1b. Summary of number of sites sampled in each basin, depth class and substrate type for Lake Erie 2002 zoobenthic survey.

Depth Class (m)	Substrate	Basin			
		West	Central	East	Total
0-2	Mud				
	Sand/Silt				
	Sand	2	9		11
	Coarse	1			1
	Hard		1	3	4
	Total	**3**	**10**	**3**	**16**
2-5	Mud				
	Sand/Silt	3	2		5
	Sand	1	6		7
	Coarse		3	3	6
	Hard				
	Total	**4**	**11**	**3**	**18**
5-10	Mud		1		1
	Sand/Silt	4	4		8
	Sand		1		1
	Coarse		3		3
	Hard		2	3	5
	Total	**4**	**11**	**3**	**18**
10-20	Mud				
	Sand/Silt		8	4	12
	Sand				
	Coarse				
	Hard				
	Total		**8**	**4**	**12**
>20	Mud				
	Sand/Silt		1	4	5
	Sand				
	Coarse				
	Hard				
	Total		**1**	**4**	**5**
Total	Mud		1		1
	Sand/Silt	7	15	8	30
	Sand	3	16		19
	Coarse	1	3		4
	Hard		6	9	15
	Total	**11**	**41**	**17**	**69**

Appendix 2. Lake Erie 2002 benthic macroinvertebrate frequency of occurrence (f), mean density (individuals m^{-2}) and percent total lake density. N=total number is sites sampled.

			Depth (m)																	
			0-2 (N=16)			>2-5 (N=18)			>5-10 (N=18)			>10-20 (N=12)			>20 (N=5)			Total (N=69)		
			f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density
Cnidaria	Hydridae	*Hydridae*	2	12.6	<1	5	325.9	**1.3**	5	198.3	<1	2	10.6	<1				14	141.5	**2.0**
Platyhelminthes	Tricladida	*Dugesia*	1	1.0	<1													1	0.2	<1
		Planariidae				2	3.7	<1	5	121.8	<1							7	32.7	<1
		Total Planariidae	1	1.0	<1	2	3.7	<1	5	121.8	<1							8	33.0	<1
	Proseriata	*Hydrolimax*							1	2.4	<1	1	3.2	<1				2	1.2	<1
	Turbellaria	*Turbellaria*	1	61.7	<1													1	14.3	<1
		Total Platyhelminthes	2	62.7	<1	2	3.7	<1	6	124.2	<1	1	3.2	<1				11	48.4	<1
Gastropoda	Bithyniidae	*Bithynia tentaculata*	1	0.9	<1				1	11.5	<1	1	29.6	<1				3	8.4	<1
	Hydrobiidae	*Amnicola limosa*	2	10.3	<1	2	19.3	<1	5	14.8	<1							9	11.3	<1
		Marstonia decepta	1	55.7	<1													1	12.9	<1
	Physidae	*Physa*													1	3.0	<1	1	0.2	<1
	Pleuroceridae	*Elimia livescens*				1	0.8	<1										1	0.2	<1
		Pleurocera acuta	1	12.6	<1	1	4.7	<1										2	4.2	<1
	Valvatidae	*Valvata perdepressa*										1	1.2	<1				1	0.2	<1
		Valvata piscinalis							1	1.6	<1							1	0.4	<1
		Valvata sincera	1	0.9	<1				1	6.6	<1				1	3.0	<1	3	2.1	<1
	Gastropoda	Total Gastropoda	4	80.4	<1	3	24.8	<1	8	34.6	<1	2	30.9	<1	2	5.9	<1	19	39.9	<1
Bivalvia	Dreissenidae	*Dreissena bugensis*	4	2712.8	**9.8**	10	2310.0	**9.4**	12	1774.4	**7.2**	9	3170.5	**8.6**	5	2633.8	**3.0**	40	2436.8	**19.0**
		Dreissena polymorpha				6	27.2	<1	4	8.2	<1	4	35.8	<1	1	11.9	<1	15	16.3	<1
		Total Dreissena	4	2712.8	**9.8**	10	2337.2	**9.5**	12	1782.6	**7.2**	9	3206.3	**8.7**	5	2645.7	**3.0**	40	2453.1	**19.5**
	Sphaeriidae	Unident Sphaeriidae							3	28.0	<1	4	187.6	<1				7	39.9	<1
		Pisidium				2	38.7	<1	5	76.5	<1	7	346.9	<1	1	106.7	<1	15	98.1	**2.5**
		Sphaerium	1	0.9	<1	2	5.8	<1	3	64.2	<1	1	30.9	<1				7	23.8	**1.2**
		Sphaerium corneum										2	21.0	<1				2	3.6	<1
		Sphaerium rhombiodium							1	5.8	<1	1	25.9	<1	1	3.0	<1	3	6.2	<1
		Total *Sphaerium*	1	0.9	<1	2	5.8	<1	4	70.0	<1	3	77.8	<1	1	3.0	<1	11	33.7	**1.4**
		Total Sphaeriidae	1	0.9	<1	3	44.4	<1	6	174.5	<1	7	612.3	**1.7**	2	109.6	<1	19	171.7	**4.7**
Hydracarina	Hydracarina	*Hydracarina*	5	115.9	<1	7	18.5	<1	5	28.7	<1	2	3.7	<1				19	39.8	<1
Amphipoda	Gammaridae	*Echinogammarus ischnus*	3	55.4	<1	5	28.2	<1	1	2.4	<1	2	71.3	<1				11	33.2	<1
		Gammarus fasciatus	4	395.2	**1.4**	3	49.7	<1	1	11.5	<1	2	32.8	<1	1	11.9	<1	11	114.2	<1
		Gammarus pseudolimneas				1	0.8	<1										1	0.2	<1
		Total Amphipoda	5	450.6	**1.6**	6	78.8	<1	2	13.9	<1	3	104.1	<1	1	11.9	<1	17	147.6	<1
Isopoda		*Caecidotea*							1	74.9	<1	4	92.6	<1				5	35.6	<1
		Caecidotea intermedius										1	1.2	<1				1	0.2	<1
		Caecidotea racovitzai				1	0.8	<1	2	68.3	<1							3	18.0	<1
		Lirceus				1	11.8	<1										1	3.1	<1
		Total Isopoda				2	12.6	<1	2	143.2	<1	4	93.8	<1				8	57.0	<1
Ephemeroptera	Caenidae	*Caenis*	1	10.6	<1	2	3.3	<1										3	3.3	<1
	Ephemeridae	*Hexagenia*				3	128.4	<1	1	34.6	<1							4	42.5	<1
		Total Ephemeroptera	1	10.6	<1	5	131.7	<1	1	34.6	<1							7	45.8	<1

(Continued)

Appendix 2. (Continued).

			Depth (m)															Total (N=69)		
			0-2 (N=16)			>2-5 (N=18)			>5-10 (N=18)			>10-20 (N=12)			>20 (N=5)					
			f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density
Trichoptera	Hydroptilidae	*Hydroptila*	2	24.9	<1	2	8.3	<1										4	7.9	<1
	Leptoceridae	*Oecetis*	1	3.3	<1	1	0.6	<1	1	0.8	<1							3	1.1	<1
		Total Trichoptera	2	28.2	<1	3	8.8	<1	1	0.8	<1							6	9.1	<1
Coleoptera	Elmidae	*Optioservus*				1	1.6	<1										1	0.4	<1
		Stenelmis				1	0.8	<1										1	0.2	<1
	Coleoptera	Total Coleoptera				1	2.5	<1										1	0.6	<1
Diptera	Ceratopogonidae	Ceratopogonidae				1	2.5	<1										1	0.6	<1
	Chironomidae	Unident Chironomidae										1	1.2	<1				1	0.2	<1
	Diamesinae	*Monodiamesa*							1	2.4	<1	1	6.4	<1				2	1.7	<1
		Potthastia				1	0.6	<1	1	0.6	<1							2	0.3	<1
		Total Diamesinae				1	0.6	<1	1	2.9	<1	1	6.4	<1				3	2.0	<1
	Chironomini	*Chironomus*	5	25.8	<1	12	152.6	<1	16	528.7	**2.1**	12	547.8	**1.5**	2	145.2	<1	47	289.5	**7.8**
		Crytpochironomus	11	107.6	<1	15	165.4	<1	10	45.9	<1	2	3.7	<1	2	41.5	<1	40	83.7	**5.6**
		Cyphomella	2	8.8	<1	1	1.2	<1										3	2.4	<1
		Dicrotendipes	2	90.8	<1	4	12.4	<1	1	2.4	<1							7	24.9	<1
		Dicrotendipes lt	2	42.1	<1	2	4.1	<1	1	0.6	<1							5	11.0	<1
		Total *Dicrotendipes*	2	133.0	<1	5	16.5	<1	2	2.9	<1							9	35.9	<1
		Hamischia grp							2	14.8	<1				1	3.0	<1	3	4.1	<1
		Microtendipes				2	10.0	<1	3	21.4	<1	2	4.3	<1				7	8.9	<1
		Microtendipes dk	3	12.9	<1													3	3.0	<1
		Parachironomus							1	0.6	<1							1	0.2	<1
		Paracladopelma							2	1.4	<1							2	0.4	<1
		Paratendipes	1	0.7	<1	2	20.6	<1										3	5.5	<1
		Phaenopsectra	1	2.0	<1	1	2.9	<1	1	0.6	<1							3	1.4	<1
		Polypedilum	2	10.9	<1	8	332.8	**1.4**	5	13.4	<1	1	2.1	<1				16	93.2	**1.6**
		Pseudochirnomus	2	63.9	<1	5	18.8	<1	4	21.9	<1				1	20.7	<1	12	26.9	<1
		Saetheria	1	7.4	<1													1	1.7	<1
		Stictochironomus	2	5.6	<1	2	12.3	<1	4	15.6	<1							8	8.6	<1
		Total Chironomini	15	378.5	**1.4**	18	733.3	**3.0**	18	667.3	**2.7**	12	557.9	**1.5**	3	210.3	<1	66	565.4	**18.2**
	Tanytarsini	Unident Tanytarsini	3	123.3	<1	2	8.3	<1	2	10.6	<1	1	2.7	<1				8	34.0	<1
		Cladotanytarsus				1	1.2	<1										1	0.3	<1
		Microspectra				1	1.6	<1	1	0.8	<1							2	0.6	<1
		Paratanytarsus	1	1.4	<1													1	0.3	**1.4**
		Rheotanytarsus				2	7.4	<1										2	1.9	<1
		Tanytarsus	4	66.4	<1	7	30.4	<1	10	992.6	**4.0**	11	432.5	**1.2**	2	47.4	<1	34	360.9	**3.9**
		Total Tanytarsini	7	191.1	<1	10	49.0	<1	11	1004.0	**4.1**	12	435.1	**1.2**	2	47.4	<1	42	398.1	**5.7**
		Unident Chironominae	1	134.0	<1	1	7.1	<1	1	1.8	<1							3	33.4	<1
		Total Chironominae	16	703.6	**2.5**	18	789.3	**3.2**	18	1673.1	**6.8**	12	993.0	**2.7**	3	257.7	<1	67	996.9	**24.0**
	Orthocladiinae	*Cricotopus*	2	15.9	<1	2	3.1	<1										4	4.5	<1
		Epoicocladius							1	1.6	<1							1	0.4	<1
		Heterotrissocladius										1	9.9	<1				1	1.7	<1
		Psectrocladius	2	4.3	<1	2	31.2	<1	2	7.7	<1							6	11.1	<1
		Tvetenia				1	0.8	<1										1	0.2	<1
		Total Orthocladiinae	2	20.2	<1	4	35.1	<1	3	9.3	<1	1	9.9	<1				10	18.0	<1

(Continued)

Appendix 2. (Continued).

			Depth (m)																	
			0-2 (N=16)			>2-5 (N=18)			>5-10 (N=18)			>10-20 (N=12)			>20 (N=5)			Total (N=69)		
			f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density
	Tanypodinae	*Ablabesmyia*				3	21.1	<1	1	0.8	<1							4	5.7	<1
		Apsectrotanypus							1	0.8	<1							1	0.2	<1
		Coelotanypus				3	158.0	<1	4	42.0	<1							7	52.2	**1.1**
		Conchapelopia	1	18.6	<1	1	0.6	<1										2	4.5	<1
		Paramerina	1	1.9	<1	2	18.9	<1	3	3.3	<1	1	4.9	<1				7	7.1	<1
		Procladius	1	3.3	<1	7	20.1	<1	11	47.0	<1	9	133.6	<1	3	23.7	<1	31	43.2	<1
		Tanypus				1	2.5	<1										1	0.6	<1
		Total Tanypodinae	2	23.7	<1	8	221.2	<1	12	93.9	<1	9	138.5	<1	3	23.7	<1	34	113.5	**2.2**
		Total Chironomidae	16	747.6	**2.7**	18	1046.2	**4.2**	18	1779.3	**7.2**	12	1149.0	**3.1**	3	281.4	<1	67	1130.7	**26.3**
Oligochaeta	Lumbriculidae	Unident Lumbriculidae	2	20.5	<1	1	11.8	<1	3	39.9	<1							6	18.2	<1
		Stylodrilus herringianus													2	201.5	<1	2	14.6	<1
		Total Lumbriculidae	2	20.5	<1	1	11.8	<1	3	39.9	<1				2	201.5	<1	8	32.8	<1
	Naididae	Unident Naididae	2	42.1	<1	3	156.2	<1	2	79.6	<1	1	2.1	<1				8	71.6	<1
		Arcteonais lomondi							1	0.8	<1							1	0.2	<1
		Dero digitata				1	2.5	<1	1	14.8	<1							2	4.5	<1
		Nais bretscheri				2	33.7	<1										2	8.8	<1
		Nais communis	1	3.7	<1													1	0.9	<1
		Nais simplex				3	4.9	<1	3	59.3	<1	1	8.6	<1				7	18.2	<1
		Nais variabilis				4	11.5	<1	5	61.7	<1							9	19.1	<1
		Total *Nais*	1	3.7	<1	7	50.2	<1	6	120.9	<1	1	8.6	<1				15	47.0	<1
		Ophidonais serpentina							2	8.2	<1							2	2.1	<1
		Piguetiella michiganensis	9	217.7	<1	13	161.1	<1	2	4.1	<1							24	93.6	**6.2**
		Specaria josinae				1	2.5	<1										1	0.6	<1
		Stylaria lacustris							2	10.7	<1	1	13.6	<1				3	5.2	<1
		Uncinais uncinata	5	78.7	<1	6	73.2	<1	1	0.8	<1	1	1.2	<1				13	37.8	**2.6**
		Vejdovskyella							1	1.2	<1	1	51.0	<1				2	9.2	<1
		Vejdovskyella intermedia	1	0.9	<1	1	2.3	<1	1	12.0	<1							3	4.0	<1
		Total *Vejdovskyella*	1	0.9	<1	1	2.3	<1	2	13.2	<1	1	51.0	<1				5	13.1	<1
		Total Naididae	12	343.2	**1.2**	17	448.0	**1.8**	11	253.2	**1.0**	3	76.6	<1				43	275.8	**10.9**
	Tubificidae	*Aulodrilus americanus*										1	9.9	<1	1	3.0	<1	2	1.9	<1
		Aulodrilus piqueti				1	21.4	<1										1	5.6	<1
		Aulodrilus pluriseta	1	0.9	<1	3	19.8	<1	6	13.2	<1							10	8.8	<1
		Total *Aulodrilus*	1	0.9	<1	4	41.1	<1	6	13.2	<1	1	9.9	<1	1	3.0	<1	13	16.3	<1
		Branchiura sowerbyi				1	1.6	<1	3	51.9	<1							4	14.0	<1
		Ilyodrilus templetoni							2	1.6	<1							2	0.4	<1
		Imm Tubificid with hair	3	50.2	<1	8	32.5	<1	12	300.9	**1.2**	7	119.0	<1	4	38.5	<1	34	122.1	**1.5**
		Imm Tubificid no hair	10	786.8	**2.8**	18	895.9	**3.6**	18	1806.9	**7.3**	12	2323.9	**6.3**	5	1665.0	**1.9**	63	1412.3	**24.3**
		Potamothrix vejdovskyi				4	8.1	<1	9	387.7	**1.6**	1	24.7	<1	2	80.0	<1	16	113.4	**1.1**
		Potamothrix moldaviensis	3	10.2	<1	9	58.4	<1	7	59.9	<1	2	26.8	<1	3	47.4	<1	24	41.3	**1.0**
		Total *Potamothrix*	3	10.2	<1	11	66.6	<1	11	447.6	**1.8**	2	51.5	<1	3	127.4	<1	30	154.7	**2.2**
		Limnodrilus cervix				1	2.4	<1	5	42.0	<1							6	11.6	<1
		Limnodrilus claparedianus							1	2.8	<1							1	0.7	<1
		Limnodrilus hoffmeisteri				7	15.6	<1	7	31.3	<1	5	13.6	<1	4	91.8	<1	23	21.3	<1
		Total *Limnodrilus*				8	18.0	<1	9	76.1	<1	5	13.6	<1	4	91.8	<1	26	33.6	<1

(Continued)

Appendix 2. (Continued).

			Depth (m)																Total (N=69)		
			0-2 (N=16)			>2-5 (N=18)			>5-10 (N=18)			>10-20 (N=12)			>20 (N=5)					
			f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density	f	Mean Density	Percent Density
		Spirosperma ferox							1	59.3	<1	6	217.8	<1	2	136.3	<1	9	63.2	**1.3**
		Tubifex tubifex													2	5.9	<1	2	0.4	<1
		Total Tubificidae	12	848.1	**3.1**	18	1055.8	**4.3**	18	2757.4	**11.2**	12	2735.7	**7.4**	5	2067.9	**2.3**	65	1817.0	**30.5**
		Total Oligochaeta	13	1211.8	**4.4**	18	1515.6	**6.2**	18	3050.5	**12.4**	12	2812.3	**7.6**	5	2269.4	**2.6**	66	2125.7	**41.9**
Hirudinea	Erpobdellidae	*Erpobdella punctata*				1	0.6	<1										1	0.2	<1
	Glossiphoniidae	*Helobdella*							4	5.8	<1	1	7.4	<1				5	2.8	<1
		Helobdella stagnalis				1	4.1	<1	5	33.7	<1	2	11.1	<1				8	11.8	<1
		Total *Helobdella*				1	4.1	<1	6	39.5	<1	3	18.5	<1				10	14.6	<1
		Total Hirudinea				2	4.7	<1	6	39.5	<1	3	18.5	<1				11	14.8	<1
		Total		5433.9	19.6		5557.9	22.6		7404.7	30.1		8044.7	21.8		5323.9	6.0		6426.45	

Appendix 3. Basin and lake-wide frequency of occurrence (f), mean density (individuals m^{-2}), lake total and within-basin percent density of all non-*Dreissena* macroinvertebrates from Lake Erie, 2002. N=total number is sites sampled.

			Basin														
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density
Cnidaria	Hydridae	*Hydridae*					10	230.1	3.4	6.3	4	19.4	<1	<1	14	141.5	3.6
Platyhelminthes	Tricladida	*Dugesia*									1	0.9	<1	<1	1	0.2	<1
		Planariidae	1	1.3	<1	<1	6	54.7	<1	1.5					7	32.7	<1
		Total Planariidae	1	1.3	<1	<1	6	54.7	<1	1.5	1	0.9	<1	<1	8	33.0	<1
	Proseriata	*Hydrolimax*									2	4.7	<1	<1	2	1.2	<1
		Turbellaria									1	58.0	<1	1.1	1	14.3	<1
		Total Platyhelminthes	1	1.3	<1	<1	6	54.7	<1	1.5	4	63.7	<1	1.2	11	48.4	1.2
Gastropoda	Bithyniidae	*Bithynia tentaculata*					2	5.4	<1	<1	1	20.9	<1	<1	3	8.4	<1
	Hydrobiidae	*Amnicola limosa*	2	16.2	<1	<1	2	6.5	<1	<1	5	19.7	<1	<1	9	11.3	<1
		Marstonia decepta									1	52.4	<1	<1	1	12.9	<1
	Physidae	*Physa*									1	0.9	<1	<1	1	0.2	<1
	Pleuroceridae	*Elimia livescens*					1	0.4	<1	<1					1	0.2	<1
		Pleurocera acuta									2	16.9	<1	<1	2	4.2	<1
	Valvatidae	*Valvata perdepressa*					1	0.4	<1	<1					1	0.2	<1
		Valvata piscinalis					1	0.7	<1	<1					1	0.4	<1
		Valvata sincera					3	3.6	<1	<1					3	2.1	<1
	Gastropoda	Total Gastropoda	2	16.2	<1	<1	10	17.0	<1	<1	7	110.7	<1	2.0	19	39.9	1.0
Bivalvia	Dreissenidae	*Dreissena bugensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		Dreissena polymorpha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
		Total Dreissena	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sphaeriidae	Unident Sphaeriidae	2	44.4	<1	1.5	5	55.3	<1	1.5					7	39.9	1.0
		Pisidium	6	162.9	<1	5.5	9	121.4	1.8	3.3					15	98.1	2.5
		Sphaerium	3	56.6	<1	1.9	4	24.9	<1	<1					7	23.8	<1
		Sphaerium corneum					2	6.1	<1	<1					2	3.6	<1
		Sphaerium rhombiodium	1	9.4	<1	<1	1	7.6	<1	<1	1	0.9	<1	<1	3	6.2	<1
		Total *Sphaerium*	4	66.0	<1	2.2	6	38.7	<1	1.1	1	0.9	<1	<1	11	33.7	<1
		Total Sphaeriidae	6	273.4	1.1	9.2	12	215.3	3.2	5.9	1	0.9	<1	<1	19	171.7	4.3
Hydracarina	Hydracarina	*Hydracarina*	3	6.7	<1	<1	9	12.6	<1	<1	7	126.8	<1	2.3	19	39.8	1.0
Amphipoda	Gammaridae	*Echinogammarus ischnus*					2	10.8	<1	<1	9	108.7	<1	2.0	11	33.2	<1
		Gammarus fasciatus					4	8.1	<1	<1	7	443.9	2.8	8.2	11	114.2	2.9
		Gammarus pseudolimneas					1	0.4	<1	<1					1	0.2	<1
		Total Amphipoda					6	19.3	<1	<1	11	552.5	3.4	10.2	17	147.6	3.7
Isopoda		*Caecidotea*					5	60.0	<1	1.6					5	35.6	<1
		Caecidotea intermedius					1	0.4	<1	<1					1	0.2	<1
		Caecidotea racovitzai					3	30.3	<1	<1					3	18.0	<1
		Lirceus									1	12.5	<1	<1	1	3.1	<1
		Total Isopoda					7	90.7	1.4	2.5	1	12.5	<1	<1	8	57.0	1.4

(Continued)

Appendix 3. (Continued).

			Basin														
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density
Ephemeroptera	Caenidae	*Caenis*					2	1.4	<1	<1	1	10.0	<1	<1	3	3.3	<1
	Ephemeridae	*Hexagenia*	4	266.6	1.1	9.0									4	42.5	1.1
		Total Ephemeroptera	4	266.6	1.1	9.0	2	1.4	<1	<1	1	10.0	<1	<1	7	45.8	1.2
Trichoptera	Hydroptilidae	*Hydroptila*									4	32.1	<1	<1	4	7.9	<1
	Leptoceridae	*Oecetis*					1	0.4	<1	<1	2	3.7	<1	<1	3	1.1	<1
	Trichoptera	Total Trichoptera					1	0.4	<1	<1	5	35.9	<1	<1	6	9.1	<1
Coleoptera	Elmidae	*Optioservus*	1	2.7	<1	<1									1	0.4	<1
		Stenelmis	1	1.3	<1	<1									1	0.2	<1
	Coleoptera	Total Coleoptera	1	4.0	<1	<1									1	0.6	<1
Diptera	Ceratopogonidae	Ceratopogonidae					1	1.1	<1	<1					1	0.6	<1
	Chironomidae	Unident Chironomidae					1	0.4	<1	<1					1	0.2	<1
	Diamesinae	*Monodiamesa*									2	7.0	<1	<1	2	1.7	<1
		Potthastia									2	1.2	<1	<1	2	0.3	<1
		Total Diamesinae									3	8.2	<1	<1	3	2.0	<1
	Chironomini	*Chironomus*	8	315.1	1.3	10.6	27	320.1	4.8	8.8	12	199.1	1.2	3.7	47	289.5	7.3
		Crytpochironomus	10	191.2	<1	6.4	25	79.5	1.2	2.2	5	24.4	<1	<1	40	83.7	2.1
		Cyphomella					3	4.0	<1	<1					3	2.4	<1
		Dicrotendipes					2	3.6	<1	<1	5	92.4	<1	1.7	7	24.9	<1
		Dicrotendipes lt									5	44.6	<1	<1	5	11.0	<1
		Total *Dicrotendipes*					2	3.6	<1	<1	7	137.0	<1	2.5	9	35.9	<1
		Hamischia grp					2	6.5	<1	<1	1	0.9	<1	<1	3	4.1	<1
		Microtendipes					1	2.2	<1	<1	6	31.1	<1	<1	7	8.9	<1
		Microtendipes dk									3	12.2	<1	<1	3	3.0	<1
		Parachironomus									1	0.6	<1	<1	1	0.2	<1
		Paracladopelma					1	0.4	<1	<1	1	0.6	<1	<1	2	0.4	<1
		Paratendipes									3	22.5	<1	<1	3	5.5	<1
		Phaenopsectra									3	5.6	<1	<1	3	1.4	<1
		Polypedilum	2	22.9	<1	<1	5	120.5	1.8	3.3	9	73.0	<1	1.3	16	93.2	2.3
		Pseudochirnomus	4	114.5	<1	3.9	4	4.5	<1	<1	4	24.3	<1	<1	12	26.9	<1
		Saetheria					1	2.9	<1	<1					1	1.7	<1
		Stictochironomus	2	20.2	<1	<1	6	9.0	<1	<1					8	8.6	<1
		Total Chironomini	11	663.9	2.7	22.4	40	553.2	8.3	15.2	15	531.2	3.3	9.8	66	565.4	14.2
	Tanytarsini	Unident Tanytarsini									8	137.9	<1	2.5	8	34.0	<1
		Cladotanytarsus					1	0.5	<1	<1					1	0.3	<1
		Microspectra	1	2.7	<1	<1	1	0.4	<1	<1					2	0.6	<1
		Paratanytarsus					1	0.5	<1	<1					1	0.3	<1
		Rheotanytarsus					2	3.3	<1	<1					2	1.9	<1
		Tanytarsus	8	57.9	<1	2.0	20	561.5	8.4	15.4	6	73.4	<1	1.4	34	360.9	9.1
		Total Tanytarsini	8	60.6	<1	2.0	22	566.2	8.5	15.6	12	211.3	1.3	3.9	42	398.1	10.0
		Unident Chironominae									3	135.4	<1	2.5	3	33.4	<1
		Total Chironominae	11	724.5	2.9	24.4	41	1119.3	16.7	30.8	15	878.0	5.4	16.2	67	996.9	25.1

(Continued)

Appendix 3. (Continued).

			Basin															
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density
	Orthocladiinae	*Cricotopus*					1	1.1	<1	<1	3	15.6	<1	<1	4	4.5	<1
		Epoicocladius	1	2.7	<1	<1									1	0.4	<1
		Heterotrissocladius									1	7.0	<1	<1	1	1.7	<1
		Psectrocladius									6	45.2	<1	<1	6	11.1	<1
		Tvetenia	1	1.3	<1	<1									1	0.2	<1
		Total Orthocladiinae	2	4.0	<1	<1	1	1.1	<1	<1	7	67.8	<1	1.2	10	18.0	<1
	Tanypodinae	*Ablabesmyia*	3	31.0	<1	1.0					1	3.1	<1	<1	4	5.7	<1
		Apsectrotanypus					1	0.4	<1	<1					1	0.2	<1
		Coelotanypus	6	325.9	1.3	11.0	1	0.4	<1	<1					7	52.2	1.3
		Conchapelopia									2	18.1	<1	<1	2	4.5	<1
		Paramerina	6	39.1	<1	1.3					1	3.5	<1	<1	7	7.1	<1
		Procladius	5	35.0	<1	1.2	16	44.8	<1	1.2	10	44.8	<1	<1	31	43.2	1.1
		Tanypus	1	4.0	<1	<1									1	0.6	<1
		Total Tanypodinae	8	435.0	1.7	14.7	16	45.5	<1	1.3	10	69.5	<1	1.3	34	113.5	2.9
		Total Chironomidae	11	1163.5	4.7	39.2	41	1166.3	17.4	32.1	15	1023.6	6.3	18.8	67	1130.7	28.5
Oligochaeta	Lumbriculidae	Unident Lumbriculidae					3	24.1	<1	<1	3	15.9	<1	<1	6	18.2	<1
		Stylodrilus herringianus									2	59.3	<1	1.1	2	14.6	<1
		Total Lumbriculidae					3	24.1	<1	<1	5	75.2	<1	1.4	8	32.8	<1
	Naididae	Unident Naididae									8	290.8	1.8	5.4	8	71.6	1.8
		Arcteonais lomondi	1	1.3	<1	<1									1	0.2	<1
		Dero digitata	2	28.3	<1	<1									2	4.5	<1
		Nais bretscheri					2	14.8	<1	<1					2	8.8	<1
		Nais communis	1	5.4	<1	<1									1	0.9	<1
		Nais simplex	2	2.7	<1	<1	5	30.0	<1	<1					7	18.2	<1
		Nais variabilis					9	32.1	<1	<1					9	19.1	<1
		Total *Nais*	3	8.1	<1	<1	12	76.9	1.2	2.1					15	47.0	1.2
		Ophidonais serpentina					2	3.6	<1	<1					2	2.1	<1
		Piguetiella michiganensis	7	261.3	1.0	8.8	17	87.4	1.3	2.4					24	93.6	2.4
		Specaria josinae	1	4.0	<1	<1									1	0.6	<1
		Stylaria lacustris					3	8.7	<1	<1					3	5.2	<1
		Uncinais uncinata	4	114.5	<1	3.9	9	32.9	<1	<1					13	37.8	<1
		Vejdovskyella									2	37.3	<1	<1	2	9.2	<1
		Vejdovskyella intermedia					3	6.7	<1	<1					3	4.0	<1
		Total *Vejdovskyella*					3	6.7	<1	<1	2	37.3	<1	<1	5	13.1	<1
		Total Naididae	9	417.5	1.7	14.1	25	216.2	3.2	5.9	9	328.1	2.0	6.0	43	275.8	6.9

(Continued)

Appendix 3. (Continued).

			Basin														
			West (N=11)				Central (N=41)				East (N=17)				Total (N=69)		
			f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density	Percent Basin Non-*Dreissena* Density	f	Mean Density	Percent Total Non-*Dreissena* Density
	Tubificidae	*Aulodrilus americanus*					1	2.9	<1	<1	1	0.9	<1	<1	2	1.9	<1
		Aulodrilus piqueti	1	35.0	<1	1.2									1	5.6	<1
		Aulodrilus pluriseta	5	37.7	<1	1.3	5	4.7	<1	<1					10	8.8	<1
		Total *Aulodrilus*	6	72.7	<1	2.5	6	7.6	<1	<1	1	0.9	<1	<1	13	16.3	<1
		Branchiura sowerbyi	2	5.4	<1	<1	2	22.0	<1	<1					4	14.0	<1
		Ilyodrilus templetoni	1	1.3	<1	<1	1	0.4	<1	<1					2	0.4	<1
		Imm Tubificid with hair	6	26.9	<1	<1	17	141.8	2.1	3.9	11	136.1	<1	2.5	34	122.1	3.1
		Imm Tubificid no hair	11	584.5	2.3	19.7	35	1049.7	15.7	28.9	17	2822.6	17.5	52.0	63	1412.3	35.5
		Potamothrix vejdovskyi					13	173.8	2.6	4.8	3	41.0	<1	<1	16	113.4	2.9
		Potamothrix moldaviensis	3	22.9	<1	<1	15	49.5	<1	1.4	6	33.5	<1	<1	24	41.3	1.0
		Total *Potamothrix*	3	22.9	<1	<1	21	223.3	3.3	6.1	6	74.4	<1	1.4	30	154.7	3.9
		Limnodrilus cervix	3	24.2	<1	<1	3	13.0	<1	<1					6	11.6	<1
		Limnodrilus claparedianus					1	1.2	<1	<1					1	0.7	<1
		Limnodrilus hoffmeisteri	7	45.8	<1	1.5	11	10.8	<1	<1	5	30.5	<1	<1	23	21.3	<1
		Total *Limnodrilus*	7	70.0	<1	2.4	14	25.1	<1	<1	5	30.5	<1	<1	26	33.6	<1
		Spirosperma ferox					7	103.7	1.6	2.8	2	6.5	<1	<1	9	63.2	1.6
		Tubifex tubifex									2	1.7	<1	<1	2	0.4	<1
		Total Tubificidae	11	783.8	3.1	26.4	37	1573.6	23.5	43.2	17	3072.8	19.1	56.6	65	1817.0	45.7
		Total Oligochaeta	11	1201.2	4.8	40.5	38	1813.8	27.1	49.9	17	3476.0	21.6	64.0	66	2125.7	53.5
Hirudinea	Erpobdellidae	*Erpobdella punctata*									1	0.6	<1	<1	1	0.2	<1
	Glossiphoniidae	*Helobdella*	3	8.1	<1	<1	2	2.5	<1	<1					5	2.8	<1
		Helobdella stagnalis	2	25.6	<1	<1	6	13.0	<1	<1					8	11.8	<1
		Total *Helobdella*	3	33.7	<1	1.1	7	15.5	<1	<1					10	14.6	<1
		Total Hirudinea	3	33.7	<1	1.1	7	15.5	<1	<1	1	0.6	<1	<1	11	14.8	<1
		Total Non-*Dreissena* Invertebrates		2966.7	11.9			3638.4	54.4			5432.6	33.7			3973.4	