ENVIRONMENTAL ASSESSMENT OF THE BENTHIC MACROINVERTEBRATE COMMUNITY OF MUSKEGON LAKE, MICHIGAN, 1999, AND EVALUATION OF CHANGES SINCE 1972

by

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For my son, Sam, an endless source
of joy and amazement.

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Introduction

Composition of the benthic macroinvertebrate community is widely considered an effective tool for evaluating environmental (trophic) conditions. Benthic macroinvertebrates are found in most habitats and relatively easy to sample quantitatively (Wiederholm 1980; Canfield *et al.* 1996). Moreover, they form stable communities that integrate conditions of both pelagic and benthic zones over relatively long periods of time (Wiederholm 1980; Nalepa 1987). Since the benthos are confined to habitat that continually receives autochthonous and allochthonous material, they serve as an integral measure of autotrophic and heterotrophic processes in lakes (Wiederholm 1980). Species assemblages and presence or absence of key "indicator" species reflect environmental conditions and can be used to assess a lake's trophic state (Wiederholm 1980; Milbrink 1983; Nalepa 1987). For example, the tubificid worm *Limnodrilus hoffmeisteri* is often found in high densities in areas with gross organic pollution; conversely, the mayfly *Hexagenia* is generally found in relatively pristine or less productive (oligotrophic) habitats (Howmiller and Scott 1977; Milbrink 1983; Schloesser *et al.* 1995).

Benthic surveys give a "snapshot" of trophic conditions in a lake at the time samples were taken and may be a reflection of recent events. However, comparisons with historical records can be used to assess trends in environmental conditions and trophic state (Nalepa *et al.* 2000). Indicator species have been particularly effective in quantifying changes based on comparisons with historical records (Carr and Hiltunen 1965; Nalepa 1991; Krieger and Ross 1993; Harman 1997; Lang 1998). As seen in the Great Lakes prior to the mid-1970s, increased densities of most benthic groups and reduced densities of intolerant taxa, generally reflected eutrophication resulting from increased nutrient loads (especially phosphorus). Nutrient abatement efforts implemented in the mid-1970s have been credited for increases in less tolerant taxa as well as an overall decrease in abundances of benthic macroinvertebrates in Lakes Michigan, Erie, and Ontario (Nalepa 1987, 1991; Schloesser *et al.* 1995). Given the difficulty of lake-

wide experimental manipulations, historical comparisons may be the only practical method to assess changes resulting from human activities (Barton and Anholt 1997). Historical records provide a baseline against which more recent studies can be compared in order to determine degree, extent, and rate of improvement (or decline) of habitat conditions in a particular lake or following a particular event (Wiederholm 1980; Nalepa 1987; Schloesser *et al.* 1995).

In this study, abundance and species composition of the benthic macroinvertebrate community in Muskegon Lake was examined. The first objective was to evaluate benthic distributions relative to known areas of environmental degradation. Sampling was mainly focused along the southern shore where most industrial discharges historically occurred. The second objective was to examine changes since the diversion of municipal and industrial wastewater to a treatment facility in 1973.

Study Area

Muskegon Lake is a large, drowned river mouth lake (1680 ha) and is directly connected to Lake Michigan, to the west, through a navigational channel. Mean depth is 7.1 m and maximum depth is 21 m, based on a low-water datum of 175.4 m above sea level for Lake Michigan (Evans 1992). Lake volume is about 119 million m^3. Mean hydraulic retention time is about 23 days. The Muskegon River enters the lake on the eastern end and is the second longest river in the state (352 km) with a 6,819-km^2 watershed. Mean annual flow is 55.5 $m^3 \cdot s^{-1}$and accounts for 95% of the flow to Muskegon Lake.

In the 1960s and early 1970s Muskegon Lake received over 1 million m^3 of wastewater from direct discharge from industrial and municipal sources daily (Evans 1992; GLC 2000). As a result, degraded conditions were observed in much of the lake as well as high sediment concentrations of heavy metals and oils (Evans 1992). Evans (1992) includes a detailed review of studies that point out areas and sources of degradation, including oil slicks on the surface, high quantities of oil and grease in the

sediments, thermal pollution, phenols, heavy metals from metal finishing operations, tainted fish, frequent algal blooms, and high nutrient concentrations. Generally, oligochaetes were dominant, and species richness and diversity were low across the lake indicating eutrophic (degraded) conditions were prevalent in 1972, especially the southeastern portion of the lake (Evans 1976).

Methods

Sample Collection

Sediment samples were collected on October 28, 29, and November 9, 1999 at each of the 27 sites (Figure 1, Table 1). Triplicate samples were taken at each site with a petite PONAR grab (15.24 cm x 15.24 cm). Fifteen of the 27 sites were also sampled for heavy metals and total organic carbon. Each sample was washed into a large tub and then washed into an elutriation device with a 0.5-mm, nitex-mesh sleeve, to remove silt and other fine particles. Material and organisms retained were then preserved in 10% buffered formaldehyde, containing rose bengal stain.

Laboratory Procedures

In the laboratory, retained residue was transferred to a white enamel pan, and all organisms were removed and sorted into groups (amphipods, oligochaetes, sphaeriids, chironomids, *Dreissena*, gastropods, and other) using a 1.75X magnifier lamp. Samples with large numbers of *Dreissena* were split (one quarter to one half) by placing the sample in a pan divided into four equal sections by lines on the bottom. A randomly selected portion was picked and appropriate factor was used to obtain the total number in the sample. All organisms were identified to the lowest practical taxonomic level. Oligochaetes were reduced proportionately with a Folsom plankton splitter whenever counts were ≥ 200 in a sample, so at least 100 were identified. Chironomids and oligochaetes were placed in lacto-no-phenol and warmed for 20 min at 60°C for clearing. Specimens were then mounted on slides in 100% glycerol for identification. The taxonomic group and the keys used for species identifications were as follows:

Oligochaetes (Kathman and Brinkhurst 1998); Chironomidae (Epler 1995); Hirudinea (Klemm 1972); Trichoptera (Wiggins 1977); and Ephemeroptera (Burks 1953). Gastropods were identified by Dr. John Burch (University of Michigan Museum of Zoology, Mollusk Division, Ann Arbor, MI).

Statistical Analysis

Spatial distribution patterns were examined using multivariate techniques. Sites with similar communities were identified by using K-means divisive classification followed by centroid cluster analysis (Schloesser *et al.* 1995). The K-means classification allows for the *a priori* selection of the number of groups to parse the sites and identifies taxa important in the grouping of sites. Selected taxa were those that fell above the inflection point on a plot of ranked F-ratios. Analysis with the K-means was conducted with 2, 4, 6, 8, and 10 groups specified, in order to evaluate the robustness of the data and to find which taxa would result in the most sites being grouped. Selected taxa were then used in centroid cluster analysis to identify site groups. Centroid cluster analysis creates groups based on similarities across sites, and the investigator cannot control the number of site groups that will result. All data were ln+1 transformed prior to analysis.

Trophic Index

The Trophic Condition Index (TCI) based on abundance of individual oligochaete species was calculated following Milbrink (1983) to evaluate conditions at each sampling site and to give an overall picture of conditions in Muskegon Lake. Each species of oligochaete was placed in one of four categories based on ecological requirements or degree of enrichment in which it is typically found (Appendix A). Group 0 includes species characteristic of oligotrophic conditions, Group 1 contains species typically found in mesotrophic or slightly enriched conditions, and Group 2 comprises species known to be tolerant of eutrophic or considerably enriched conditions. Group 3 contains only *Limnodrilus hoffmeisteri* and *Tubifex tubifex* because these species can tolerate gross

organic pollution. The Trophic Condition Index (TCI) was calculated:

$$TCI = c * \frac{1/2\,\Sigma n_0 + \Sigma n_1 + 2\Sigma n_2 + 3\Sigma n_3}{\Sigma n_0 + \Sigma n_1 + \Sigma n_2 + \Sigma n_3}$$

Where n_0, n_1, n_2, and n_3 are the total number of oligochaetes·m^{-2} in each of the four ecological groups. The coefficient "c" adjusts the result based on the total abundance of oligochaetes following:

C=1 when	abundance (n) > 3,600 specimen·m^{-2}
C= 3/4	1,200< n < 3,600
C= 1/2	400< n < 1,200
C= 1/4	130< n < 400
C= 0	n < 130

Another TCI was calculated based on species of chironomids (Winnell and White 1985). The index is basically a modification of Howmiller and Scott (1977), but chironomids are used instead of oligochaetes. The chironomid TCI used here differs from the TCI used for oligochaetes in that it has three ecological categories instead of four (i.e., 0-2) and does not have the "c" coefficient to adjust for total abundance. The trophic tolerance of species follows that of Winnell and White (1985). When a species was encountered that was not classified in Winnell and White (1985) who dealt with Southeastern Lake Michigan, the biotic index by Hilsenhoff (1987) and regional tolerance values from Barbour *et al.* (1999) were used to make classifications. The classification schemes of both Hilsenhoff (1987) and Barbour *et al.* (1999) were on a ten-point scale, and were partitioned among the ecological groups within the TCI. The chironomid TCI was calculated in order to make comparisons with the 1972 data.

Historical Comparisons

Data collected in the present study were compared with data collected in 1972 (Evans 1976). The 1972 study sampled at 52 sites with a petite PONAR, and sediments were washed through a 0.60-mm-mesh screen. Sites in the present study were matched

with sites sampled in 1972 as closely as possible, based on geographic proximity and depth. Since oligochaetes were not identified in 1972, oligochaete taxa were lumped into a single group (as oligochaetes). The following metrics were calculated for each year: Shannon-Weaver diversity with $\log_2$, as in Evans (1976), oligochaete-chironomid ratio (calculated as density of oligochaetes/ density of oligochaetes + density of chironomids and reported as a percentage), mean number of taxa at each site, proportion of oligochaetes, and the chironomid TCI. The oligochaete-chironomid ratio generally reflects the tendency for tolerant oligochaete species to increase their abundance relative to sedentary chironomids in conditions of nutrient enrichment (Wiederholm 1980). As a result, higher percentages indicate increased abundance of oligochaetes and lower lake quality (Evans 1992). The oligochaete-chironomid ratio was calculated in the current study for comparison with data from 1972. Differences in benthic densities and metrics at paired sites between the two years (1972 vs. 1999) were evaluated using the Mann-Whitney U-test.

Evaluation of changes since 1972 were generally limited to comparisons of broader benthic groups, (i.e., total oligochaetes, total chironomids, etc.) because the surveys in 1972 and 1999 were conducted at different times of the year. The only species that were considered directly were *Pisidium* sp. and *Gammarus* sp., since they tend to vary less within a year and were sampled when young of the year were large enough to be collected quantitatively (Wiederholm 1980). Species (when possible; i.e., *Coelotanypus concinnus*) or genera (i.e., *Procladius* sp.) of Chironomidae were used to calculate the TCI. Another reason for limiting comparisons to general groups is because of differences in taxonomic resolution; oligochaetes were only identified as "oligochaetes" in the 1972 study. It is thought that general groups could give a clearer impression of community changes over time.

Results

Chemistry

Sediment samples were analyzed for heavy metals (including arsenic, barium, cadmium, chromium, copper, nickel, lead, zinc, mercury, and selenium) and total organic carbon (TOC) at sites Musk-1 through Musk-16A (Figure 1) (see Rediske *et al.* 1998, for methods). Highest concentrations for heavy metals were observed at either Musk-5, 6, 7, or 8. Lowest concentrations were consistently found at Musk-4, 12, or 16A. Concentrations ranged from 640 $mg \cdot kg^{-1}$ (dry weight) to levels that were undetectable. Generally, zinc, barium, and lead had the highest mean concentrations with 196 ± 44 $mg \cdot kg^{-1}$ (range 13-640 $mg \cdot kg^{-1}$), 93 ± 13 $mg \cdot kg^{-1}$ (range 10-180 $mg \cdot kg^{-1}$), and 90 ± 20 $mg \cdot kg^{-1}$ (range 5.8-280 $mg \cdot kg^{-1}$), respectively (Table 2). Mercury and selenium had the lowest mean concentrations (0.55 ± 0.13 $mg \cdot kg^{-1}$ and 0.51 ± 0.03 $mg \cdot kg^{-1}$, respectively), and both were undetectable at sites Musk-4, 9, and 12 (Table 2). Selenium only was undetectable at Musk-16A (Table 2). Total organic carbon was variable and ranged from <0.5 to 8.0 % (Table 2). Regression analysis of TOC and proximity to the river mouth indicated they were not significantly related.

Taxa Abundances and Composition

Results of the enumeration and identification of the benthos sampled at 27 sites in 1999 identified a total of 55 taxa, with an average of 10 ± 2.48 taxa per site (range 6-15, Table 3, Figure 1, Appendices A and B). Total density was generally high and ranged between 2,585 and 49,124 $organisms \cdot m^{-2}$ with 19 of 27 sites having >5,000 $organisms \cdot m^{-2}$ (Table 4). Oligochaeta were the most abundant group at all but two of the sites sampled, and densities ranged from 1,767$\cdot m^{-2}$-10,489$\cdot m^{-2}$ (Table 4). Oligochaetes accounted for 12-91% of all organisms collected and exceeded 50% at 20 of the sites sampled (Table 4). The proportion of oligochaetes was the lowest at sites Musk-9 (26.9%) and Musk-12 (12.4%), where *Dreissena* exceeded 15,000$\cdot m^{-2}$ (see figure 1 for site locations). Immature tubificids accounted for 72% (range 35-95%) of the total abundance of

oligochaetes at all sites; the remaining 28% included 18 positively identified taxa (Appendix A). Three oligochaete species, *Aulodrilus pigueti, Limnodrilus hoffmeisteri*, and *Quistadrilus multisetosus* were most common and found at most sites (Appendix A). *Aulodrilus pigueti* occurred at all sites except E-40, and mean abundance was 596 $\pm$ 108·m^{-2} (range 43-2,415·m^{-2}). *Quistadrilus multisetosus* was found at all sites, except E-40, and mean abundance was 224 $\pm$ 52·m^{-2} (range 14-1,335·m^{-2}). Generally considered one of the most tolerant species, *L. hoffmeisteri* was found at all but four sites (Musk-4, Musk-7, Musk-15, and Musk-16A), and mean abundance was 76 $\pm$ 16·m^{-2} (range 14-301·m^{-2}).

Densities of Chironomidae ranged between 1,435·m^{-2} and 273·m^{-2} and were the second-most abundant taxa group at 16 of the 27 sites sampled (Table 4 and Appendix B). A total of 14 taxa was identified (Appendix A). *Chironomus* sp. and *Procladius* sp. were found at all sites except Musk-6 and D-46 (Appendix A). Mean abundance of *Chironomus* sp. was 370 $\pm$ 65·m^{-2} (range 14-1206·m^{-2}) and was generally the most common chironomid encountered. *Procladius* sp. abundance was low, not exceeding 273·m^{-2} and averaged124 $\pm$ 14·m^{-2} across all sites. With the exception of *Coelotanypus concinnus* and *Cryptochironomus* sp., remaining species were found infrequently and were generally low in abundance. Not found at 10 sites, *C. concinnus* tended to be relatively low in abundance ranging from 14-474·m^{-2} (mean 141 $\pm$ 47), with the exception of sites Musk-5 and B-30 with 976 and 718·m^{-2}, respectively, accounting for 78 and 85% of the Chironomidae abundance at these sites. *Cryptochironomus* sp. occurred at all but three sites; however, abundance was low, ranging from 172-14·m^{-2} with a mean of 64 $\pm$ 10·m^{-2} over all sites.

Densities of Sphaeriidae were variable, ranging from not being found at Musk-1 and 4, to low abundance (44·m^{-2}) at 2ML, and to relatively high abundance (1,607·m^{-2}) at Musk-5 (Table 4). *Pisidium* was the predominant genus, ranging from 22-1,550·m^{-2} with 16 of the sites having abundances greater than 200·m^{-2} (Appendix A).

Amphipoda, which included three taxa (*Gammarus* sp., *Hyalella azteca*, and *Echinogammarus ischnus*), were found at all but three sites. However, abundance was generally low ($\leq 359 \cdot m^{-2}$) except at three sites (Table 4). Relatively high abundances of 1,249, 616, and $947 \cdot m^{-2}$ were found at Musk-4, Musk-12, and E-40, respectively. *Gammarus* sp. tended to be the dominant taxa of the three identified, and was found at all but four sites (Appendix A). *Gammarus* sp. abundance was generally the determinant of abundance for the amphipods as a group, with a maximum of $1{,}206 \cdot m^{-2}$ and a minimum of $14 \cdot m^{-2}$. The exotic amphipod *Echinogammarus ischnus* was found at three of the sites sampled (Musk-9, Musk-12, and E-40) in relatively low abundance, from $21\text{-}57 \cdot m^{-2}$.

Sites where oligochaetes were not the most abundant group were Musk-9 and Musk-12. These two sites had high densities of *Dreissena polymorpha*, $25{,}611 \cdot m^{-2}$ and $40{,}860 \cdot m^{-2}$, respectively (Table 4). Overall, densities of *Dreissena*, with the exception of the above sites and site 16A ($5{,}626 \cdot m^{-2}$), were relatively low and did not exceed $359 \cdot m^{-2}$.

The remaining groups, i.e. Turbellaria, Polychaeta, Hirudunea, Gastropoda, Isopoda, Ceratopogonidae, Chaoboridae, Ephemeroptera, and Trichoptera were generally found in low abundance and/or occurred infrequently in Muskegon Lake (other in Table 4). Abundances of the remaining groups and constituent taxa can be found in Appendices A and B. The taxonomic groups described in more detail above, the oligochaetes, Sphaeriidae, *Dreissena*, Chironomidae, and amphipods accounted for 89-100% of the total abundance at all sites, except E-40 in which the above groups accounted for 74% of the total abundance (Table 4).

Distribution Relative to the River Mouth

In order to determine the potential effects of the river input on the benthic community, nine sites were chosen in the deeper region of the lake and were generally located along the submerged river channel. Total abundance declined with increased distance from the river mouth (east to west). There was a significant negative relationship between abundance and distance ($p = 0.04$, $r^2 = 0.48$, Figure 2). A similar

negative relationship was found with *Quistadrilus multisetosus* ($p= 0.002$, $r^2= 0.75$) (Figure 3). In addition, the number of taxa ($p= 0.06$, $r^2= 0.41$) (Figure 4) and total oligochaete abundance ($p= 0.07$, $r^2= 0.39$) (Figure 5) indicated a similar negative relationship to distance from the river mouth, however were less significant. Trends for *Chironomus* sp. were contrary to findings above, where density increased as distance from the river increased ($p= 0.02$, $r^2= 0.57$) (Figure 6). No other metrics or taxonomic groups showed significant relationships.

Trophic Condition Index, Diversity, and Oligochaete-Chironomid ratio

Generally the oligochaete Trophic Condition Index (oligochaete TCI) indicated that communities at each of the sites were characteristic of mesotrophic to eutrophic conditions (Table 3), and that no communities were found to be either indicative of oligotrophic conditions or conditions of gross organic pollution. The mean trophic index score was 1.43 (range 0.78-1.94). Twelve sites (Musk-3, 4, 11, 13, 14, CML, 2ML, B-30, C-40, D-40, D-46, and E-40) had trophic index scores ≥ 1.5 (tending toward eutrophic conditions) eight of which were at depths > 10 m. (Table 3). The 15 remaining sites (Musk-1, 5, 6, 7, 8, 9, 10, 12, 15, 16A, AML, BML, 1ML, 3ML, and 4ML,) had trophic index scores that ranged from 0.78 to 1.48, conditions that tended to be more mesotrophic or meso-eutrophic. Ten of the mesotrophic sites were at depths < 10 m, three of these sites (Musk-5, 6, and 7) had scores < 1. In addition, results indicated a significant positive linear relationship ($p= 0.0007$, $r^2= 0.37$) between depth and the trophic index (Figure 7). The chironomid TCI indicated that all sites in the lake tended to be eutrophic, and no scores were below 1.8 (Table 3).

Species diversity scores ranged from 1.09 to 3.5 but tended to be relatively high. Twenty of the sites sampled had diversity scores ≥ 2.3, and only two sites (Musk-12 and CML) had values <2.00 (Table 3).

The oligochaete-chironomid ratio (O/C) ranged from 67% to 99% (Table 3). Twenty-four of the sites had an O/C ≥ 80%, of which 14 had an O/C ≥ 95%. The

sites, BML, 1ML, 2ML, and E-40, all had scores of 67% and 74%. A significant trend between depth and the O/C was found ($p= 0.02$, $r^2= 0.19$) where the O/C increased while depth decreased (Figure 8), which generally reflected the increase in abundance of *Chironomus* sp. with depth.

Cluster Analysis

In general, clusters were similar across all of the attempts with the different number of groups specified in the K-means classification. The taxa that were used to determine site groups with the centroid cluster analysis were *Aulodrilus americanus*, *A. pigueti*, *A. pluriseta*, *Ilyodrilus templetoni*, *Limnodrilus cervix* var., immature tubificids without hair chaetae, *Amnicola* sp., *Bithynia* sp., *Valvata tricarinata*, *Dreissena*, *Chironomus* sp., and *Ceolotanypus concinnus*. The four site groupings that resulted from the centroid cluster analysis included 18 of the 27 sites (Table 5, Figure 9, Appendix C). The four site groups resulting from the cluster analysis span the entire lake and can generally be referred to by where they occur in the lake (Figure 10, Appendix C). From east to west, the southeastern (SE) cluster was located along the eastern shore near the South Channel of the Muskegon River and the B.C. Cobb power plant. The Hartshorn Anchorage (HA) group is an embayment on the southern shore near the Hartshorn Municipal Marina. The west central (WC) grouping is generally in open lake and occurs in northern central and western areas of the lake. Finally, the south western (SW) cluster was located in the southwestern corner of the lake. The mean depth of the SE group was 9.3 m, and taxa and indices generally indicated that this area was the most enriched of the site groups (Table 5). The site grouping HA was the shallowest with a mean depth of 7.2 m. The indices and taxa present, especially the oligochaete TCI and the density of *A. pigueti,* suggest that this area had the best environmental conditions (Table 5). The WC and the SW groupings were the deepest and were generally similar, probably because of some spatial overlap of the site groups (Table 5, Figure 10). The community observed at these two site groups likely is a reflection of depth.

Generally, the benthic macroinvertebrate densities tended to increase with trophic status (from oligochaete TCI); the SE site group had the highest total benthos with 9,375 animals·m^{-2} as well as the highest mean density of oligochaetes (7,932·m^{-2}, Table 5). *Aulodrilus* spp. were most abundant (2,554·m^{-2}) at the SW site group, followed by the HA group (682·m^{-2}) and the WC site group (535·m^{-2}, Table 5). The SE group had the lowest mean density of *Aulodrilus* spp. at 379·m^{-2}. Mean abundance of *Aulodrilus pigueti*, a mesotrophic indicator, was highest at the HA site group with 651·m^{-2}; whereas, the densities of the other three site groups were similar with 326, 379, and 486·m^{-2} at SE, WC, and SW, respectively. The tolerant species *Limnodrilus hoffmeisteri* was found in low abundance across all site groups, however, they were relatively abundant at the SE site with 154·m^{-2}; reduced densities may be more important an indicator of environmental conditions than moderately high densities. Another tolerant species, *Quistadrilus multisetosus*, was found in highest abundance at the SE site group (279·m^{-2}), while the other clusters had substantially lower densities than the SE group, the lowest being at the SW site group with 64·m^{-2} (Table 5)

The mean density for total chironomids was similar across all site groups with 631, 762, 909, and 758 chironomids·m^{-2} at SE, SW, WC, and HA, respectively (Table 5). *Chironomus* sp. generally increased moving west, reaching their highest density (708·m^{-2}) at the SW site group; however, they were lowest at the HA site group (55·m^{-2}), not at the SE group (169·m^{-2}, Table 5). The predatory midges, *Cryptochironomus* sp., were generally low in abundance, but were essentially equal at the two eastward site groups (100·m^{-2} at SE and 108·m^{-2} at HA). The westward site groups were also very nearly equal (29·m^{-2} at WC and 19·m^{-2} at SW), but had lower densities than the eastern sites (Table 5). Another predatory midge, *Coelotanypus concinnus*, generally had low densities over all groups; the HA group had the highest density (502m^{-2}), while SE and WC were the only other groups to have *C. concinnus* densities, which were relatively low (104 and 14·m^{-2}. respectively) (Table 5). *Procladius* sp. was generally found in relatively

similar densities at all of the site groups; highest was at SE (226·m^{-2}), and lowest density was at WC with 82·m^{-2} (Table 5).

The dominant amphipods, *Gammarus* sp., had generally higher densities in the western end of the lake than the eastern end (Table 5). However, there was not a significant relationship between *Gammarus* sp. densities and distance from the river mouth.

Historical Comparisons

A total of 15 sites sampled in 1999 was matched with sites sampled in 1972 (Evans 1976). Five of the sites sampled, in 1999, were based on sites from the 1972 study (Evans 1976), while the 10 sites remaining were paired based on depth and general location. Sites compared spanned the length of the lake, were located predominantly along the southern shoreline, and included depths between 4.1 and 14.1 m (Table 6). Mann-Whitney U tests on 11 selected metrics indicated that all differences were significant with the exception of the chironomid-based TCI (Table 6). Lack of significant differences with the chironomid TCI reflects similarities in species composition between years (Figure 11). Mean densities of select benthic taxa were higher in 1999 than densities observed in 1972 (Table 6). Mean total benthos was significantly higher in 1999 than in 1972 whether or not *Dreissena* was included (Figure 12A and 12B). Total oligochaete density was higher in 1999 at most sites compared (Figure 13). Densities of Chironomidae (Figure 14), *Gammarus* sp. (Figure 15), and *Pisidium* sp. (Figure 16) were higher in 1999 at all sites compared. In addition, mean densities for *Gammarus* sp. and *Pisidium* sp. found in 1999, were nearly 14 and 55 times the densities found in 1972, respectively (Table 6). Such increases in benthic taxa could be interpreted as response to enrichment; however when differences in metrics are considered, it appears that increases in densities of benthic taxa were a response to improved environmental conditions (Table 6). Shannon-Weaver diversity and the number of taxa calculated for the matched sites were higher in 1999 (Figure 17 and

18, respectively). Conversely, both the proportion of oligochaetes and the O/C were lower, in 1999, at most of the sites compared (Figures 19A, B and 20), and suggest that oligochaete densities have decreased relative to other member of the benthic community.

Discussion

Present Trophic Status

The oligochaete TCI indicated that Muskegon Lake generally tended to be meso-eutrophic. However, scores were variable (range 0.74-1.94) and were independent of any river influences. The TCI scores suggested the presence of consistent organic enrichment. Generally, densities of mesotrophic indicator species were dominant over eutrophic indicator species at a majority (15 of 27) of the sites, suggesting that mesotrophic conditions might also tend to prevail. The species *Aulodrilus pigueti*, a mesotrophic indicator, had the highest densities of the oligochaetes at most of the sites sampled. Also, *Limnodrilus hoffmeisteri* (generally indicative of gross organic pollution) occurred frequently, but was usually in low abundance. Lower densities of *L. hoffmeisteri* suggested that Muskegon Lake was not subject to extreme amounts of organic enrichment. The TCI used is weighted to account for total abundance and, since it incorporates species composition and tolerances, the index may accurately characterize conditions at individual sites rather than using total abundances alone as an index of organic enrichment. Higher trophic scores do not always correspond with sites that had the higher oligochaete densities because changes in water or habitat quality are not always accompanied by equal changes in densities of tolerant or non-tolerant forms (Rabeni *et al.* 1985).

Distribution Relative to River Mouth and TOC Levels

The Muskegon River has one of the largest drainage basins in Michigan and as a result may have substantial effects on habitat conditions in Muskegon Lake. The significant regressions between the distance from the river mouth and species richness, total benthos, total oligochaete density, *Chironomus* sp., and *Quistadrilus multisetosus*

support the contention that the river is contributing substantial amounts of organic matter to Muskegon Lake. Freedman *et al.* (1979) indicated the Muskegon River was the major source of nutrients to Muskegon Lake, before and after wastewater diversion; this still seems to be the case. Decreasing numbers of benthos downstream suggest that much of the input from the Muskegon River settles quickly upon entering the lake and the community at the western end of the lake may reflect increased depth and possibly effects of intrusion of Lake Michigan water.

Generally, TOC levels in the sediments of Muskegon Lake fall within the range found in Lake Michigan (0.04–8.25%) and Lake Ontario (3-4%)(Johnson and Brinkhurst 1971; Cahill 1981), but were greatly reduced when compared to the Bay of Quinte, which had high organic matter (28%) in the sediments (Johnson and Brinkhurst 1971). Low TOC levels observed in Muskegon Lake suggest that sedimentation rate was such that much of the settling material was utilized. Further, areas with higher sedimentation rates can support higher densities of macroinvertebrates (Robbins *et al.* 1989). Higher densities of macroinvertebrates found in the eastern end of the lake reflected higher sedimentation rates, likely allochthonous material from the river (Table 4). Lower densities in the more westerly areas of the lake suggested sedimentation rates were lower there.

Spatial Differences in the Benthos and Community Descriptors of Habitat Quality

Generally, the cluster analysis resulted in four distinct groups of sites. However, there was some spatial overlap among the site groups in the western area of the lake (WC and SW). Western site groups were similar for nine of the selected metrics and taxa of the 15 used to characterize site groups (Table 5). Similarities included depth, trophic condition, species richness, species diversity, and abundances for total oligochaetes, *A. pigueti*, *Chironomus* sp., *Coelotanypus concinnus*, and *Procladius* sp.. These similarities suggested that habitats were also similar. The WC and SW site groups could have been combined into one larger site group; however, they were kept separate so they would

provide more resolution of differences across the lake. Despite similarities between the two western site groups, the SW group had relatively higher mean densities for total benthos, total oligochaetes, total *Aulodrilus* spp., *A. pigueti*, *Gammarus* sp., total Chironomidae, and *Chironomus* sp.; suggesting the SW site may be more productive. Localized conditions may exist at these site groups as a result of point and non-point sources into the lake as well as circulation patterns and colder water from Lake Michigan. The sites could generally be classified by the TCI as meso-eutrophic, since the mean TCI for both sites was approximately 1.5.

The SE site group is nearest the Muskegon River and so habitat in this area may reflect the influence of the river. The trophic scores for the SE site group were the highest of all the site groups (Table 5), indicating that conditions tended to be eutrophic. Species diversity was the lowest of all site groups, while the number of taxa was relatively high. The mean densities for total benthos and oligochaetes (Table 5) were highest at the SE site group suggesting organic enrichment may be substantial. The mesotrophic indicator species, *Aulodrilus pigueti*, was the dominant oligochaete found at the SE site group, however, the tolerant species *Quistadrilus multisetosus* and *Limnodrilus hoffmeisteri* were also relatively abundant when compared with the other site groups. Also, one of the most tolerant chironomids, *Procladius* sp., exhibited highest densities at the SE group, and the dominant amphipod *Gammarus* sp. was rare. Presence of *A. pigueti* and the relatively high number of taxa (Table 5) suggest that conditions in southeastern Muskegon Lake were not as degraded as other areas in the Great Lakes (see Schloesser *et al.* 1995; Canfield *et al.* 1996). The presence of *Q. multisetosus, L. hoffmeisteri,* and *Procladius* sp. in higher densities at the SE site group than what was found at the other site groups (Table 5) suggests that inputs of organic matter from the river were substantial. In addition, this site group is at the end of a long reach where prevailing winds are generally from the west (off Lake Michigan). Such winds could be responsible for "concentrating" mats of floating algae at the eastern end of the lake

(personal observation by the author), where sinking and subsequent decomposition could affect habitat conditions. Several studies have reported that accumulations of drifting algae in sandy bottom areas, can induce hypoxia and anoxia, alter community structure (i.e., dominance of tolerant and opportunistic species and reduction in biomass and diversity of mud-dwelling fauna), and affect predator-prey interactions by inducing escape-reactions (Nicolls *et al.* 1981; Bonsdorff 1991; Norkko and Bonsdorff 1996a, b, c; Hansen and Kristensen 1997). This may be especially important at the time of our sampling in fall 1999, since algal mats could be in some advanced state of decomposition at this time of year. While the benthic community in the SE site group is not indicative of anoxia, the potential exists for algal mats to contribute to the overall enrichment of the sediments in this area of the lake.

When just considering the benthic community, the HA site group appeared to have the best habitat in the lake. The TCI for this group was the lowest in the lake, and the number of taxa and species diversity was highest (Table 5). In addition, the density of total oligochaetes and the dominance of *Aulodrilus pigueti* were consistent with conditions tending toward mesotrophic. The composition of the community generally indicated that HA, potentially, had better quality habitat than the other site groups. However, the density of *Coelotanypus concinnus* was highest of all the site groups, suggesting conditions may not actually be what were predicted by the TCI. The predatory midges (including *C. concinnus* and *Procladius* sp.) are generally pollution tolerant and can be found in a wide range of habitats (Berg 1995). Higher diversity and species richness may be a reflection of the depth in the area being considered (7.2 m); both parameters tend to increase in shallower waters (Brinkhurst 1974). The abundance of the benthos has also been linked to depth, which generally decreases as depth increases (Brinkhurst 1974; Barton and Griffiths 1984). By this reasoning the HA site group should have the highest abundance of total benthos of all the site groups. This was not the case; the total benthos abundance of HA was very similar to that found at the SW

site group, an area approximately 5 m deeper on the western side of the lake. Brinkhurst (1974) also found that some species of oligochaetes (i.e., *Limnodrilus hoffmeisteri, Aulodrilus pluriseta, Ilyodrilus templetoni,* and *Tubifex tubifex)* were also found in higher densities in shallow water than in deeper water. Again this was not the case at the HA site group, where oligochaete abundance was the lowest of all the site groups. While species diversity and the number of taxa may reflect shallower depths in the HA site, total abundance and oligochaete abundance do not. The lower densities found in the HA site group suggest that factors other than organic enrichment are affecting the benthic community.

Examination of TOC levels indicated that sites within the HA group are consistent with other sites across the lake, with the exception of Musk-7, which contained 8% TOC (the highest in the lake) (Table 2). The HA site group is mostly located in a relatively sheltered embayment and, as such, may be sufficiently removed from the mouth of the river and the main flow of water through the lake that it may not act as a settling area for organic matter in Muskegon Lake. Consequently, it may not have the capacity to support as dense a benthic population as other areas of the lake. The highest level for TOC is in the Hartshorn Anchorage (Musk-7) and may be affected by the outfall from a storm sewer drain (Division Street). In addition, an oily sheen and hydrocarbon odor was present when samples were collected and may account for the increased TOC levels.

Toxicity was measured at some of the HA sites, and may have impacted the benthos at these sites (Richard R. Rediske, Grand Valley State University, Annis Water Research Institute, Muskegon Michigan, personal communication). The tests indicated that the sediments at Musk-5 and 6, exhibited toxicity in 10-day survival tests with the amphipod *Hyalella azteca* (percent survival was significantly different from control, (see Rediske *et al.* 1998, for methodology). Percent survival was not significantly different from the control at Musk-7, which was particularly surprising, considering the close proximity of this site to Musk-5 and 6 (which were between 60 and 90 m apart).

It is likely that toxicity was the result of a combination of heavy metal contaminants measured in the area (Richard R. Rediske, personal communication) possibly resulting from effluent discharges of past foundry and metal finishing operations. Historically, Musk-7 may not have been subject to as much metal laden effluent as Musk-5 and 6. Concentrations of metals including arsenic, barium, cadmium, chromium, copper, nickel, lead, zinc, and mercury in the Hartshorn Anchorage were consistently the highest in the lake (Richard R. Rediske, personal communication). Probable effect concentrations (PECs) are the pollutant concentrations above which adverse effects on sediment-dwelling organisms are likely to be observed (Macdonald *et al.* 2000; Ingersoll *et al.* 2001). Concentrations for several of the heavy metals found at sites in the HA site group (specifically Musk-5 and 6, Table 2) exceeded the PECs established by MacDonald *et al.* (2000) for freshwater ecosystems (Table 2). Using a database of 1,657 samples from 92 published reports that included tests with *Hyalella azteca, Chironomus tentans, C. riparius, Hexagenia limbata, Lumbriculus variegatus, Ceriodaphnia dubia, Daphnia magna,* and *Vibrio fisheri,* Ingersoll *et al.* (2001) found an increase in toxicity with an increase in concentrations of contaminants across geographic regions and determined that PECs could be reliably used to predict toxicity of sediments. The reports by both MacDonald *et al.* (2000) and Ingersoll *et al.* (2001) present strong support for sediment toxicity from a combination of metal contaminants affecting the benthos at the HA site group.

Concentrations of metals may be continually "re-circulated" through the benthos; stratigraphic analysis of sediment cores, taken when macroinvertebrates were collected, indicate that approximately the top 5 cm of sediment were well mixed at Musk-5, 6, and 7 (Richard R. Rediske, personal communication). Such mixing, if frequent, could result in prolonged exposure of the macroinvertebrate community to toxic levels of several heavy metals and may actually serve to concentrate contaminants near the sediment surface. Bioavailability of the heavy metals may also be a factor affecting the

community at the HA sites. Relatively low levels of organic matter and larger grain size (sand) found at the HA sites may serve to enhance the availability of contaminants to the benthos (Gossiaux *et al.* 1993 Richard R. Rediske, personal communication). Lack of toxic effects of sediment exposure at Musk-7 may reflect reduced concentrations of metals compared with Musk-5 and 6, as well as increased TOC levels, which may serve as complexing agents, reducing bioavailability (Table 2). Further research is needed to fully understand the extent and frequency of sediment mixing and how it may affect contaminants and exposure to the benthos at the HA sites.

While the SW, WC, and SE site groups appear to correlate well with distance from the mouth of the Muskegon River, this was not the case with the HA sites. The SE site was generally the most productive based on benthos and appeared heavily influenced by the Muskegon River. The SW and WC sites were rather similar with regard to macroinvertebrate composition, a condition that may reflect spatial similarities. The SW and WC sites may also reflect effects of depth on the benthic community. Results of the macroinvertebrate survey of the HA site group are misleading. The species composition, densities of organisms (especially oligochaetes and total benthos), and trophic condition indicated consistent relatively low levels of organic enrichment, which may be the case. However, toxicity of the sediments and apparent effects on the benthos warrant revision of considering the HA site as "the best" habitat in the lake. This situation illustrates a shortcoming in using benthic community metrics, generally designed to evaluate organic enrichment, in assessing pollution impacts when contaminants such as heavy metals are likely having adverse effects on macroinvertebrates.

Changes in the Benthos Between 1972 and 1999

The overall, highly significant increase in most groups in 1999 compared with 1972 is generally indicative of improving conditions in Muskegon Lake (Table 6). On average, most major taxa, including total densities, increased with maximum increases occurring in *Pisidium* sp. (54 fold) and *Gammarus* sp. (14 fold). Such increases in

benthic fauna could be interpreted as worsening conditions in response to enrichment. Historically, increases in (or high) densities of benthos (especially oligochaetes and chironomids) in the Great Lakes have been considered indicative of degraded conditions or eutrophication (Carr and Hiltunen 1965; Nalepa and Thomas 1976; Krieger 1984; Lang 1985; Winnell and White 1985; Nalepa 1987; Harman 1997). In the current study it was determined that some areas, especially those near the river, had fauna and densities that suggest enrichment was substantial. However, concurrent with increases of benthic groups, there occurred a significant reduction in the proportion of oligochaetes, oligochaete/chironomid ratio, and significant increases in the number of taxa and species diversity. Collectively these suggest that while production of benthic groups in Muskegon Lake remains high, changes since 1972 reflect generally improved environmental conditions. Krieger and Ross (1993) found increases in the number of taxa, Chironomidae and Sphaeriidae, and reduced proportion of oligochaetes was particularly indicative of improved conditions in the Cleveland Harbor area of Lake Erie.

Only the chironomid TCI was not significantly different between the 2 years (Table 6). The numerically dominant species in both years were *Chironomus* sp., *Cryptochironomus* sp., *Coelotanypus concinnus*, and *Procladius* sp. (all indicative of eutrophic conditions). Further, there were only two other taxa (*Tanytarsus* sp. and *Dicrotendipes* sp.) common between the two years, despite the occurrence of 14 taxa in each year at the sites compared. As argued previously, the chironomids may reflect changes on a shorter time scale because of life history (Armitage 1995) and are generally quicker to recolonize following disturbance because dispersion of eggs is greater (Lang and Lods-Crozet 1997). Effects of a large sewage spill into eastern Muskegon Lake in spring 1999 may have masked the TCI by eliminating or reducing less tolerant species from areas sampled. Further sampling is required to determine if the chironomid community found in 1999 is the norm or if there was indeed an impact from the sewage spill.

Generally, conditions in 1972 could be considered a product of "cultural eutrophication" resulting from the discharge of more than 1,135,550 m^3/day (Evans 1992) of combined municipal and industrial wastewater into the lake. Mean surface concentration of total phosphorus in 1972 was 67 $\mu g \cdot L^{-1}$, mean chlorophyll *a* was 25 $\mu g \cdot L^{-1}$, and Secchi depth averaged 1.5 m (Freedman *et al.* 1979; Evans 1992); all three of these exceed levels indicative of eutrophic conditions (Wetzel 1983). High algal productivity such as that seen in Muskegon Lake in 1972 resulting from high nutrient loads is often responsible for oxygen deficient or anoxic conditions in the hypolimnion and subsequently the sediments (Brinkhurst 1974). Freedman *et al.* (1979) found extended periods of anoxic conditions during summer 1972, but the duration was variable, possibly due to mixing from ship traffic, circulation patterns, and storms. However, following such mixing "events", dissolved oxygen concentrations were probably reduced rapidly as the water column re-stratified. With reduced hypolimnetic oxygen levels/anoxia, recorded in Muskegon Lake in 1972, conditions may have favored tolerant oligochaetes resulting in their dominance in the benthos as well as restricting many of the less-tolerant invertebrates (Krieger and Ross 1993). By 1975, surface concentrations of total phosphorus and chlorophyll *a* decreased by 37% and 62%, respectively (Freedman *et al.* 1979; Evans 1992). However, chlorophyll *a* (9.5 $\mu g \cdot L^{-1}$) and Secchi depth (approximately 1.5 m) (which changed little) suggested eutrophic conditions persisted, and anoxia was still observed (Freedman *et al.* 1979). Likewise benthos was dominated by oligochaetes, while total densities decreased (Evans 1992), suggesting the lake remained sufficiently degraded to favor the oligochaetes. By 1994-1997, surface concentrations of chlorophyll *a* (range 7–11 $\mu g \cdot L^{-1}$) and total phosphorus (range 20–26 $\mu g \cdot L^{-1}$) were reduced below levels considered indicative of eutrophic conditions (Gary Fahnenstiel, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan, unpublished data). Secchi disc measurements over the period (1994-97) were generally between 2 and 4 m; in 2001 Secchi depth never exceeded 2 m

(Doran Mason, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan, unpublished data). Resuspension of sediments may occur frequently in Muskegon Lake and could, historically, be responsible for reducing Secchi depths. Increases in macroinvertebrate densities and reduction in oligochaete dominance in Muskegon Lake may be due to reduced extent or duration of summer anoxia in response to wastewater diversion and nutrient reduction. If indeed anoxia has decreased since wastewater diversion, it potentially alleviated conditions that may have suppressed the entire community and thus would allow for the increases in the benthos observed in this study. In Lake Erie, the reduction in the extent and duration of anoxia has been suggested (Makarewicz and Bertram 1991) and would represent a "major improvement in habitat quality" (Krieger and Ross 1993).

Overall, it appears that nutrients rather than toxic pollutants had the overall greatest effect on Muskegon Lake benthos. Historically, the benthos has been subjected to high amounts of organic as well as chemical pollutants from a paper mill, chemical plants, and metal foundry and finishing operations (Evans 1992, and Richard R. Rediske, personal communication). These discharges were sources of heavy metals, PAHs, wood pulp, sulfides, fuel oil, and PCBs to the lake. Toxicity in conjunction with anoxia induced by high nutrient loads, may suppress all macroinvertebrates, and a reduction in contaminant and nutrient inputs (via wastewater diversion) would likely lead to an increase in species diversity and higher productivity of common taxa (Krieger and Ross 1993). However, with the exception of nickel and zinc, which were both higher in 1972, there was no significant difference between concentrations of several heavy metals between 1999 and 1972 (Table 7). Concentrations of cadmium, chromium, and lead all exceeded PECs (Macdonald *et al.* 2000) in both years, while zinc exceeded the PEC in 1972, but not in 1999. It is possible that toxicity did have an effect on the benthos in 1972 when considering changes between 1972 and 1999 and finding no differences between heavy metal concentrations, it becomes evident that nutrient and organic

enrichment was the main reason for a degraded benthos in 1972.

It is worth noting that only three sites were compared for heavy metals in 1972 and 1999, and it is likely that some areas of Muskegon Lake that were "hot spots" where toxicity was found in 1999 (i.e. Musk-5, 6, 7 and 16A) may have showed toxic effects in 1972. Generally, metal concentrations at the 1972 sites used in the comparison (between 1972 and1999) were similar to the mean concentration at all 13 sites where metal concentrations were measured in 1980 (Evans 1992) and could be considered representative of overall conditions in the lake at that time. Lack of difference in heavy metal concentrations between 1972 and 1999 suggests sediment mixing may be an important process in Muskegon Lake in prolonging exposure of the benthos to heavy metals.

Effects of the Zebra Mussel

When evaluating changes over time in the benthos, the invasion of the zebra mussel (*Dreissena polymorpha*) cannot be ignored. The progress and effects of the invasion of *Dreissena* in the Laurentian Great Lakes has been well documented (Griffiths 1993; Fahnenstiel *et al.* 1995; Nalepa and Fahnenstiel 1995; Dermott and Kerec 1997; Ricciardi *et al.* 1997; Stewart *et al.* 1998; Haynes *et al.* 1999). Generally, these studies make comparisons (when possible) of data prior to the invasion with data collected during and after establishment of *Dreissena* populations. For Muskegon Lake, the most extensive survey prior to this study was conducted in 1972, with follow up surveys in 1975 and 1980. The latter two surveys were conducted at progressively fewer sites.

Generally, *Dreissena* attains highest densities on hard substrates in littoral habitats (Griffiths 1993; Stewart and Haynes 1994; Nalepa and Fahnenstiel 1995; Howell *et al.* 1996; Ricciardi *et al.* 1997; Stewart *et al.* 1998). *Dreissena* has, however, been found in high numbers on soft substrates in Lake Erie and Michigan, but were not found in high densities on soft substrates in Saginaw Bay, Lake Huron (Nalepa and Fahnenstiel 1995) and in this study. In addition to high densities, *Dreissena* alters habitat structure

by forming dense beds which create refugia for other macroinvertebrates, resulting in increases in biomass, abundance, and diversity of non-*Dreissena* organisms (Griffiths 1993; Stewart and Haynes 1994; Ricciardi *et al.* 1997). Experiments with artificial substrates indicated macroinvertebrate abundance was higher in the presence of *Dreissena* than on substrates without a layer of *Dreissena* or on substrates with intact empty shells and that the interstices as well as deposition of feces and pseudofeces enhanced densities of deposit-feeding organisms (Ricciardi *et al.* 1997). In deepwater areas with soft sediments, where *Dreissena* densities are generally lower, there has also been a decline in other macroinvertebrates, possibly as a result of reduced transport of phytoplankton biomass from shallow habitats to deepwater regions (Dermott and Kerec 1997; Nalepa *et al.* 1998; Haynes *et al.* 1999; Nalepa *et al.* 2000; Strayer and Smith 2001). Declines of the amphipod *Diporeia* in Lake Michigan and Lake Erie may, in part, be a result of food limitation caused by filtering activities of *Dreissena* (Dermott and Kerec 1997; Nalepa *et al.* 1998; Nalepa *et al.* 2000). Strayer and Smith (2001) found a decrease in total benthos of deep-water areas in the Hudson River and attributed decreases in densities to loss of sedimenting food. The population of *Dreissena* in 1992 was estimated to be capable of filtering the inner bay of Saginaw Bay, Lake Huron, 1.3 times a day (Fanslow *et al.* 1995). High filtering rates of dense populations of *Dreissena* have been linked to decreases in concentrations of chlorophyll *a* and total phosphorus and an increase in Secchi disk transparency (Griffiths 1993; Fahnenstiel *et al.* 1995; Howell *et al.* 1996). In inner Saginaw Bay, chlorophyll decreased by 59%, total phosphorus decreased by 43%, and Secchi disk depth increased 60%, following heavy colonization by *Dreissena*; such reductions were found regardless of mussel density at a particular sampling site (Fahnenstiel *et al.* 1995).

Dreissena became established in southeastern Lake Michigan in 1989 (Nalepa *et al.* 1998) and was probably found in Muskegon Lake by the early 1990s. The impact that *Dreissena* has had on Muskegon Lake is difficult to discern (partially because

data are lacking). As noted previously, by 1995–97, levels of chlorophyll *a* and total phosphorus were greatly reduced compared with 1972, and water clarity as measured by Secchi disk had increased. These changes may have been a result of nutrient reductions, establishment of *Dreissena*, or a combination of both. High densities of *Dreissena* were found at sites Musk-9, 12, and 16A (range 5,626–40,860·m^{-2}) and may reflect the presence of coarser material found in the samples (i.e., wood chips, coarse sand, and gravel). Densities at the other sites were generally low (range 14–359·m^{-2}) and were likely due to sandy substrate at almost all of the sites sampled. Densities of *Dreissena* were probably higher in areas closer to shore than we sampled, especially in rocky areas and on seawalls, which provide ample surface area for attachment. The fact that there was an overall increase in the benthos (excluding *Dreissena*) since 1972 at sites in the deeper soft-bottom areas in Muskegon Lake suggests *Dreissena* likely had little influence on the benthos at these sites. Further, regression analysis indicated no significant relationship between *Dreissena* and oligochaete densities or between *Dreissena* and *Gammarus* sp., although they were found in relatively high abundance at Musk-12 where *Dreissena* densities exceeded 40,000·m^{-2}. However, *Gammarus* sp. densities were at a maximum at Musk-4, where no *Dreissena* were found (Appendix A). The sphaeriid clams, *Pisidium* sp., also have been found to decrease following the introduction of *Dreissena* in southern Lake Michigan (Nalepa *et al.* 1998) and eastern Lake Erie (Dermott and Kerec 1997). In 1999, *Pisidium* sp. densities in Muskegon Lake were higher than densities found in 1972, indicating that *Dreissena* did not negatively affect these taxa. The increases in oligochaetes, *Gammarus* sp., *Pisidium* sp., and total benthos at soft bottom areas together with no significant relationships between any of the above taxa and *Dreissena*, strongly supports nutrient reduction as the likely reason for temporal changes. Moreover, the significant positive relationship between distance from the river mouth (likely the largest source for recent nutrient levels in Muskegon Lake) and total benthos density (Figure 2) demonstrates the influence of the river on the lake. This is not

to say that *Dreissena* colonization did not have an impact on the benthos of Muskegon Lake, but impacts may be more localized in shallower areas where higher densities may be found.

Conclusions

Based on indices derived from the benthic macroinvertebrate community, Muskegon Lake in 1999 was determined to be meso-eutrophic to eutrophic. Oligochaete densities and the trophic condition index (TCI) based on oligochaete species composition support these conclusions. The community was largely dominated by *Aulodrilus pigueti* (a mesotrophic indicator) and *Quistadrilus multisetosus* (a eutrophic indicator). Significant relationships between distance from the Muskegon River mouth and number of taxa, total benthos, total oligochaete density, *Chironomus sp.*, and *Q. multisetosus* suggests that organic inputs from the river may be substantial but relatively labile, given that TOC levels were similar to those found in the more enriched areas of Lake Michigan.

Cluster analysis of the benthic community resulted in four groupings of sites. The group closest to the river mouth, SE, consisted of species indicative of enriched conditions, likely due to its proximity to the river. The two groups in the western end of the lake, WC and SW, were similar in community composition and reflected similarities in depth and location within the lake. The community at the HA group indicated that better environmental conditions existed at these sites. Sites in this group had the shallowest mean depth, and metrics such as Shannon-Weaver diversity, number of taxa, and TCI suggested better habitat conditions compared with other site groups. However, sediment toxicity from heavy metals was found that might have affected conditions at this group. Concentrations of some metals found at a few of the sites within the HA group were higher than anywhere else in the lake. Moreover, six of the 10 metals measured exceeded the probable effect concentration (PECs) above which adverse effects could be expected more times than not. Generally, the clusters indicated improving conditions with increased distance from the river mouth.

Comparisons between benthic communities in 1972 and 1999 indicated substantial changes in environmental conditions since diversion of wastewater, beginning

in 1973. Increases in total benthos, oligochaetes, chironomids, *Gammarus* sp., and *Pisidium* sp., coupled with increased Shannon-Weaver diversity, number of taxa, and especially a decrease in proportion of oligochaetes, are indicative of generally improved environmental conditions. Decreases in surface chlorophyll *a* and total phosphorus concentrations are further evidence that overall conditions have improved since 1972. The reduction of nutrient concentrations in Muskegon Lake and a subsequent decrease in primary production may have lead to a decrease in the duration and extent of summer anoxia, which potentially could have suppressed the entire benthos. Finally, it appears that changes in Muskegon Lake were driven by the diversion of municipal and industrial wastewater rather than by colonization of the lake by *Dreissena*, which likely occurred in the early 1990s. Increases in oligochaete and *Pisidium* sp. densities at soft-bottom areas in Muskegon Lake, rather than reductions as seen in Lake Michigan and Lake Erie and lack of correlation between *Dreissena* densities and oligochaete densities, support discharge diversion as the main impetus for observed changes. Moreover, the significant negative relationship between distance from the river mouth with total benthos and oligochaete densities demonstrates the influence of contributions of nutrients from the river as the major factor promoting benthic macroinvertebrate distribution patterns. Consistent concentrations of some heavy metals between the 2 years suggest sediment mixing and resuspension may be important.

Future research should be directed toward determination and remediation of continuing sources of degradation. This may require further scrutiny of tributaries to Muskegon Lake as well as investigation of storm sewers and discharges that occur during storm events. The present study may have benefited from additional collections of benthos during other times of the year to rule out seasonal variation in the benthic community. In addition, collections at more of the historical sites would have strengthened evaluation of changes over time by allowing more sites to be compared.

Table 1: Coordinates and depth at sites sampled by petite PONAR for benthic macroinvertebrates in Muskegon Lake, Michigan, fall 1999.

Site	Lat	Long	Depth (m)
Musk-1	43° 13.387	86° 18.690	12.0
Musk-3	43° 13.418	86° 17.219	12.2
Musk-4	43° 13.365	86° 17.345	12.8
Musk-5	43° 13.953	86° 15.922	6.4
Musk-6	43° 13.986	86° 15.922	4.1
Musk-7	43° 14.007	86° 15.925	7.9
Musk-8	43° 14.082	86° 16.261	8.2
Musk-9	43° 14.381	86° 15.781	7.5
Musk-10	43° 14.631	86° 15.561	7.4
Musk-11	43° 14.723	86° 15.391	8.8
Musk-12	43° 14.562	86° 14.961	4.2
Musk-13	43° 14.897	86° 15.182	9.6
Musk-14	43° 15.040	86° 15.112	8.6
Musk-15	43° 14.604	86° 16.461	9.6
Musk-16A	43° 14.457	86° 15.479	5.4
1ML	43° 13.39	86° 18.98	11.5
2ML	43° 14.21	86° 18.27	16
3ML	43° 13.47	86° 17.87	20.4
4ML	43° 14.79	86° 15.88	10.2
AML	43° 13.21	86° 18.47	16.6
BML	43° 14.12	86° 16.63	11
CML	43° 14.96	86° 15.12	9.4
B30	43° 14.91	86° 15.70	8.7
C40	43° 14.35	86° 16.40	11.4
D40	43° 13.67	86° 17.00	12.5
D46	43° 13.75	86° 17.17	14.1
E40	43° 13.95	86° 18.83	12.2

Table 2: Heavy metals (mg·kg^{-1}, dry weight) and total organic carbon (TOC, % dry weight) in Muskegon Lake PONAR samples collected in fall 1999. Probable effect concentrations (PECs) were from MacDonald *et al.* (2000) (see text for explanation). Data are courtesy of R. Rediske, Grand Valley State University, Annis Water Resources Institute, Muskegon, Michigan. See Table 1 for location of sites.

Site	TOC	Arsenic	Barium	Cadmium	Chromium	Copper	Nickel	Lead	Zinc	Mercury	Selenium
Musk-1	4.5	10	130	3.9	150	63	24	120	260	0.38	0.72
Musk-3	5.5	6.1	130	2.0	71	52	19	83	190	0.20	0.44
Musk-4	<0.5	5.2	14	0.13	4.8	4.0	2.0	5.8	13	U	U
Musk-5*	4.1	11	180	12	210	260	38	270	600	1.7	0.49
Musk-6*	5.3	9.5	180	7.9	160	260	38	280	640	1.7	0.53
Musk-7*	8.0	11	120	4.2	120	100	29	140	290	0.56	0.48
Musk-8*	4.9	8.5	130	4.4	107	83	25	125	255	0.52	0.68
Musk-9	<0.5	5.6	20	0.38	9.6	6.8	3.4	12	30	U	U
Musk-10	1.1	6.2	110	2.9	77	58	22	89	200	0.34	0.58
Musk-11	4.3	6.8	110	2.3	61	49	20	67	160	0.26	0.59
Musk-12	<0.5	5.2	10	0.078	2.8	3.4	2.6	6.2	14	U	U
Musk-13	4.2	10	97	3.1	80	39	19	63	160	0.25	0.38
Musk-14	2.3	5.2	88	1.1	30	33	14	31	100	0.14	0.38
Musk-15	2.5	5.8	120	2.5	68	46	19	64	160	0.26	0.42
Musk-16	1.4	3.7	33	1.3	20	16	6.8	31	67	0.14	U
Mean(S.E.)	3.30(0.58)	7.1(0.64)	93(13)	3.28(0.78)	71.9(17.8)	66.7(18.9)	17.7(2.8)	90.1(20.3)	196(44)	0.55(0.13)	0.51(0.03)
PEC		33	N/A	4.98	111	149	48.6	128	459	1.06	N/A

"U" Indicates undetectable levels.

* Indicates sites that were in the Hartshorn Anchorage group from cluster analysis.

Table 3: Benthic data collected from Muskegon Lake, Michigan, fall 1999. Values for Trophic Condition Index using oligochaetes (based on Milbrink 1983) and chironomids (based on Howmiller and Scott 1977), Shannon-Weaver diversity ($\log_2$), oligochaete-chironomid ratio (Olig/Olig+Chir, see text for explanation), and number of taxa. See Table 1 for site locations.

Site	Trophic Condition (Oligochaete)	Trophic Condition (Chironomid)	Species Diversity	Olig/Olig+Chir	Number of Taxa
Musk-1	1.48	1.98	3.07	0.89	6
Musk-3	1.62	2.00	2.57	0.83	9
Musk-4	1.88	2.00	2.52	0.93	8
Musk-5	0.81	2.00	3.21	0.95	13
Musk-6	0.78	2.00	3.29	0.95	11
Musk-7	0.91	2.00	3.27	0.92	13
Musk-8	1.39	2.00	2.96	0.91	12
Musk-9	1.16	1.95	2.23	0.96	15
Musk-10	1.03	1.97	3.30	0.99	11
Musk-11	1.94	2.00	2.11	0.96	10
Musk-12	1.18	1.94	1.09	0.98	12
Musk-13	1.78	1.95	2.15	0.95	8
Musk-14	1.57	1.89	2.44	0.97	12
Musk-15	1.29	1.97	2.30	0.95	8
Musk-16A	1.13	1.94	2.53	0.95	13
AML	1.38	2.00	3.50	0.81	6
BML	1.47	2.00	3.30	0.73	10
CML	1.93	1.84	1.67	0.98	10
IML	1.11	2.00	2.92	0.67	7
2ML	1.50	2.00	3.32	0.74	11
3ML	1.28	1.98	3.48	0.86	9
4ML	1.94	1.91	2.24	0.95	7
B-30	1.10	2.00	2.96	0.97	10
C-40	1.80	1.97	2.52	0.95	8
D-40	1.66	2.00	2.76	0.80	8
D-46	1.60	2.00	2.53	0.89	7
E-40	1.88	1.95	2.82	0.73	14

Table 4: Mean abundance in animals·m^{-2} (and relative densities, %) of major taxonomic groups collected in Muskegon Lake, Michigan, fall 1999. See Table 1 for location of sites.

Site	Oligochaetes	Chironomids	Sphaeriids	Amphipods	*Dreissena*	Other	Total
Musk-1	3,802(81.8)	646(13.9)	0(0)	43(0.9)	0(0)	158(3.4)	4,649
Musk-3	6,132(76.5)	1,392(17.4)	115(1.4)	144(1.8)	29(0.4)	200(2.5)	8,012
Musk-4	8,461(81.4)	646(6.2)	0(0)	1,249(12.0)	0(0)	43(0.4)	10,399
Musk-5	2,395(38.0)	1,249(19.8)	1,607(25.5)	287(4.6)	359(5.7)	402(6.4)	6,299
Musk-6	2,511(50.4)	690(13.9)	646(13.0)	359(7.2)	316(6.3)	458(9.2)	4,980
Musk-7	2,740(55.0)	559(11.2)	904(18.2)	29(0.6)	316(6.3)	430(8.6)	4,978
Musk-8	3,458(66.7)	647(12.5)	632(12.2)	57(1.1)	14(0.3)	373(7.2)	5,181
Musk-9	6,898(26.9)	703(2.7)	329(1.3)	200(0.8)	15,758(61.5)	1,723(6.7)	25,611
Musk-10	2,669(48.2)	559(10.1)	1,521(27.5)	43(0.8)	129(2.3)	616(11.1)	5,537
Musk-11	8,986(86.5)	833(8.0)	388(3.7)	43(0.4)	14(0.1)	129(1.2)	10,393
Musk-12	6,111(12.4)	273(0.6)	689(1.4)	616(1.3)	40,860(83.2)	575(1.2)	49,124
Musk-13	5,554(83.0)	632(9.4)	258(3.9)	0(0)	0(0)	244(3.6)	6,688
Musk-14	9,094(81.5)	631(5.7)	876(7.8)	86(0.8)	14(0.1)	459(4.1)	11,160
Musk-15	10,489(87.2)	660(5.5)	546(4.5)	172(1.4)	14(0.1)	143(1.2)	12,024
Musk-16A	6,674(47.8)	401(4.1)	445(3.2)	14(0.1)	5,626(40.3)	804(5.8)	13,964
AML	1,767(68.4)	488(18.9)	158(6.1)	29(1.1)	14(0.5)	129(5.0)	2,585
BML	1,779(57.4)	746(24.1)	173(5.6)	100(3.2)	86(2.8)	215(6.9)	3,099
CML	8,093(90.5)	431(4.8)	287(3.2)	28(0.3)	0(0)	100(1.1)	8,939
IML	2,424(57.7)	1,435(34.1)	215(5.1)	29(0.7)	14(0.3)	86(2.0)	4,203
2ML	1,918(53.0)	818(22.6)	44(1.2)	496(13.7)	108(3.0)	237(6.5)	3,621
3ML	2,725(66.4)	531(12.9)	215(5.2)	301(7.3)	187(4.6)	143(3.5)	4,102
4ML	6,801(84.2)	660(8.2)	488(6.0)	0(0)	0(0)	129(1.6)	8,078
B-30	2,912(55.5)	847(16.1)	1,234(23.5)	0(0)	57(1.1)	200(3.8)	5,250
C-40	5,770(84.8)	301(4.4)	158(2.3)	28(0.4)	57(0.8)	488(7.2)	6,802
D-40	4,534(73.8)	1,234(20.1)	86(1.4)	57(0.9)	72(1.2)	157(2.6)	6,140
D-46	4,175(78.2)	517(9.7)	244(4.6)	57(1.1)	0(0)	343(6.4)	5,336
E-40	1,937(37.2)	861(16.5)	86(1.7)	947(18.2)	0(0)	1,377(26.4)	5,208

Table 5: Metrics and benthic organisms (S.E.) used to characterize Muskegon Lake site groups using cluster analysis, 1999. Trophic Condition is based on chironomid densities adapted from Howmiller and Scott (1977). Species diversity is the Shannon-Weaver index (log_2). *Aulodrilus* spp. is the sum of all of the *Aulodrilus* species observed at sites in the groupings. Densities are in animals·m^{-2}. There were 18 sites (see Table 1) used in this analysis.

	South East (SE)	**Hartshorn Anchorage (HA)**	**West Central (WC)**	**South West (SW)**
Number of sites	4	6	5	3
Depth (m)	9.3(0.32)	7.2(0.72)	15.3(1.62)	12.1(0.38)
Trophic Condition	1.81(0.09)	1.00(0.09)	1.52(0.09)	1.49(0.22)
N taxa	10(0.76)	12(0.47)	8(0.8)	7(0.51)
Species Diversity	1.05(0.07)	2.24(0.11)	1.51(0.21)	1.23(0.22)
Total Benthos	9,295(984)	6,879(221)	4,650(791)	6,418(1995)
Total Oligochaeta	7,932(824)	2,782(154)	3,343(781)	4,897(1826)
Total *Aulodrilus* spp.	379(162)	682(175)	535(148)	2,554(1354)
Aulodrilus pigueti	326(169)	651(170)	379(123)	486(65)
Limnodrilus hoffmeisteri	154(51)	17(4)	118(22)	29(22)
Quistadrilus multisetosus	279(123)	139(57)	145(32)	64(49)
Gammarus sp.	29(13)	117(55)	172(90)	416(395)
Total Chironomidae	632(82)	648(107)	675(163)	909(263)
Chironomus sp.	169(48)	55(36)	544(138)	708(249)
Coelotanypus concinnus	104(30)	502(126)	14(8)	0(0)
Procladius sp.	226(28)	91(22)	82(18)	148(53)

Table 6: Mean (S.E.) and Mann-Whitney U test p values for selected benthic taxa and metrics of 15 matched pairs of sites in Muskegon Lake, Michigan, between 1972 and 1999. General groups were used because sampling occurred at different times of the year in each year. Trophic Condition Index (chironomids) is based on Howmiller and Scott (1977). Densities of benthic groups are in animals m^{-2}. Proportion of oligochaetes (Prop. olig) and the oligochaete/chironomid ratio are percentages. Diversity is the Shannon-Weaver index (log_2). "Excl. ZM" indicates *Dreissena* abundance has been excluded from the calculation.

	1972	1999	p-value
Total Benthos	2,858(710)	9,652(2918)	0.0002
Total Benthos (Excl. ZM)	2,858(710)	6,452(598)	0.001
Total Oligochaeta	2,558(717)	4,562(664)	0.003
Total Chironomidae	158(45)	677(75)	0.00002
Gammarus sp.	12(7)	165(54)	0.0007
Pisidium sp.	9(5)	493(118)	0.0001
Prop. olig (Excl. ZM)	85(3)	68(4)	0.005
Oligochaete/Chironomid	92(2)	84(2)	0.008
Trophic Condition	1.85(0.13)	1.97(0.01)	0.14
Diversity (olig lumped)	0.68(0.11)	1.66(0.17)	0.0003
Number of Taxa	3(0.27)	10(0.64)	0.000002

Table 7: Mean heavy metal concentrations ($mg \cdot kg^{-1}$, dry weight) from sediment samples at three sites in Muskegon Lake, Michigan for 1972 and 1999. Only metals at three sites could be compared because of limited coverage in 1972. However, the sites are widely spread and give an indication of contaminant concentration across the lake. The p-values are derived from Mann-Whitney U-tests. Data, for 1999, are courtesy of R. Rediske, Grand Valley State University, Annis Water Resources Institute, Muskegon Michigan.

	1972	1999	p-value
Arsenic	18(1.8)	11.1(2.0)	0.08
Cadmium	10(1.5)	9.2(1.9)	0.83
Chromium	274(47.6)	247(99.4)	0.51
Copper	94(12.2)	75(5.1)	0.13
Nickel	39(3.7)	26(0.9)	0.05
Lead	165(11.8)	140(15.3)	0.27
Zinc	475(16.8)	300(34.6)	0.05
Mercury	0.6(0.1)	0.6(0.1)	0.83

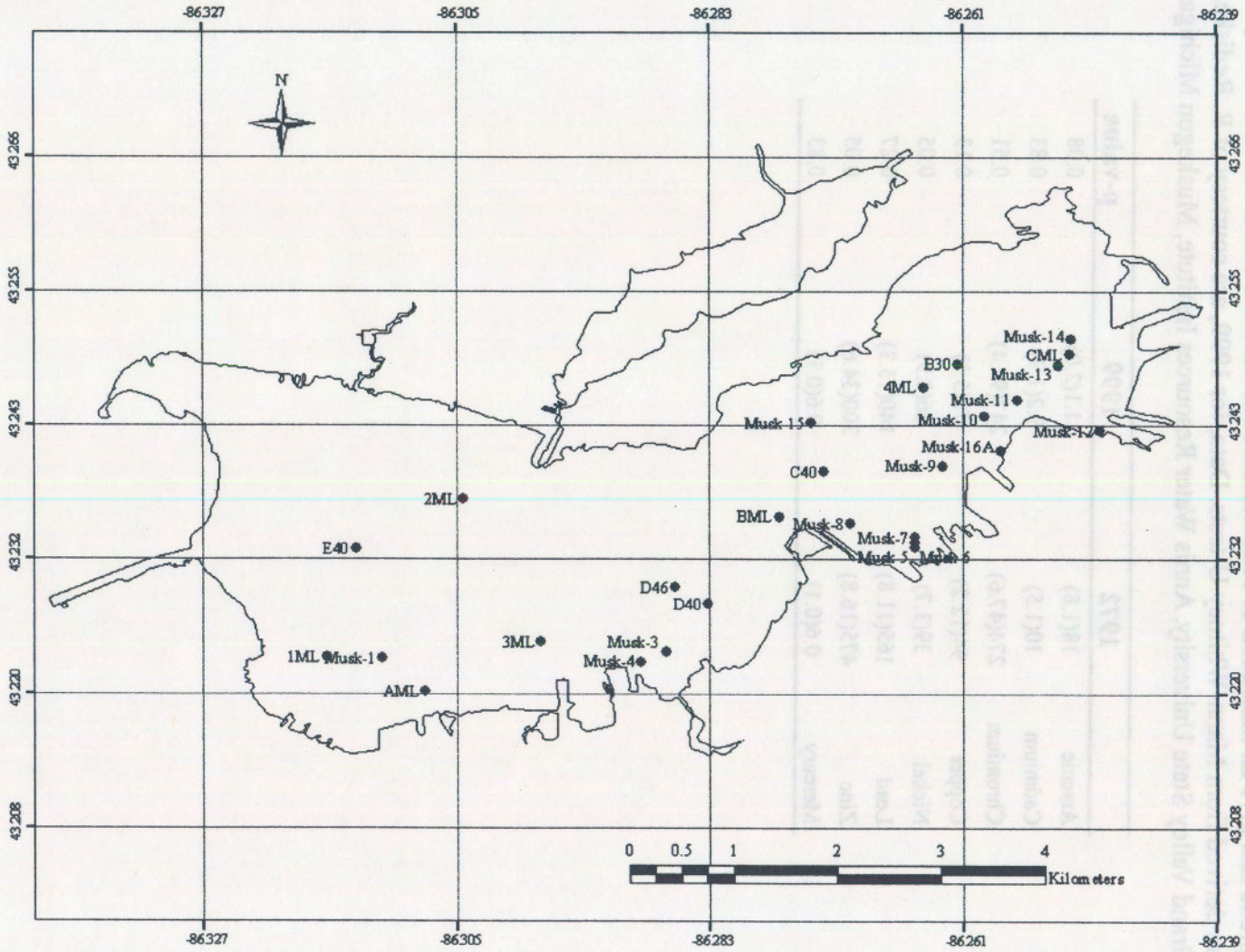


Figure 1: Map of Muskegon Lake, Michigan with 27 sites sampled in fall 1999. See Table 1 for site coordinates.

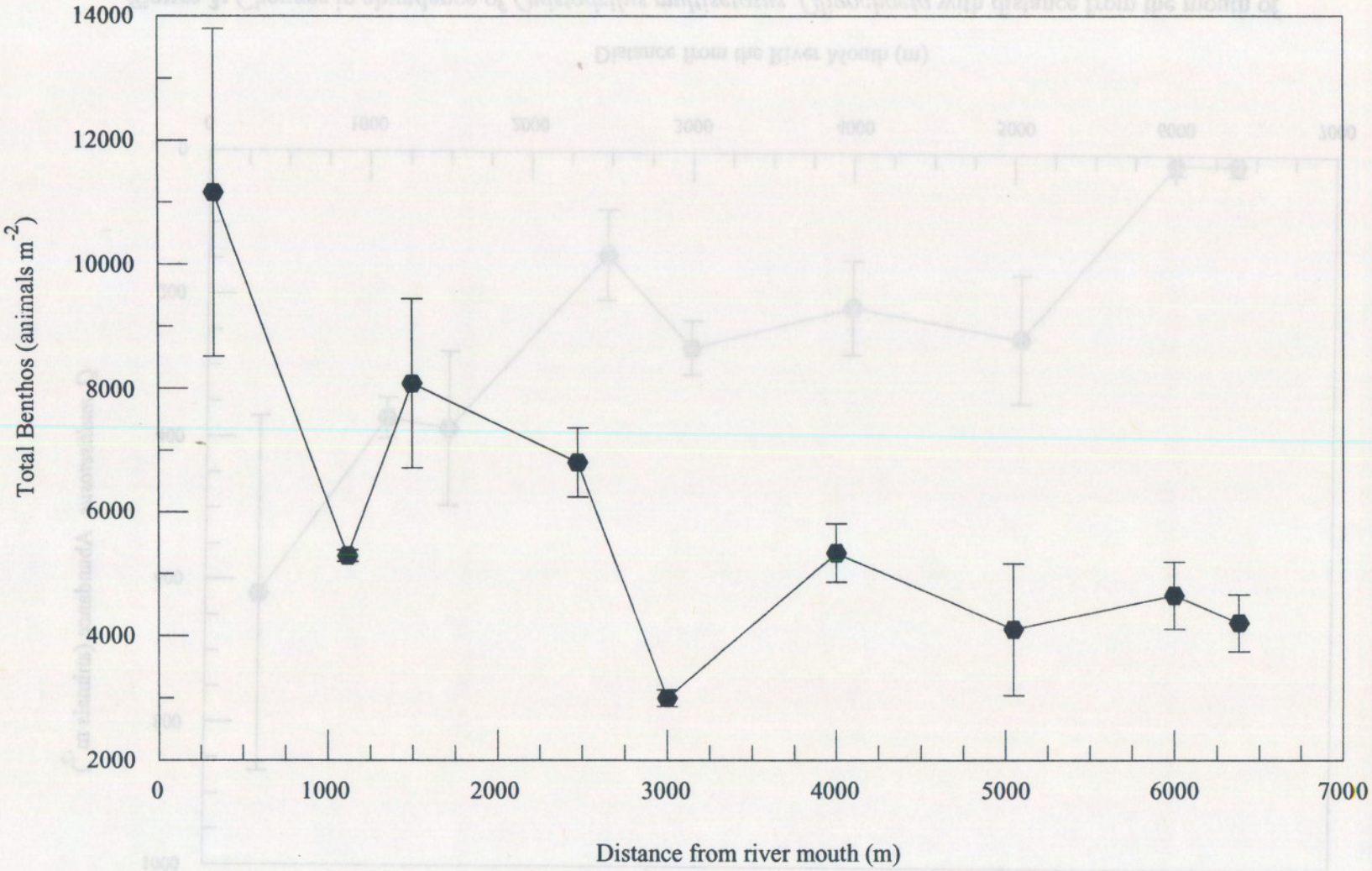


Figure 2: Changes in total benthic abundance with distance from the mouth of the Muskegon River (moving west) in Muskegon Lake in 1999. The relationship was significant at $p<0.05$ with $r^2= 0.48$ (n= 9).

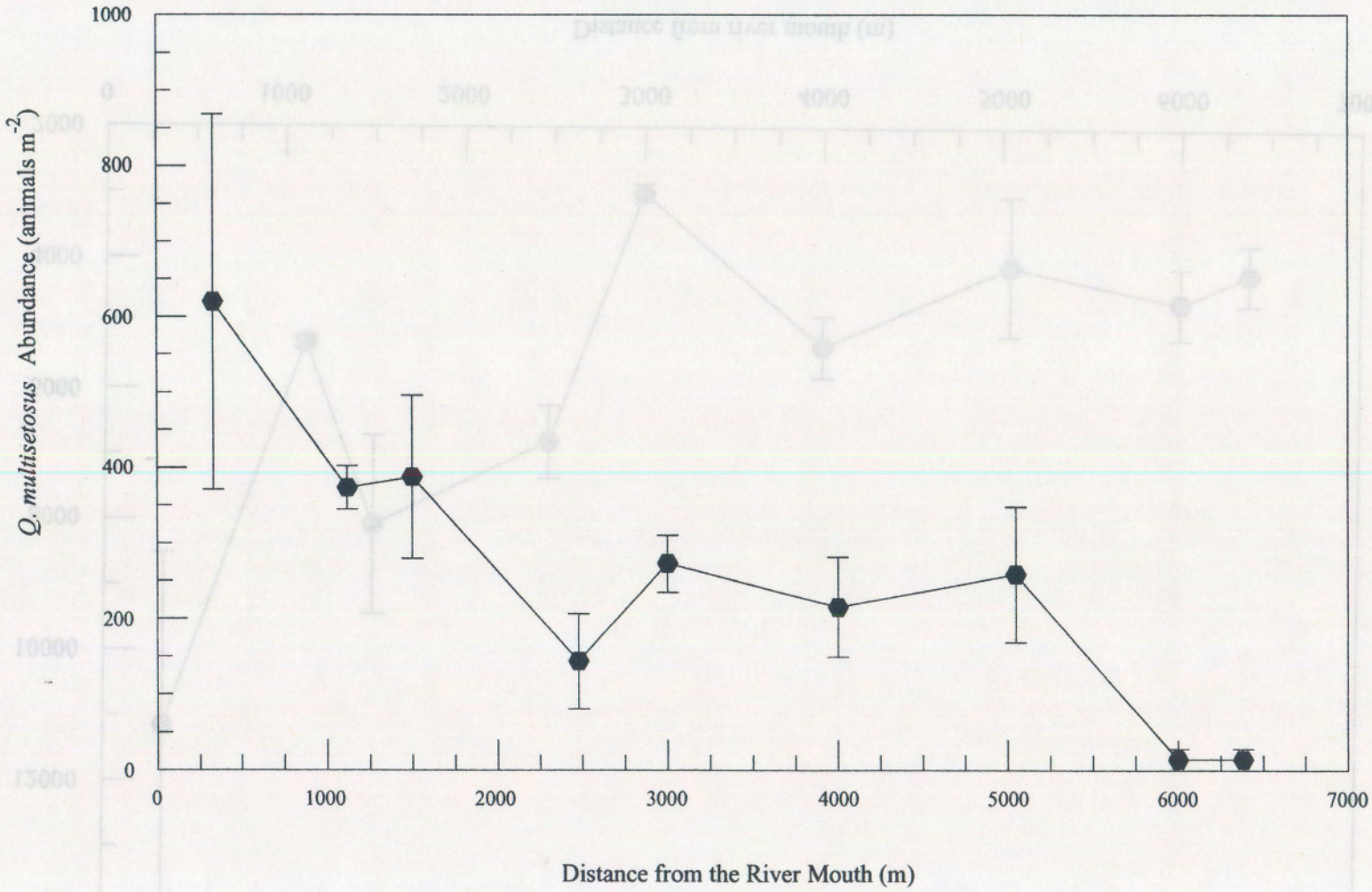


Figure 3: Changes in abundance of *Quistadrilus multisetosus*, *Oligochaeta* with distance from the mouth of the Muskegon River (moving west) in Muskegon Lake in 1999. The relationship was significant at $p<0.01$ with $r^2= 0.75$ (n= 9).

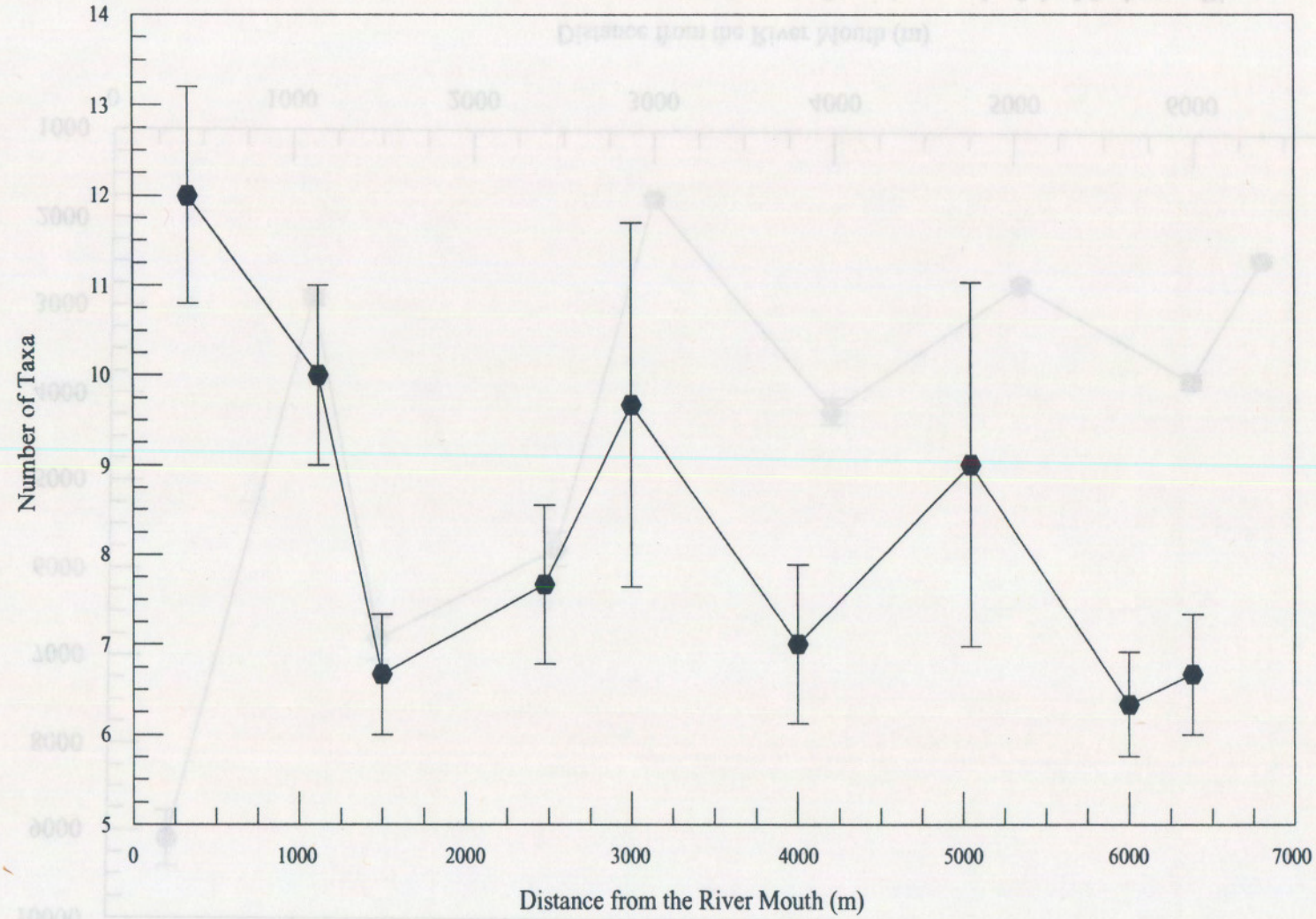


Figure 4: Changes in number of taxa with distance from the mouth of the Muskegon River (moving west) in Muskegon Lake, Michigan, 1999. This relationship is significant at $p<0.10$ with $r^2= 0.41$ (n= 9).

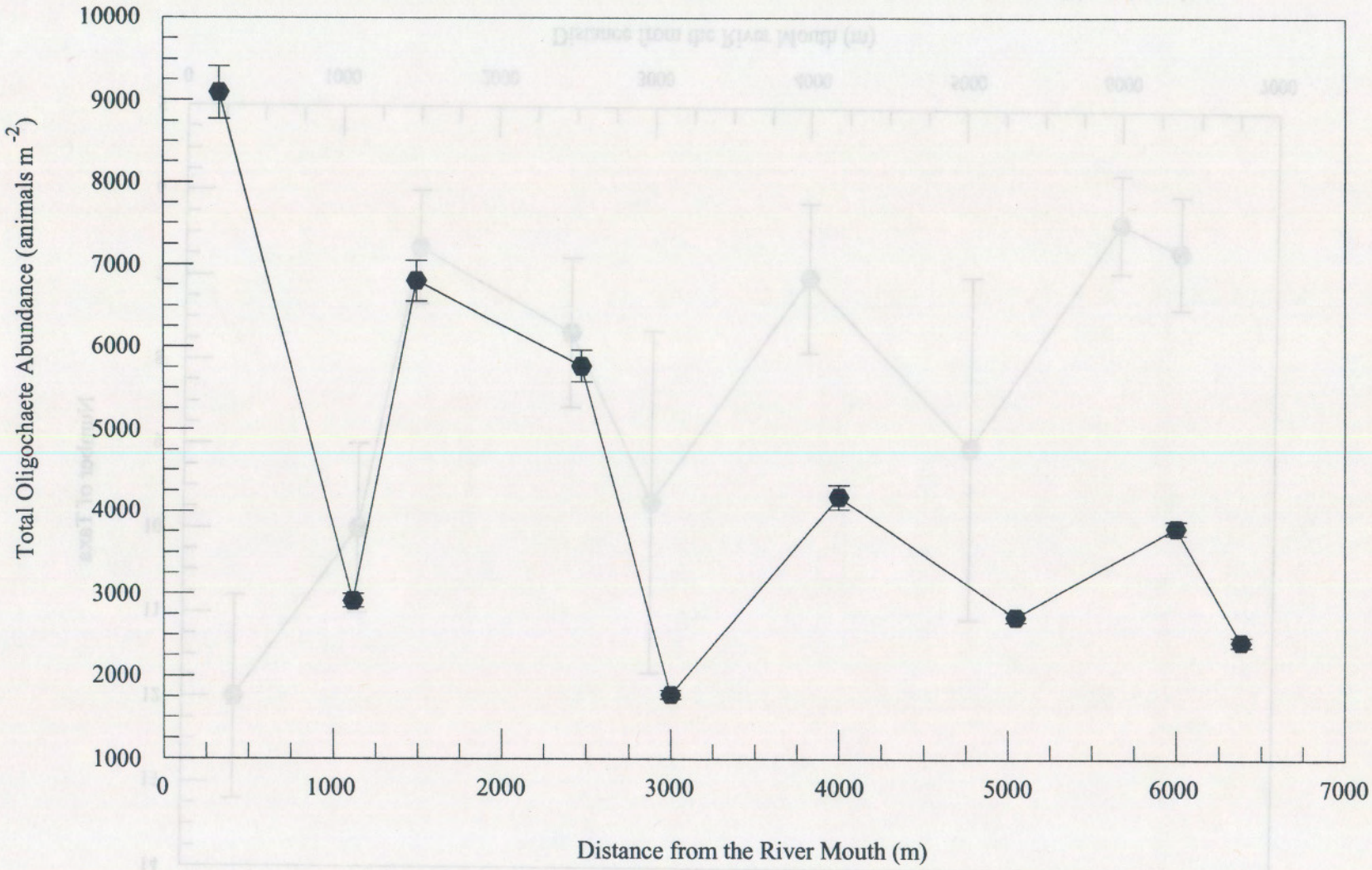


Figure 5: Changes in total oligochaete abundance with distance from the mouth of the Muskegon River (moving west) in Muskegon Lake in 1999. This relationship is significant at $p<0.10$ with $r^2= 0.39$ (n= 9).

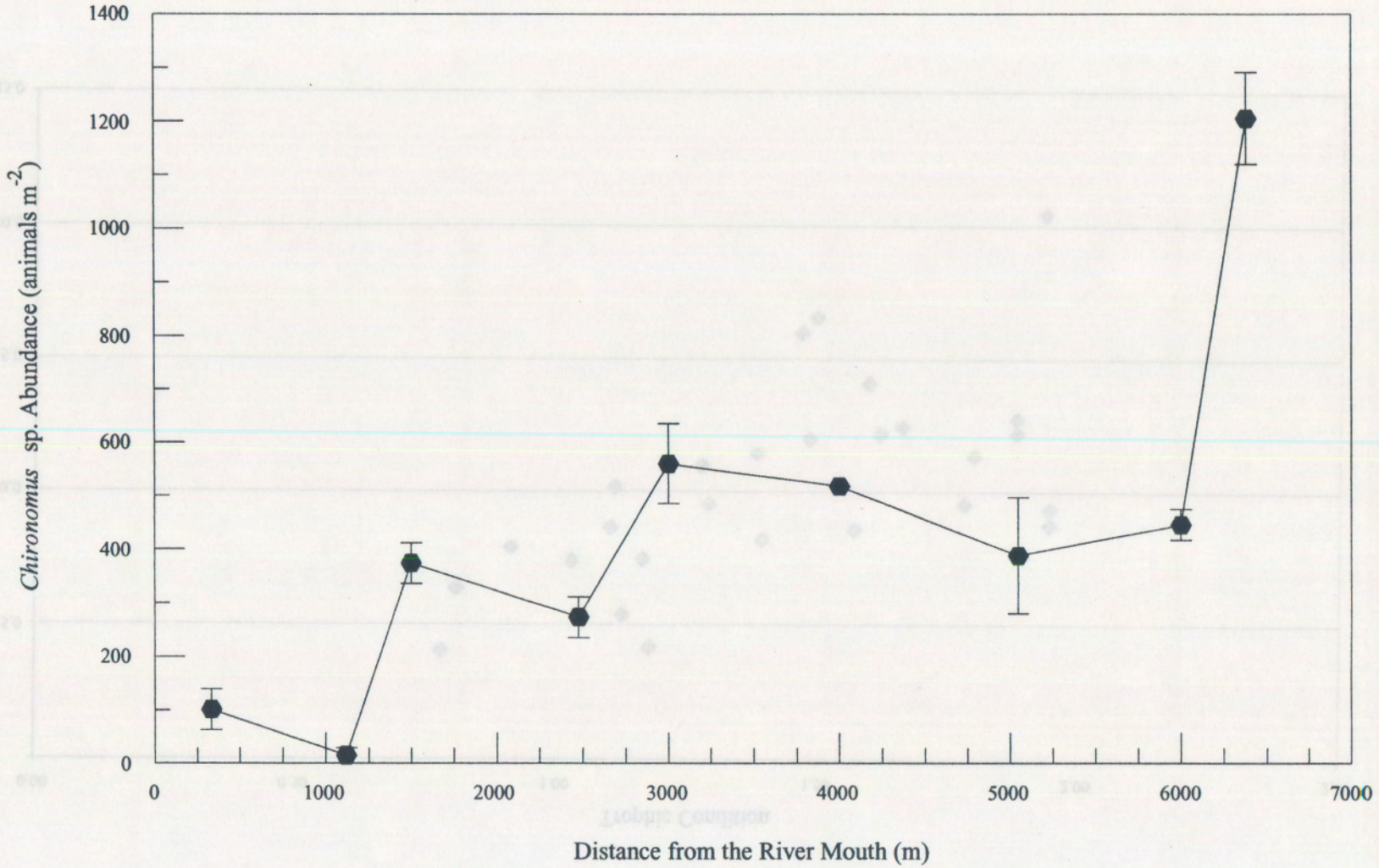


Figure 6: Changes in *Chironomus* sp. abundance with distance from the mouth of the Muskegon River (moving west) in Muskegon Lake in 1999. This relationship is significant at $p<0.05$ with $r^2= 0.57$ (n= 9).

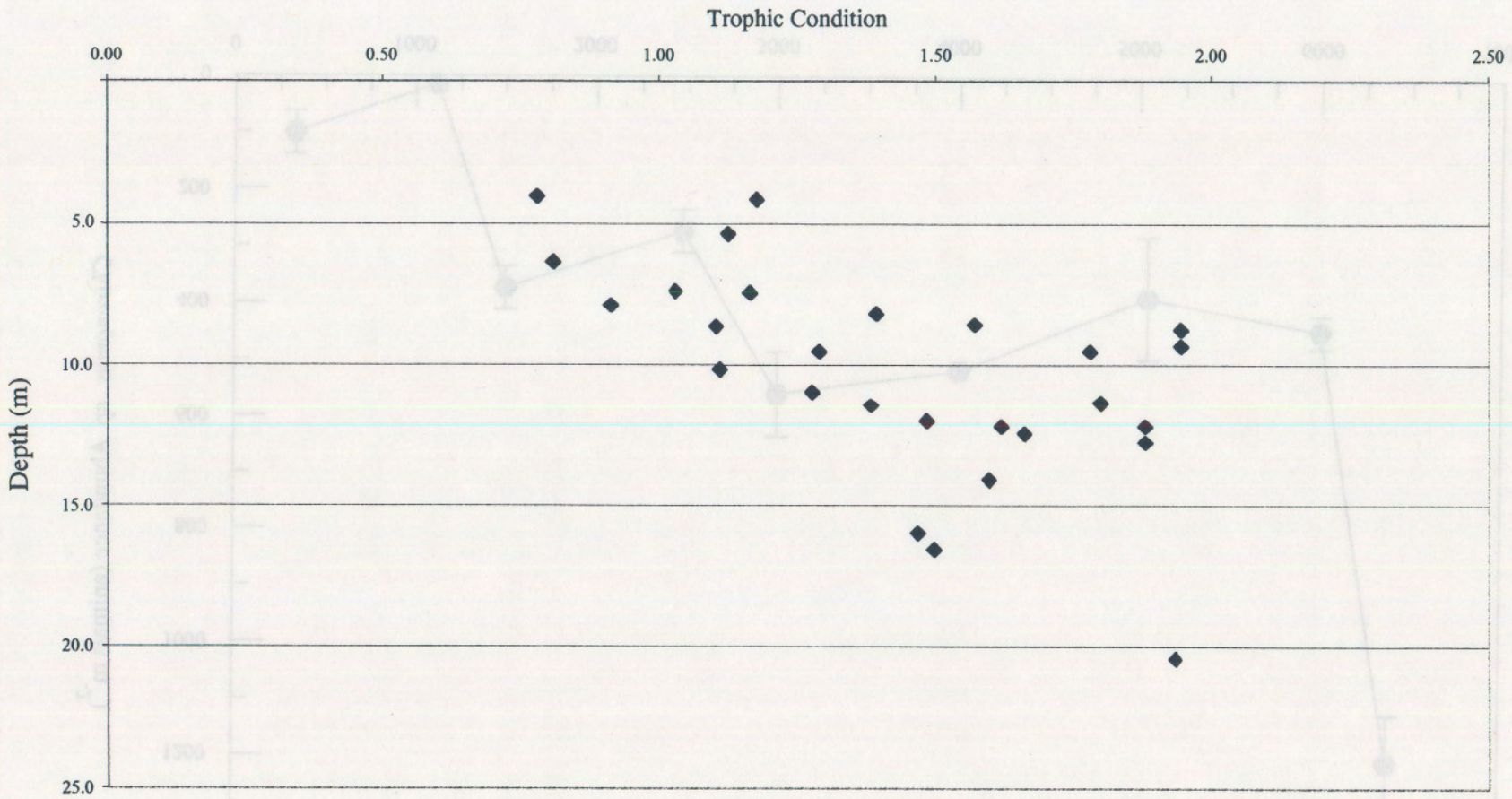


Figure 7: Significant relationship ($p<0.01$, $r^2= 0.37$, $n=27$) between depth and oligochaete Trophic Condition Index (Milbrink 1983) in Muskegon Lake, 1999, generally reflecting poorer conditions with increasing depth.

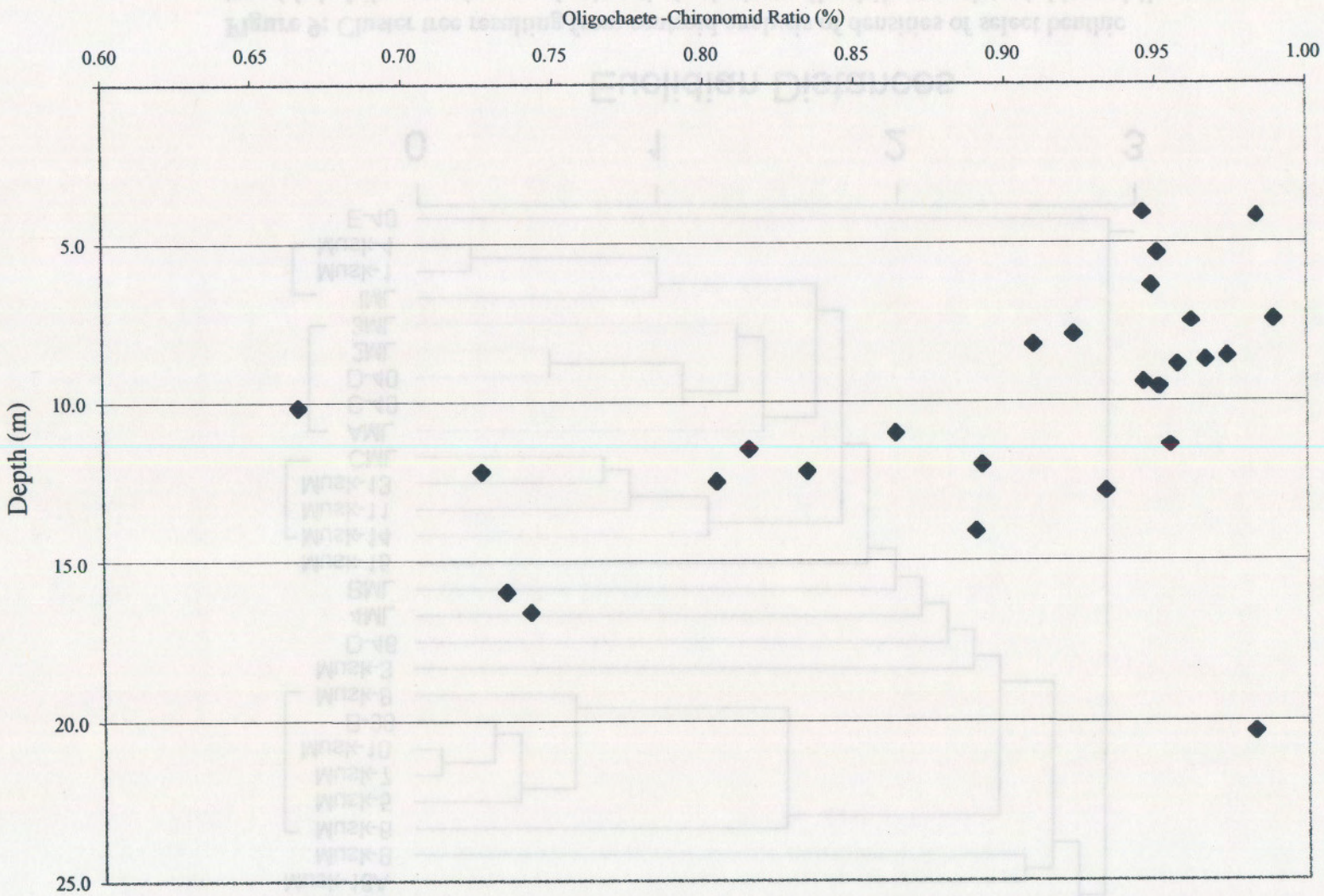


Figure 8: Significant relationship ($p<0.05$, $r^2= 0.19$, $n= 27$) between depth and oligochaete-chironomid ratio in Muskegon Lake, 1999. The trend indicates a tendency for chironomid density to increase in deeper water.

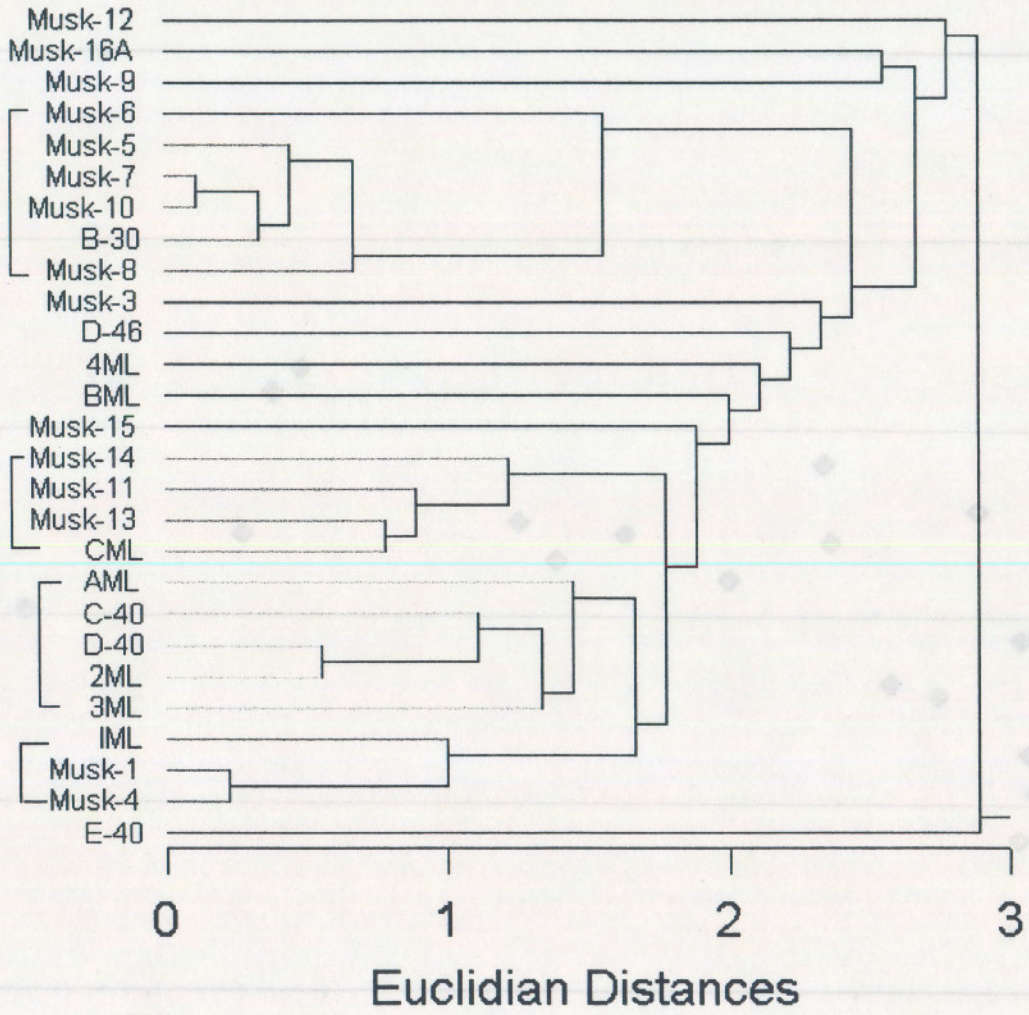


Figure 9: Cluster tree resulting from centroid analysis of densities of select benthic taxa (*Aulodrilus americanus*, *A. pigueti*, *A. pluriseta*, *Ilyodrilus templetoni*, *Limnodrilus cervix* var., immature tubiţcids without hair chaetae, *Amnicola* sp., *Bithynia* sp., *Valvata tricarinata*, *Dreissena*, *Chironomus* sp., and *Ceolotanypus concinnus*) from Muskegon Lake, 1999. See Table 1 for site locations.

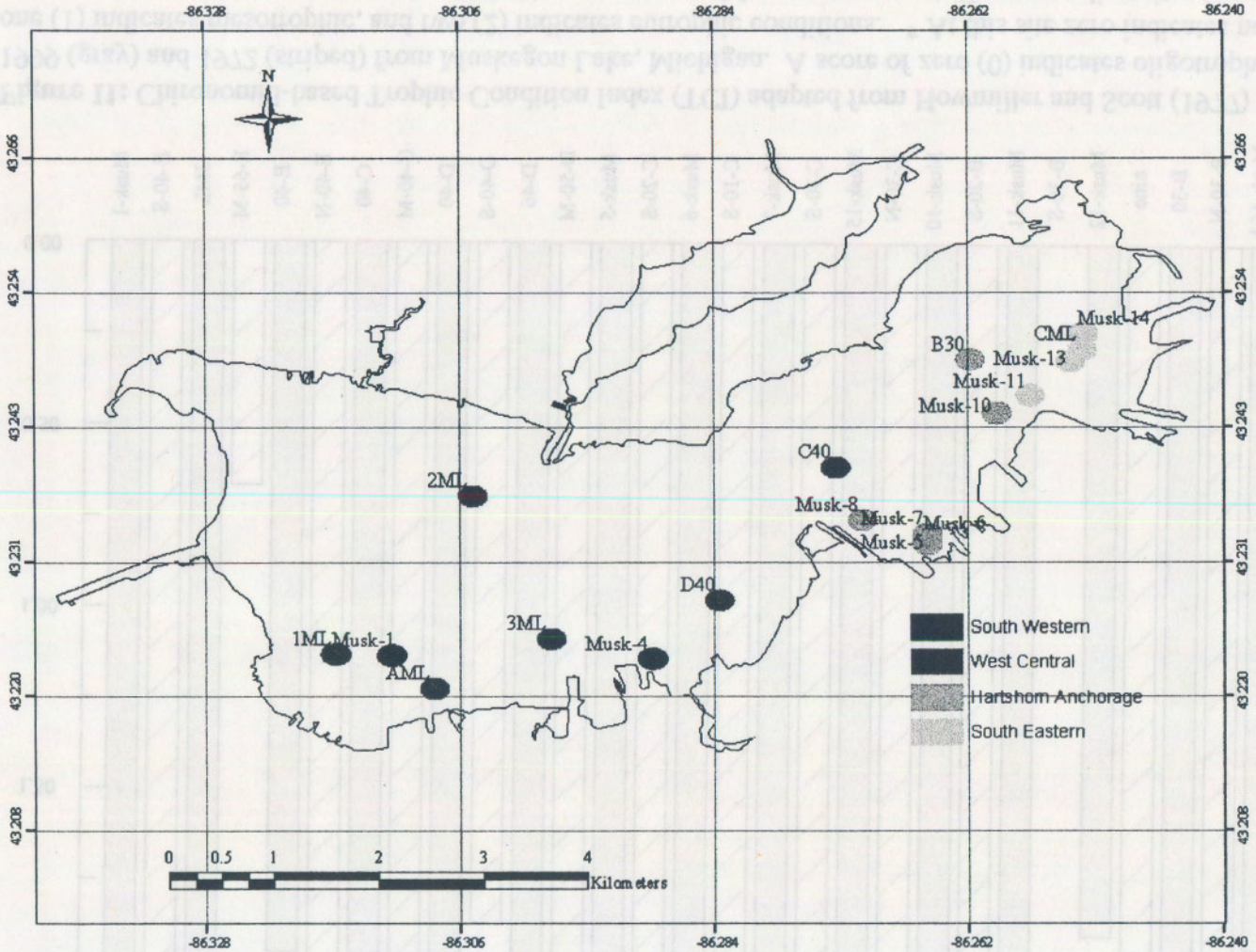


Figure 10: Site groups resulting from cluster analysis of selected benthic taxa abundances (*Aulodrilus americanus*, *A. pigueti*, *A. pluriseta*, *Ilyodrilus templetoni*, *Limnodrilus cervix* var., immature tubificids without hair chaetae, *Amnicola* sp., *Bithynia* sp., *Valvata tricarinata*, *Dreissena*, *Chironomus* sp., and *Ceolotanypus concinnus*) sampled in Muskegon Lake, 1999.

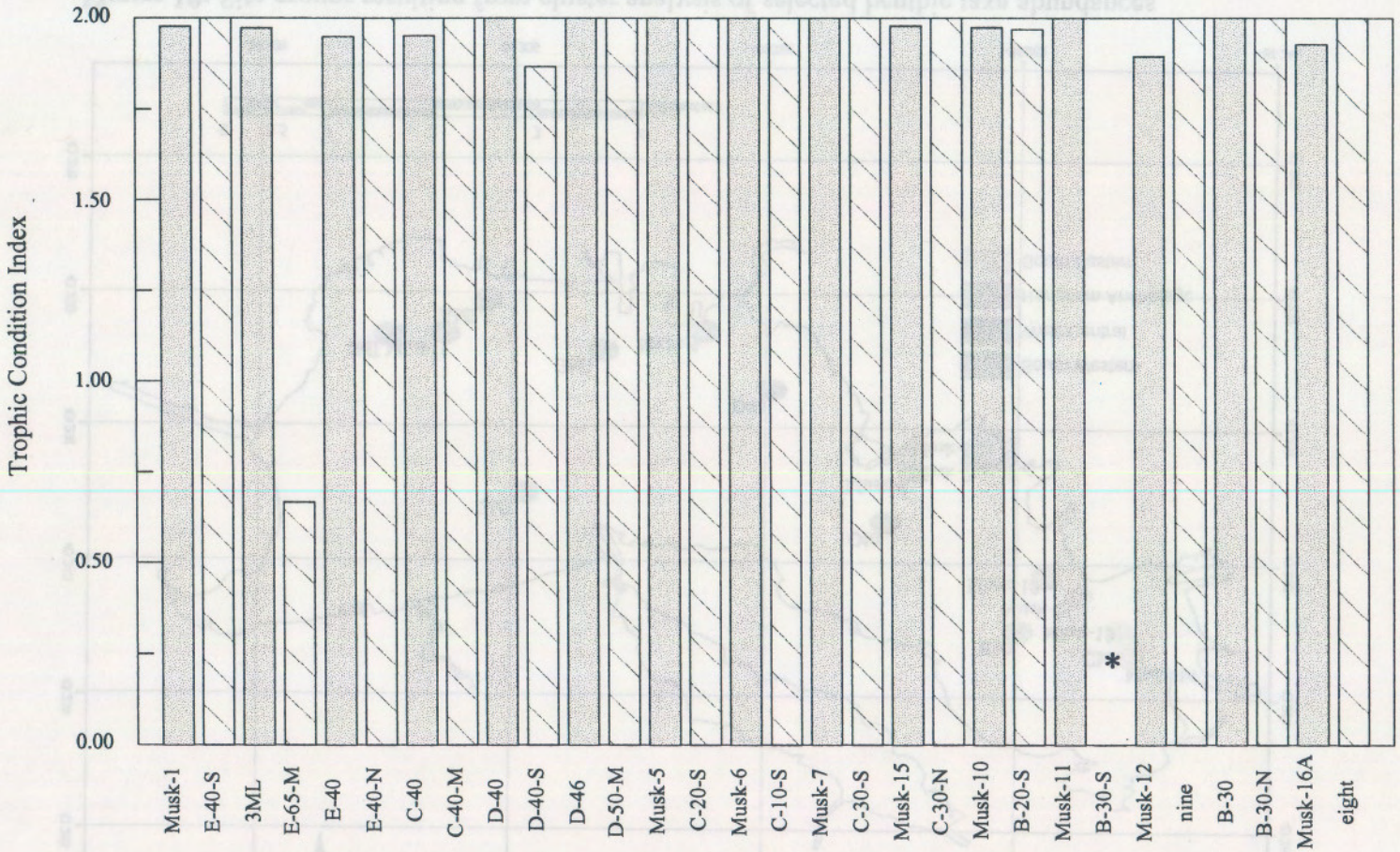
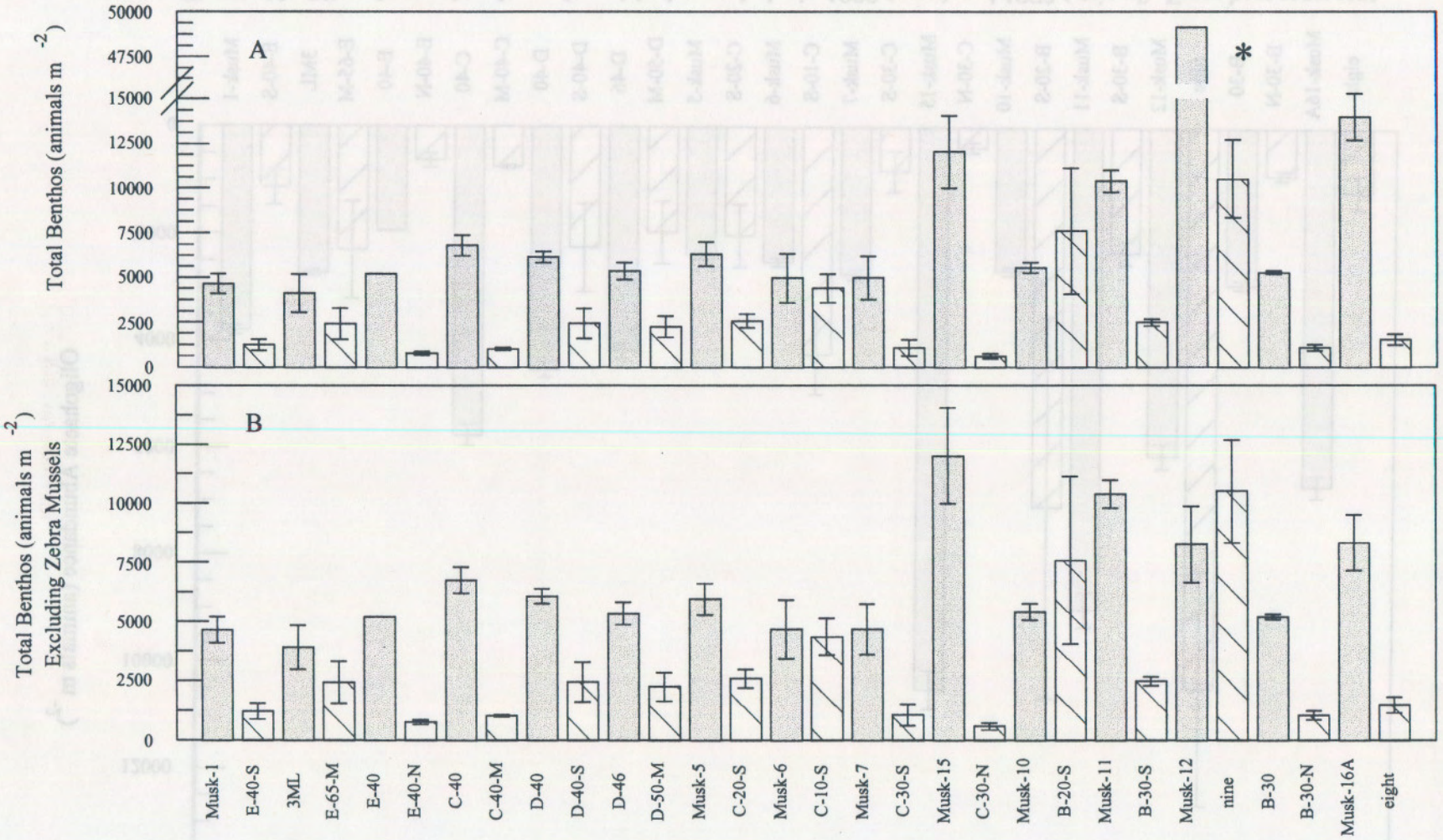


Figure 11: Chironomid-based Trophic Condition Index (TCI) adapted from Howmiller and Scott (1977) for 1999 (gray) and 1972 (striped) from Muskegon Lake, Michigan. A score of zero (0) indicates oligotrophic, one (1) indicates mesotrophic, and two (2) indicates eutrophic conditions. * At this site zero indicates no score because chironomids were absent in 1972. Sites are arranged from west to east. Corresponding sites from 1972 are immediately to the right of the 1999 bar. See Table 1 for site locations.



Figures 12A and 12B: Total benthos abundance from Muskegon Lake in 1999 (gray) and 1972 (striped). (A) includes zebra mussels (* S.E. at this site was 13,219 and was not included in order to discern the densities at other sites); (B) does not include zebra mussel densities. Error bars represent standard error. Corresponding sites from 1972 are immediately to the right of the 1999 bar. Sites are arranged west to east. See Table 1 for site locations.

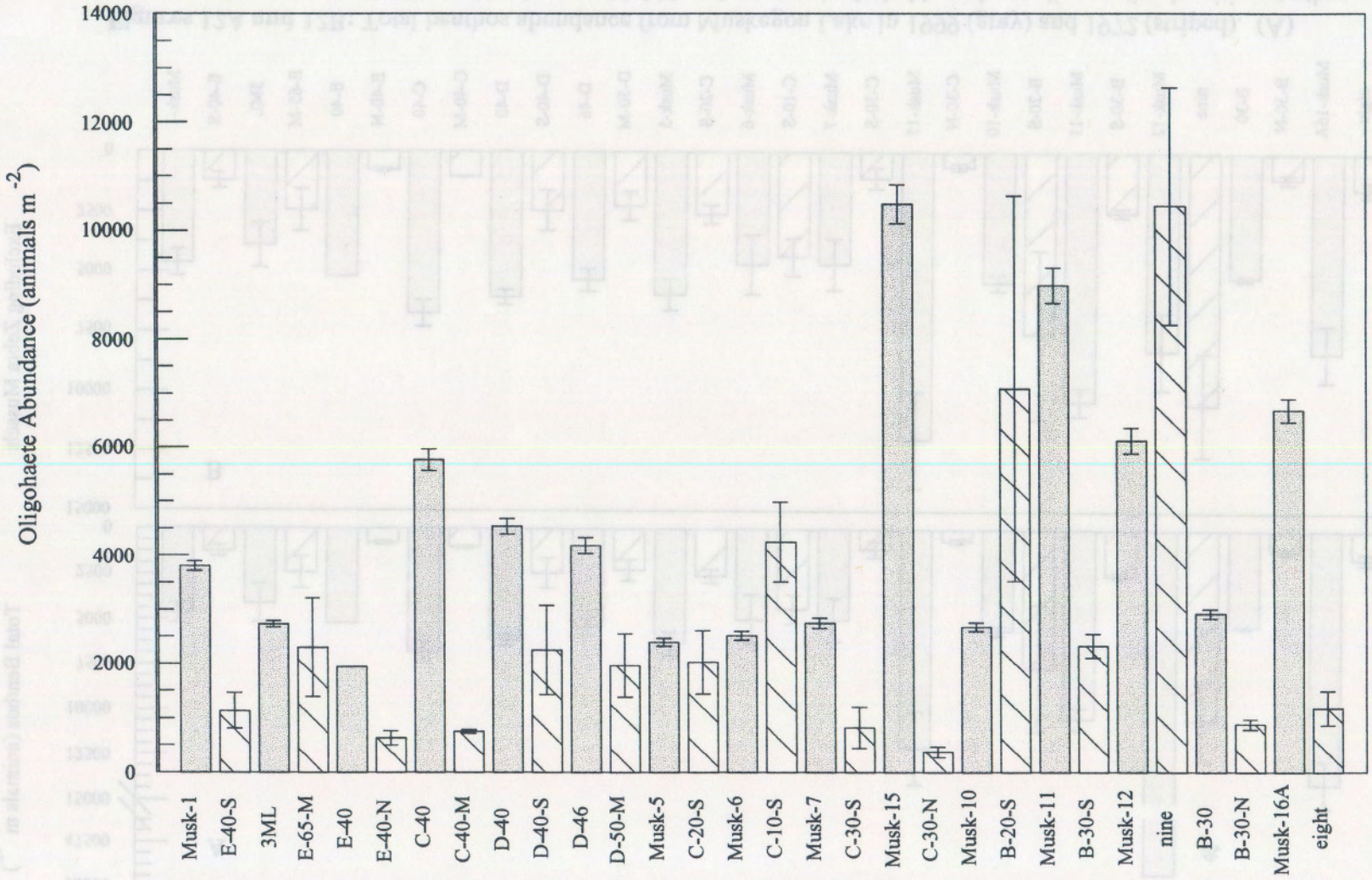


Figure 13: Oligochaete abundance from Muskegon Lake in 1999 (gray) and 1972 (striped). Error bars represent standard error. Sites are arranged from west to east. Corresponding sites from 1972 are immediately to the right of the 1999 bar. See Table 1 for site locations.

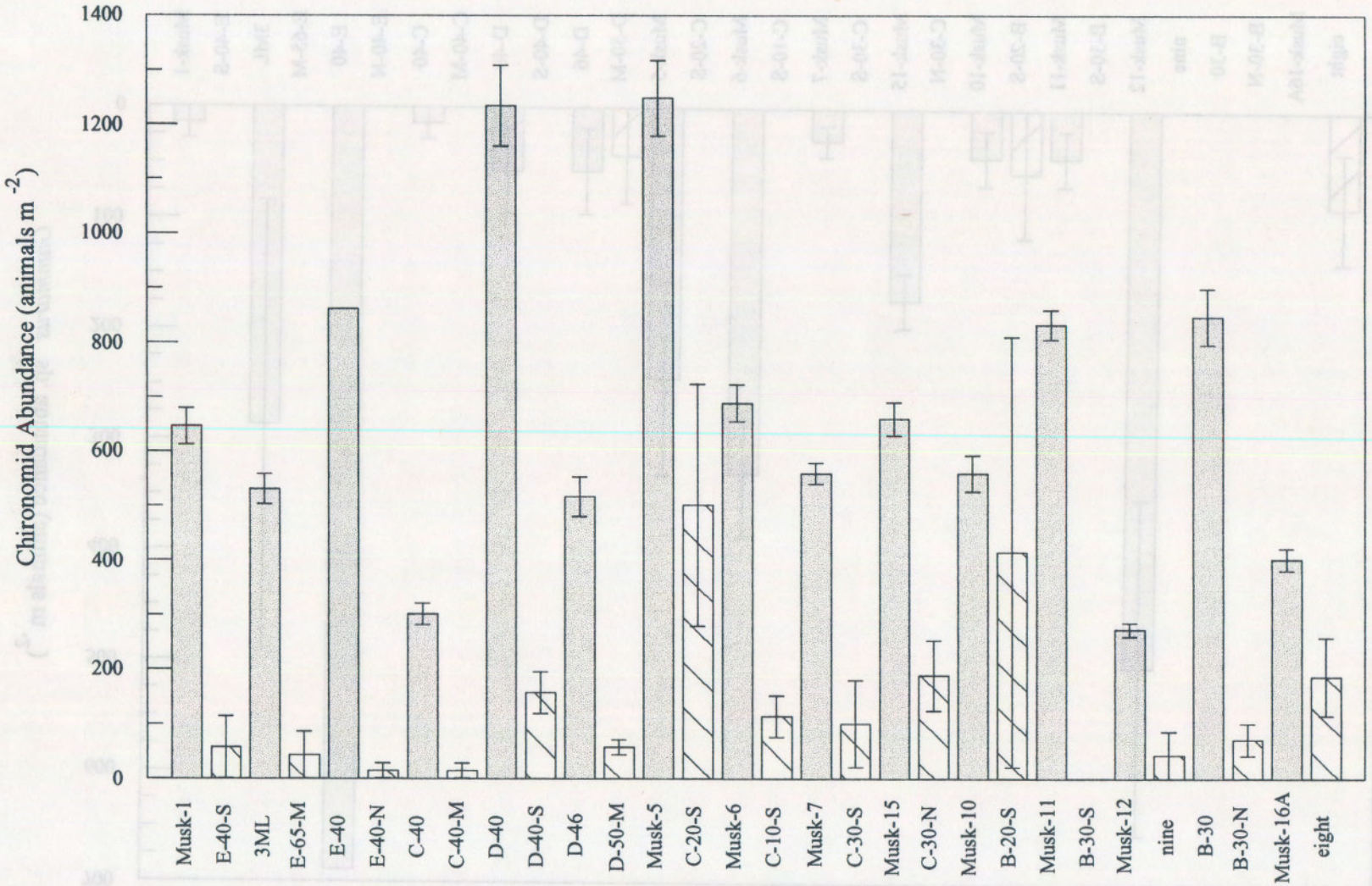


Figure 14: Total chironomid abundance from 1972 (striped) and 1999 (gray) in Muskegon Lake. Error bars indicate standard error. Corresponding sites from 1972 are immediately to the right of the 1999 bar. See Table 1 for site locations.

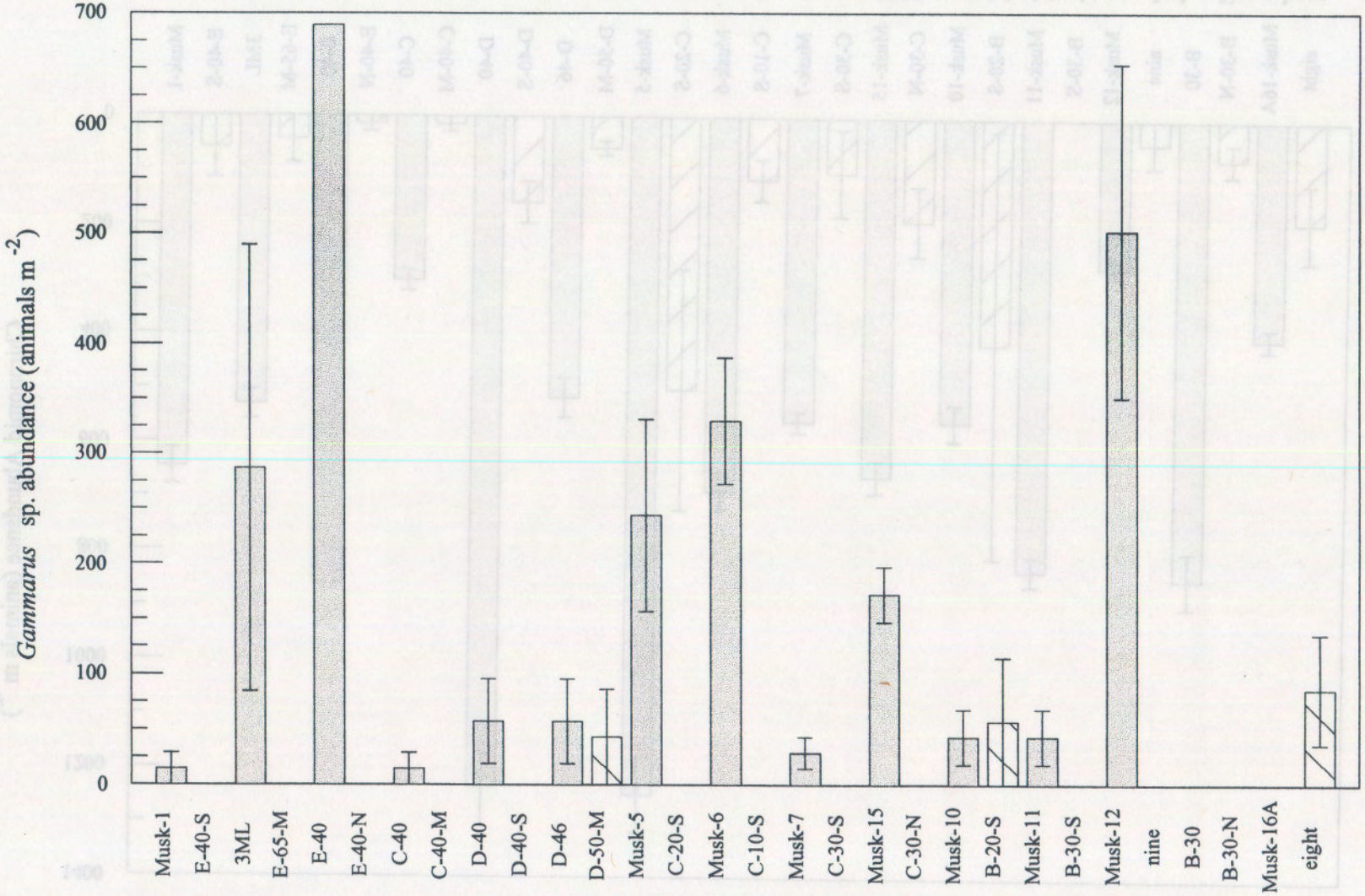


Figure 15: *Gammarus* sp. abundance from Muskegon Lake in 1999 (gray) and 1972 (striped). Error bars represent standard error. Corresponding sites from 1972 are immediately to the right of the 1999 bar. Sites are arranged west to east. See Table 1 for site locations.

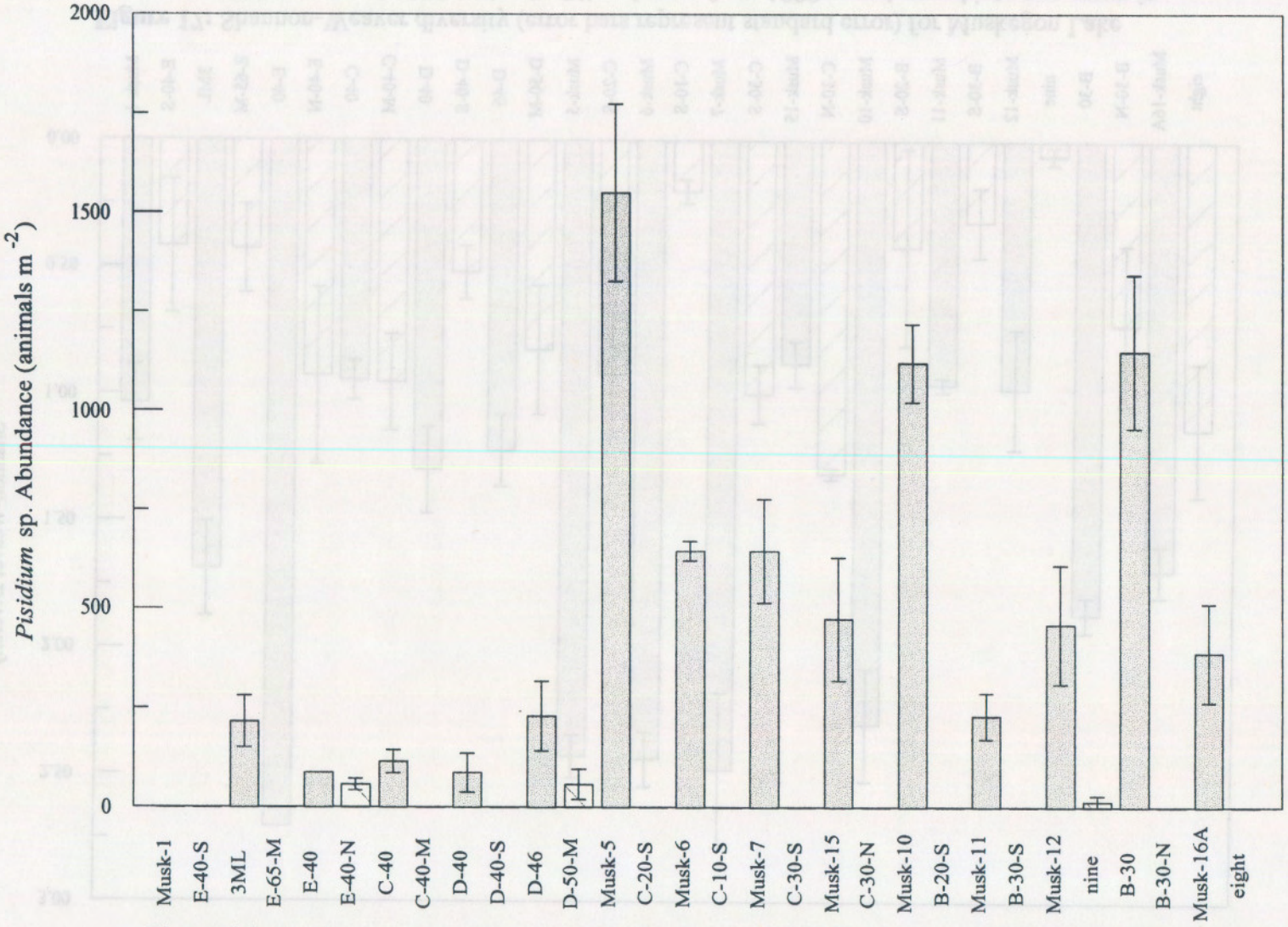


Figure 16: *Pisidium* sp. abundance from Muskegon Lake in 1999 (gray) and 1972 (striped). Error bars represent standard error. Corresponding sites from 1972 are immediately to the right of the 1999 bar. Sites are arranged west to east. See Table 1 for site locations.

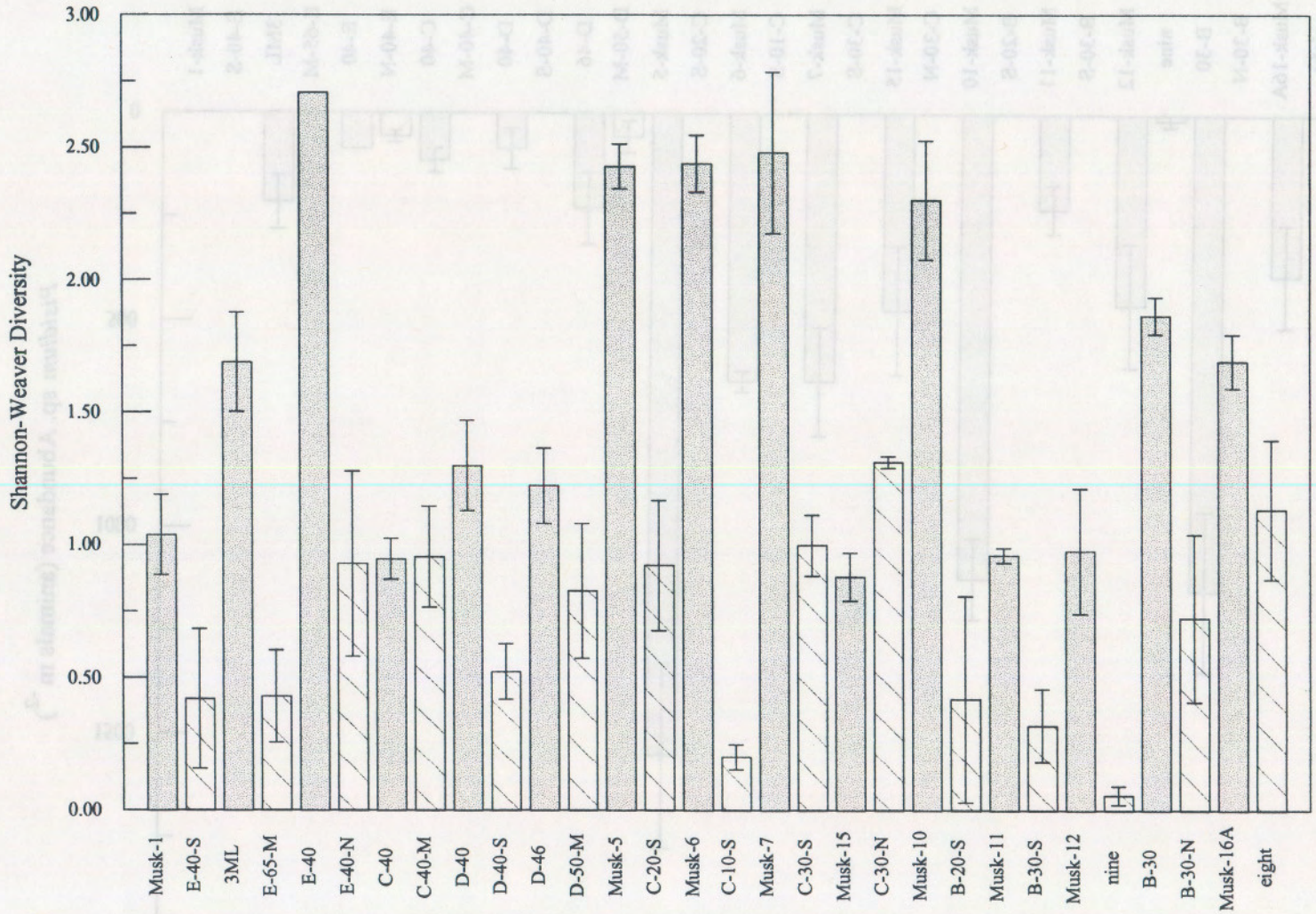


Figure 17: Shannon-Weaver diversity (error bars represent standard error) for Muskegon Lake benthos in 1999 (gray) and 1972 (striped). Oligochaetes from 1999 were lumped into one group in order to compare with 1972. Sites are arranged from west to east. Corresponding sites from 1972 are immediately to the right of the 1999 bar. See Table 1 for site locations.

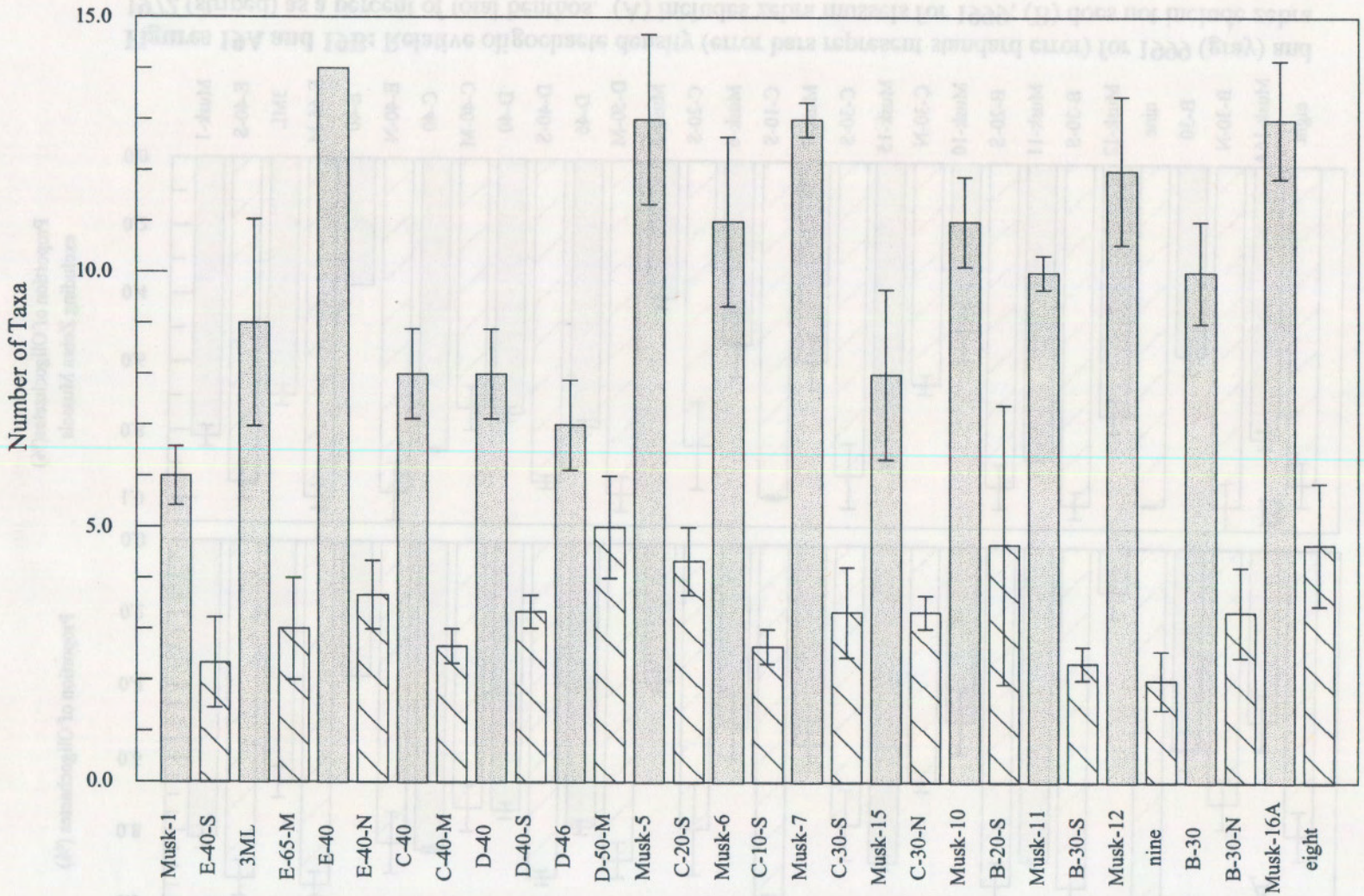
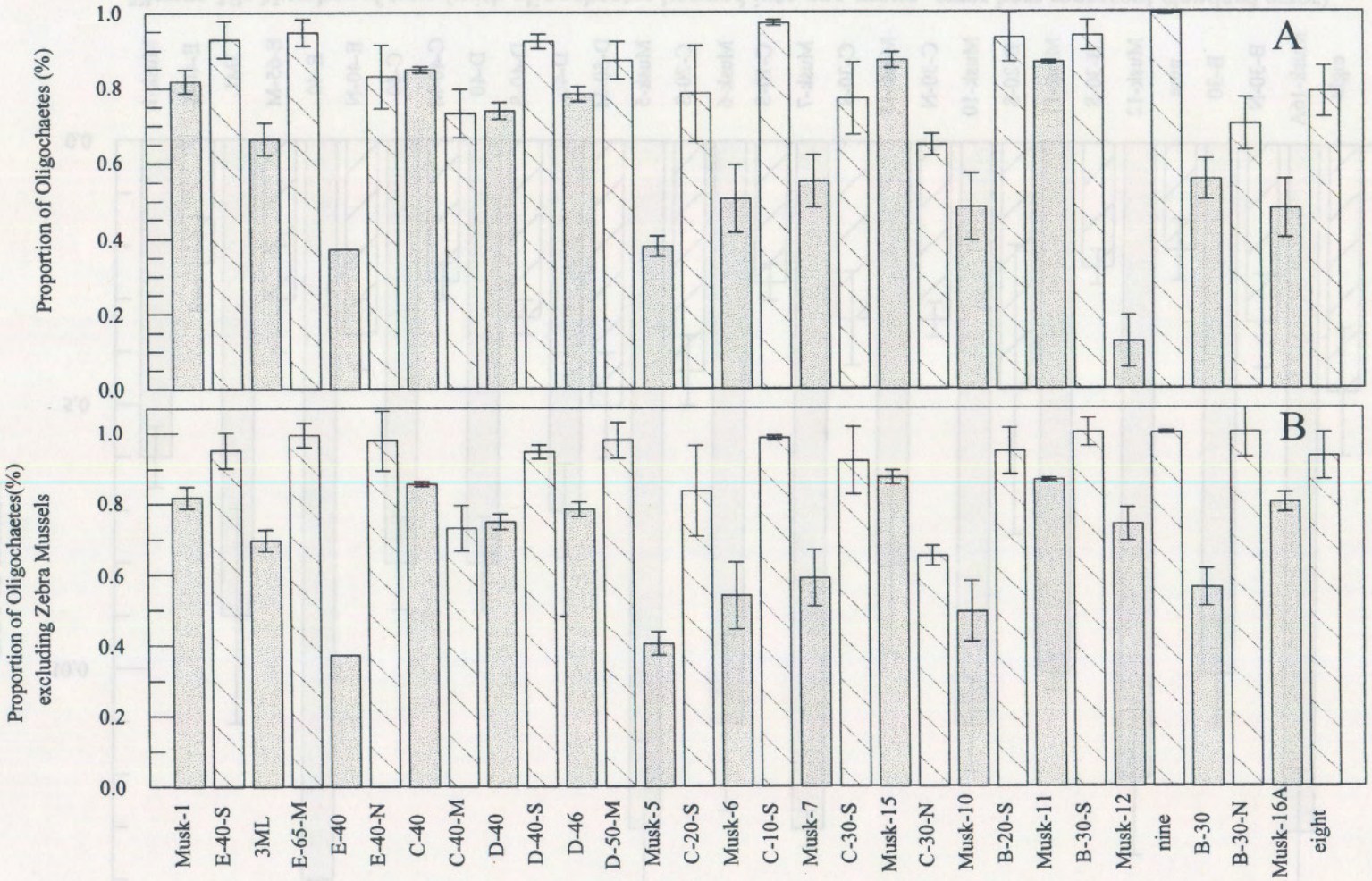


Figure 18: Number of taxa (with oligochaetes lumped into one group, error bars represent standard error) for 1999 (gray) and 1972 (striped). Sites are arranged from west to east. Corresponding sites from 1972 are immediately to the right of the 1999 bar. See Table 1 for site locations.



Figures 19A and 19B: Relative oligochaete density (error bars represent standard error) for 1999 (gray) and 1972 (striped) as a percent of total benthos. (A) includes zebra mussels for 1999; (B) does not include zebra mussels. Sites are arranged from west to east. Corresponding sites from 1972 are immediately to the right of the 1999 bar. See Table 1 for site locations.

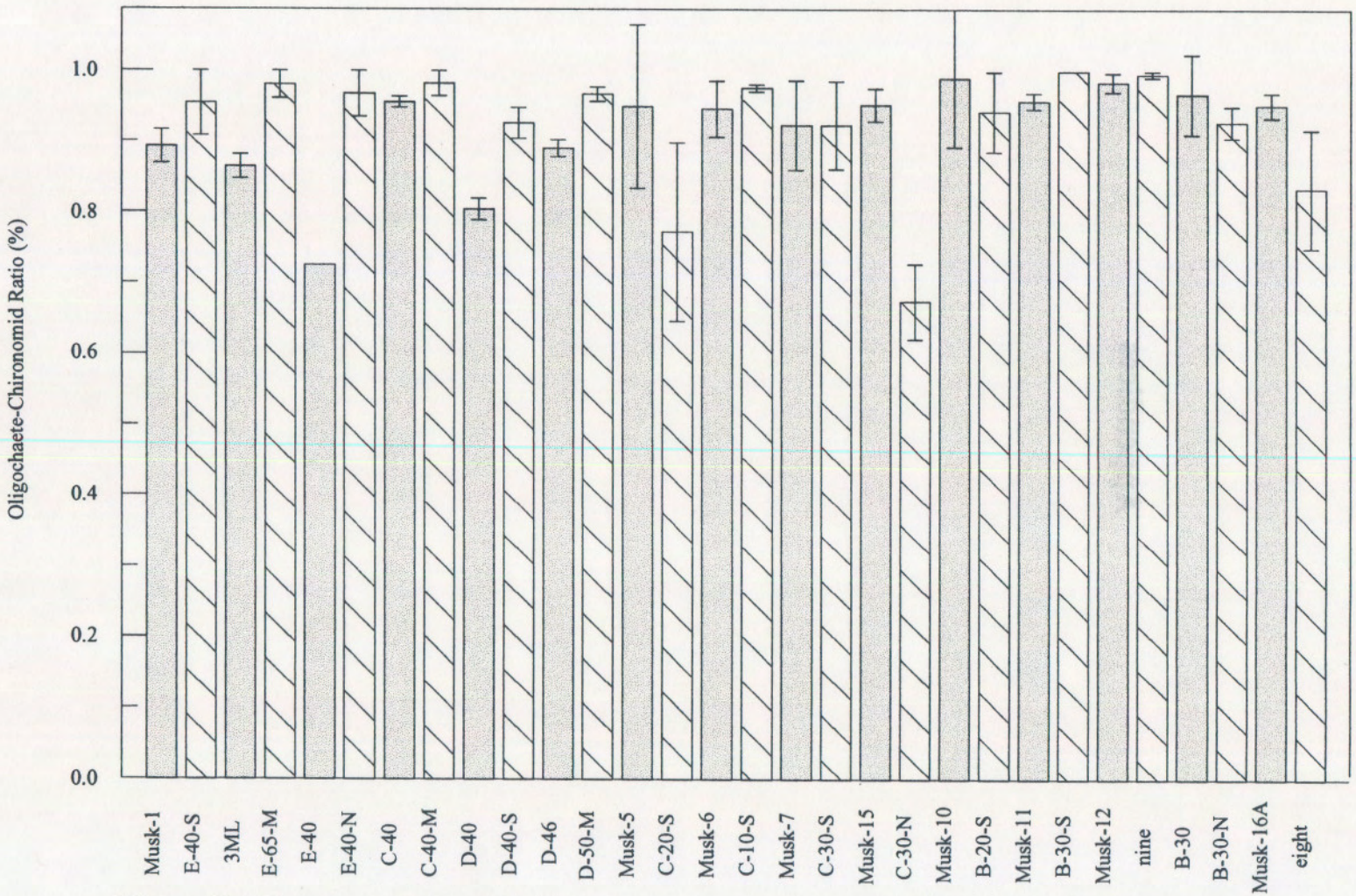


Figure 20: Oligochaete-chironomid ratio (%, error bars represent standard error) for 1999 (gray) and 1972 (striped). Sites are arranged from west to east. Corresponding sites from 1972 are immediately to the right of the 1999 bar. See Table 1 for site locations.

Appendices

Appendix A: Mean animals·m^{-2} ± S.E. for sites sampled in Muskegon Lake, Michigan, fall 1999. Numbers in parentheses indicate ecological classification for use in the Trophic Condition Index (Milbrink 1983). See Table 1 for site locations.

Station	Musk-1	Musk-3	Musk-4	Musk-5	Musk-6	Musk-7	Musk-8	Musk-9	Musk-10	Musk-11
Taxa										
Turbellaria	14 ± 14	14 ± 14	43	144 ± 14	86 ± 25	57 ± 38	72 ± 52	1249 ± 1035	158 ± 38	29 ± 14
Oligochaeta										
Lumbriculidae										
Stylodrilus heringianus (0)	0	0	0	0	0	0	14 ± 14	0	0	0
Naididae										
Arcteonais lomondi (1)	14 ± 14	0	0	0	0	0	14 ± 14	0	0	0
Dero digitata (2)	258 ± 66	14 ± 14	0	14 ± 14	0	14 ± 14	0	170 ± 170	29 ± 14	79 ± 45
Dero flabelliger (2)	0	0	0	14 ± 14	0	0	0	0	0	0
Piguetiella michiganensis (1)	0	0	0	0	0	0	0	0	0	0
Salvina appendulata (1)	0	0	0	0	0	14 ± 14	0	114 ± 114	14 ± 14	0
Tubificidae										
Aulodrilus americanus (1)	0	0	0	0	14 ± 14	0	0	113 ± 113	0	0
Aulodrilus limnobius (1)	172 ± 50	14 ± 14	81	14 ± 14	57 ± 57	86 ± 66	0	57 ± 57	14 ± 14	27 ± 27
Aulodrilus pigueti (1)	359 ± 152	460 ± 51	570	1134 ± 288	1220 ± 546	344 ± 132	258 ± 114	2415 ± 1942	445 ± 117	136 ± 72
Aulodrilus pluriseta (2)	1076 ± 305	0	4556	0	0	0	0	0	0	53 ± 27
Ilyodrilus templetoni (2)	14 ± 14	79 ± 59	81	0	0	0	0	0	0	0
Isocheatides freyi (2)	86 ± 50	0	81	0	0	14 ± 14	0	0	0	0
Limnodrilus cervix variant (2)	0	0	0	0	0	0	0	0	0	26 ± 26
Limnodrilus hoffmeisteri (3)	72 ± 14	76 ± 17	0	14 ± 14	29 ± 14	0	29 ± 14	29 ± 29	14 ± 14	106 ± 24
Limnodrilus maumeensis (2)	0	14 ± 14	0	0	0	0	0	0	0	0
Limnodrilus udekemianus (2)	0	0	0	0	0	0	0	0	0	0
Potamothrix moldaviensis (1)	0	0	0	0	0	0	0	0	0	0
Quistadrilus multisetosus (2)	14 ± 14	508 ± 216	163	14 ± 14	14 ± 14	57 ± 57	187 ± 38	1335 ± 1120	187 ± 38	296 ± 99
Immatures w/o hair chaetae	1378 ± 25	3752 ± 610	2115	990 ± 282	1033 ± 326	1938 ± 634	2411 ± 197	2422 ± 1003	1507 ± 538	6404 ± 597
Immatures w/hair chaetae	359 ± 63	1215 ± 299	814	201 ± 94	144 ± 63	273 ± 144	545 ± 94	243 ± 135	459 ± 100	1859 ± 354
Polychaeta										
Manayunkia speciosa	0	0	0	0	0	0	0	0	14 ± 14	0
Hirudinea										
Glossiphoniidae										
Alboglossiphonia heteroclita	0	0	0	0	0	0	0	0	0	0
Helobdella stagnalis	29 ± 14	0	0	0	0	0	0	0	0	0
Helobdella elongata	0	0	0	0	0	0	0	0	0	43 ± 43
Mollusca										
Gastropoda										
Amnicola sp.	0	57 ± 38	0	57 ± 14	100 ± 52	100 ± 52	29 ± 14	144 ± 103	172 ± 75	0
Bithynia sp.	0	0	0	14 ± 14	14 ± 14	0	0	29 ± 29	0	0
Valvata tricarinata	0	0	0	144 ± 38	187 ± 72	144 ± 52	57 ± 14	43 ± 43	43 ± 25	0
Valvata sincera	0	0	0	0	0	0	0	0	0	0
Bivalvia										
Pisidium sp.	0	86 ± 50	0	1550 ± 224	646 ± 25	646 ± 132	431 ± 66	258 ± 114	1119 ± 99	230 ± 57
Sphaerium sp.	0	29 ± 14	0	43 ± 25	0	244 ± 14	201 ± 80	57 ± 38	402 ± 137	158 ± 63
Musculium sp.	0	0	0	14 ± 14	0	14 ± 14	0	14 ± 14	0	0
Dreissena polymorpha	0	29 ± 14	0	359 ± 175	316 ± 123	316 ± 132	14 ± 14	15758 ± 15715	129 ± 75	14 ± 14
Isopoda										
Caecidotea	0	0	0	0	0	29 ± 29	43 ± 0	158 ± 137	0	0
Amphipoda										
Gammarus sp.	14 ± 14	144 ± 29	1206	244 ± 87	330 ± 57	29 ± 14	57 ± 29	57 ± 38	43 ± 25	43 ± 25
Hyalella azteca	29 ± 14	0	43	43 ± 43	29 ± 29	0	0	86 ± 66	0	0
Echinogammarus ischnus	0	0	0	0	0	0	0	57 ± 38	0	0
Diptera										
Ceratopogonidae*	0	0	0	0	0	0	0	0	0	0
Probezzia sp.	0	0	0	0	0	14 ± 14	14 ± 14	0	14 ± 14	0
Chaoboridae										
Chaoborus sp.	115 ± 52	129 ± 75	0	29 ± 14	57 ± 38	57 ± 29	158 ± 29	86 ± 66	215 ± 90	57 ± 14
Chironomidae										
Chironominae										
Chironomus sp.	445 ± 29	1163 ± 197	474	14 ± 14	0	57 ± 38	230 ± 63	115 ± 29	14 ± 14	258 ± 43
Cladopelma sp.	0	0	86	0	0	0	0	0	0	0
Cryptochironomus sp.	0	57 ± 29	43	115 ± 76	144 ± 63	172 ± 25	115 ± 63	144 ± 29	14 ± 14	144 ± 29
Cryptochironomus digitatus	0	0	0	0	0	0	0	0	0	0
Dicrotendipes sp.	0	0	0	0	0	0	0	14 ± 14	0	0
Paratanytarsus sp.	0	0	0	0	0	0	0	0	0	0
Polypedilum sp.	0	0	0	0	0	0	0	0	0	0
Tanytarsus sp.	14 ± 14	0	0	0	0	0	0	0	0	0
Tribelos jucundum	0	0	0	0	0	0	0	0	0	0
Orthocladiinae										
Heterotrissocladius oliveri	0	0	0	0	0	0	0	0	0	0
Tanypodinae										
Ablabesmyia annulata	0	0	0	0	0	0	0	14 ± 14	14 ± 14	0
Coelotanypus concinnus	0	14 ± 14	0	976 ± 486	474 ± 124	223 ± 57	144 ± 38	215 ± 86	474 ± 217	187 ± 57
Conchapelopia sp.	0	0	0	0	0	0	0	14 ± 14	0	0
Procladius sp.	187 ± 38	158 ± 63	43	144 ± 29	72 ± 72	100 ± 38	158 ± 38	187 ± 52	43 ± 43	244 ± 57
Ephemeroptera										
Caenis sp.	0	0	0	0	0	0	0	0	0	0
Trichoptera										
Ocetis sp.	0	0	0	14 ± 14	14 ± 14	29 ± 29	0	0	0	0
Neureclipsis sp.	0	0	0	0	0	0	0	14 ± 14	0	0

*Heads were too damaged to identify, most likley these were *Probezzia* sp.

Appendix A: Continued.

Station	Musk-12	Musk-13	Musk-14	Musk-15	Musk-16A	AML	BML	CML
Taxa								
Turbellaria	388 ± 179	0	330 ± 94	14 ± 14	201 ± 63	0	72 ± 14	14 ± 14
Oligochaeta								
Lumbriculidae								
Stylodrilus heringianus (0)	0	0	0	0	0	0	0	0
Naididae								
Arcteonais lomondi (1)	0	0	0	0	34 ± 34	0	0	0
Dero digitata (2)	168 ± 120	14 ± 14	0	150 ± 82	0	29 ± 14	0	0
Dero flabelliger (2)	0	0	0	0	0	0	0	0
Piguetiella michiganensis (1)	104 ± 104	0	0	0	0	0	0	0
Salvina appendulata (1)	0	0	0	0	0	0	0	0
Tubificidae								
Aulodrilus americanus (1)	0	0	0	0	220 ± 79	0	0	0
Aulodrilus limnobius (1)	27 ± 27	0	30 ± 30	157 ± 96	121 ± 80	0	57 ± 57	0
Aulodrilus pigueti (1)	725 ± 44	177 ± 91	834 ± 452	1601 ± 682	1611 ± 442	72 ± 52	43 ± 0	158 ± 80
Aulodrilus pluriseta (2)	14 ± 14	43 ± 25	0	150 ± 82	0	144 ± 52	43 ± 0	57 ± 57
Ilyodrilus templetoni (2)	29 ± 29	0	0	0	0	144 ± 29	0	0
Isocheatides freyi (2)	0	0	0	55 ± 55	0	14 ± 14	86 ± 50	14 ± 14
Limnodrilus cervix variant (2)	0	26 ± 26	14 ± 14	0	0	29 ± 29	0	14 ± 14
Limnodrilus hoffmeisteri (3)	88 ± 47	137 ± 26	70 ± 50	0	0	100 ± 14	57 ± 14	301 ± 197
Limnodrilus maumeensis (2)	0	0	0	0	0	57 ± 38	0	14 ± 14
Limnodrilus udekemianus (2)	0	0	0	0	30 ± 30	29 ± 14	0	72 ± 52
Potamothrix moldaviensis (1)	14 ± 14	0	0	0	0	0	0	0
Quistadrilus multisetosus (2)	14 ± 14	72 ± 38	620 ± 249	232 ± 122	216 ± 77	144 ± 57	273 ± 38	129 ± 66
Immatures w/o hair chaetae	4654 ± 937	4247 ± 883	6335 ± 1082	6951 ± 1842	4192 ± 1209	617 ± 187	1076 ± 132	6803 ± 3248
Immatures w/hair chaetae	274 ± 98	838 ± 289	1191 ± 254	1193 ± 466	250 ± 22	388 ± 43	144 ± 38	531 ± 166
Polychaeta								
Manayunkia speciosa	0	14 ± 14	0	0	0	0	0	0
Hirudinea								
Glossiphoniidae								
Alboglossiphonia heteroclita	0	0	0	0	0	0	0	0
Helobdella stagnalis	0	0	0	0	0	0	0	0
Helobdella elongata	0	0	0	0	0	0	0	0
Mollusca								
Gastropoda								
Amnicola sp.	115 ± 14	0	0	0	388 ± 188	0	0	0
Bithynia sp.	0	0	0	0	14 ± 14	0	14 ± 14	0
Valvata tricarinata	29 ± 14	0	0	29 ± 29	72 ± 29	0	0	0
Valvata sincera	0	0	0	0	29 ± 14	0	14 ± 14	14 ± 14
Bivalvia								
Pisidium sp.	459 ± 150	144 ± 76	445 ± 251	474 ± 155	388 ± 124	158 ± 72	144 ± 87	201 ± 117
Sphaerium sp.	230 ± 76	100 ± 63	431 ± 217	72 ± 72	57 ± 14	0	29 ± 29	86 ± 25
Musculium sp.	0	14 ± 14	0	0	0	0	0	0
Dreissena polymorpha	40860 ± 13976	0	14 ± 14	14 ± 14	5626 ± 1730	14 ± 14	86 ± 66	0
Isopoda								
Caecidotea	0	0	29 ± 29	0	0	0	29 ± 14	0
Amphipoda								
Gammarus sp.	502 ± 152	0	57 ± 38	172 ± 25	0	29 ± 29	100 ± 52	14 ± 14
Hyalella sp.	14 ± 14	0	29 ± 29	0	14 ± 14	0	0	14 ± 14
Echinogammarus sp.	100 ± 14	0	0	0	0	0	0	0
Diptera								
Ceratopogonidae*	0	29 ± 29	43 ± 43	0	0	0	0	0
Probezzia sp.	0	14 ± 14	14 ± 14	0	0	0	0	43 ± 43
Chaoboridae								
Chaoborus sp.	0	187 ± 100	43 ± 25	100 ± 52	57 ± 38	129 ± 43	86 ± 25	29 ± 14
Chironomidae								
Chironominae								
Chironomus sp.	43 ± 25	244 ± 52	100 ± 38	431 ± 132	287 ± 87	388 ± 174	560 ± 75	72 ± 14
Cladopelma sp.	0	0	0	0	0	0	0	0
Cryptochironomus sp.	29 ± 14	43 ± 25	144 ± 14	72 ± 38	43 ± 0	14 ± 14	86 ± 25	72 ± 29
Cryptochironomus digitatus	0	0	0	14 ± 14	0	0	0	0
Dicrotendipes sp.	0	0	0	0	0	0	0	0
Paratanytarsus sp.	0	0	0	14 ± 14	0	0	0	0
Polypedilum sp.	29 ± 29	0	0	0	0	0	0	0
Tanytarsus sp.	0	0	0	0	0	0	0	0
Tribelos jucundum	0	0	0	0	0	0	0	0
Orthocladiinae								
Heterotrissocladius oliveri	0	0	0	0	14 ± 14	0	0	0
Tanypodinae								
Ablabesmyia annulata	0	29 ± 14	57 ± 14	0	0	0	0	43 ± 25
Coelotanypus concinnus	0	43 ± 25	86 ± 25	43 ± 43	0	0	0	100 ± 63
Conchapelopia sp.	0	0	0	0	0	0	0	0
Procladius sp.	172 ± 114	273 ± 100	244 ± 115	86 ± 66	57 ± 29	86 ± 43	100 ± 14	144 ± 52
Ephemeroptera								
Caenis sp.	29 ± 29	0	0	0	0	0	0	0
Trichoptera								
Ocetis sp.	14 ± 14	0	0	0	43 ± 25	0	0	0
Neureclipsis sp.	0	0	0	0	0	0	0	0

*Heads were too damaged to identify, most likley these were *Probezzia* sp.

Appendix A: Continued.

Station	1ML	2ML	3ML	4ML	B-30	C-40	D-40	D-46	E-40
Taxa									
Turbellaria	0	43 ± 43	14 ± 14	0	29 ± 14	29 ± 29	14 ± 14	57 ± 38	1033
Oligochaeta									
Lumbriculidae									
Stylodrilus heringianus (0)	0	0	0	0	0	0	0	0	0
Naididae									
Arcteonais lomondi (1)	0	0	14 ± 14	0	0	0	0	0	0
Dero digitata (2)	43 ± 25	0	0	0	14 ± 14	57 ± 57	14 ± 14	14 ± 14	43
Dero flabelliger (2)	0	0	0	0	0	0	0	0	0
Piguetiella michiganensis (1)	0	0	0	0	0	0	0	0	0
Salvina appendulata (1)	0	0	0	0	0	0	0	0	0
Tubificidae									
Aulodrilus americanus (1)	0	0	0	0	0	0	0	0	0
Aulodrilus limnobius (1)	86 ± 86	0	43 ± 25	14 ± 14	0	72 ± 38	115 ± 115	0	0
Aulodrilus pigueti (1)	531 ± 283	129 ± 43	617 ± 311	330 ± 63	502 ± 63	402 ± 274	675 ± 337	344 ± 179	0
Aulodrilus pluriseta (2)	230 ± 38	22 ± 22	100 ± 52	0	0	201 ± 94	86 ± 43	57 ± 57	0
Ilyodrilus templetoni (2)	14 ± 14	22 ± 22	86 ± 43	14 ± 14	0	29 ± 14	43 ± 25	29 ± 14	0
Isocheatides freyi (2)	0	0	14 ± 14	0	0	29 ± 14	57 ± 57	158 ± 117	0
Limnodrilus cervix variant (2)	0	22 ± 22	0	14 ± 14	0	29 ± 14	14 ± 14	0	0
Limnodrilus hoffmeisteri (3)	14 ± 14	129 ± 0	43 ± 0	301 ± 108	14 ± 14	172 ± 43	144 ± 100	57 ± 38	43
Limnodrilus maumeensis (2)	0	65 ± 65	43 ± 25	14 ± 14	0	14 ± 14	14 ± 14	57 ± 29	0
Limnodrilus udekemianus (2)	0	43 ± 43	0	57 ± 29	14 ± 14	14 ± 14	14 ± 14	14 ± 14	0
Potamothrix moldaviensis (1)	0	0	0	0	0	0	0	0	0
Quistadrilus multisetosus (2)	14 ± 14	65 ± 22	258 ± 90	388 ± 108	373 ± 29	144 ± 63	115 ± 14	215 ± 66	0
Immatures w/o hair chaetae	1119 ± 179	1184 ± 280	1105 ± 201	4966 ± 1054	1550 ± 326	3846 ± 273	2870 ± 476	3000 ± 169	1851
Immatures w/hair chaetae	373 ± 38	237 ± 22	402 ± 29	703 ± 166	445 ± 80	761 ± 199	373 ± 125	230 ± 166	0
Polychaeta									
Manayunkia speciosa	0	0	0	0	0	0	0	0	0
Hirudinea									
Glossiphoniidae									
Alboglossiphonia heteroclita	0	0	0	0	0	0	0	0	43
Helobdella stagnalis	0	0	0	0	0	0	0	0	0
Helobdella elongata	0	0	0	0	0	0	0	0	0
Mollusca									
Gastropoda									
Amnicola sp.	0	22 ± 22	0	0	14 ± 14	43 ± 43	29 ± 14	57 ± 29	0
Bithynia sp.	0	0	0	0	0	0	0	0	43
Valvata tricarinata	0	0	0	14 ± 14	29 ± 14	0	0	14 ± 14	0
Valvata sincera	0	43 ± 43	14 ± 14	0	14 ± 14	0	0	0	0
Bivalvia									
Pisidium sp.	172 ± 25	22 ± 22	215 ± 66	445 ± 63	1148 ± 193	115 ± 29	86 ± 50	230 ± 87	86
Sphaerium sp.	43 ± 25	22 ± 22	0	43 ± 43	86 ± 43	43 ± 25	0	14 ± 14	0
Musculium sp.	0	0	0	0	0	0	0	0	0
Dreissena polymorpha	14 ± 14	108 ± 108	187 ± 128	0	57 ± 38	57 ± 14	72 ± 29	0	0
Isopoda									
Caecidotea	0	0	0	0	14 ± 14	0	0	14 ± 14	215
Amphipoda									
Gammarus sp.	29± 29	474 ± 86	287 ± 202	0	0	14 ± 14	57 ± 38	57 ± 38	689
Hyalella sp.	0	22 ± 22	14 ± 14	0	0	14 ± 14	0	0	43
Echinogammarus sp.	0	0	0	0	0	0	0	0	215
Diptera									
Ceratopogonidae*	0	0	0	0	0	0	0	0	0
Probezzia sp.	14 ± 14	0	0	0	0	0	14 ± 14	0	0
Chaoboridae									
Chaoborus sp.	72 ± 52	129 ± 43	115 ± 29	115 ± 14	86 ± 25	416 ± 63	100 ± 52	201 ± 76	43
Chironomidae									
Chironominae									
Chironomus sp.	1206 ± 86	624 ± 22	388 ± 108	373 ± 38	14 ± 14	273 ± 38	1048± 160	517 ± 0	646
Cladopelma sp.	0	0	0	0	0	0	0	0	0
Cryptochironomus sp.	14 ± 14	43 ± 0	29 ± 14	14 ± 14	86 ± 25	0	57 ± 38	0	43
Cryptochironomus digitatus	0	0	0	0	0	0	0	0	0
Dicrotendipes sp.	0	0	0	0	0	0	0	0	0
Paratanytarsus sp.	0	0	0	0	0	0	0	0	0
Polypedilum sp.	0	0	14 ± 14	0	0	0	0	0	0
Tanytarsus sp.	0	0	0	0	0	0	0	0	0
Tribelos jucundum	0	0	0	0	0	0	0	0	43
Orthocladiinae									
Heterotrissocladius oliveri	0	0	0	0	0	0	0	0	0
Tanypodinae									
Ablabesmyia annulata	0	0	0	0	0	14 ± 14	0	0	0
Coelotanypus concinnus	0	43 ± 0	14 ± 14	43 ± 43	718 ± 175	0	14 ± 14	0	0
Conchapelopia sp.	0	0	0	72 ± 72	0	0	0	0	0
Procladius sp.	215 ± 0	108 ± 22	86 ± 25	158 ± 52	29 ± 14	14 ± 14	115 ± 52	0	129
Ephemeroptera									
Caenis sp.	0	0	0	0	14 ± 14	0	0	0	0
Trichoptera									
Ocetis sp.	0	0	0	0	0	0	0	0	0
Neureclipsis sp.	0	0	0	0	0	0	0	0	0

*Heads were too damaged to identify, most likley these were *Probezzia* sp.

Appendix B: Total abundance in animal·m^{-2} ± S.E. of general benthic taxonomic groups collected from Muskegon Lake in fall 1999. Numbers in parentheses next to group names are number of positively identified taxa in each group. See Table 1 for site locations.

Site	Musk-1	Musk-3	Musk-4	Musk-5	Musk-6	Musk-7	Musk-8	Musk-9	Musk-10	Musk-11	Musk-12	Musk-13	Musk-14	Musk-15
Turbellaria (1)	14 ± 14	14 ± 14	43	144 ± 14	86 ± 25	57 ± 38	72 ± 52	1249 ± 1035	158 ± 38	29 ± 14	388 ± 179	0	330 ± 94	14 ± 14
Oligochaeta (18)	3802 ± 84	6132 ± 193	8461 ± 244	2395 ± 73	2511 ± 77	2740 ± 97	3458 ± 122	6898 ± 172	2669 ± 79	8986 ± 327	6111 ± 232	5554 ± 213	9094 ± 318	10489 ± 351
Polychaeta (1)	0	0	0	0	0	0	0	0	14 ± 14	0	0	14 ± 14	0	0
Hirudinea (3)	29 ± 10	0	0	0	0	0	0	0	0	43 ± 14	0	0	0	0
Gastropoda (4)	0	57 ± 14	0	215 ± 32	301 ± 43	244 ± 36	86 ± 14	216 ± 31	215 ± 41	0	144 ± 27	0	0	29 ± 7
Sphaeriidae (3)	0	115 ± 25	0	1607 ± 507	646 ± 215	904 ± 185	632 ± 125	329 ± 75	1521 ± 327	388 ± 68	689 ± 133	258 ± 38	876 ± 146	546 ± 147
Dreissena (1)	0	29 ± 14	0	359 ± 175	316 ± 123	316 ± 132	14 ± 14	15758 ± 15715	129 ± 75	14 ± 14	40860 ± 13976	0	14 ± 14	14 ± 14
Isopoda (1)	0	0	0	0	0	29 ± 29	43 ± 0	158 ± 137	0	0	0	0	29 ± 29	0
Amphipoda (3)	43 ± 8	144 ± 48	1249 ± 395	287 ± 75	359 ± 105	29 ± 10	57 ± 19	200 ± 10	43 ± 14	43 ± 14	616 ± 150	0	86 ± 16	172 ± 57
Ceratopogonidae (1)	0	0	0	0	0	14 ± 7	14 ± 7	0	14 ± 7	0	0	43 ± 8	57 ± 15	0
Chaoboridae (1)	115 ± 52	129 ± 75	0	29 ± 14	57 ± 38	57 ± 29	158 ± 29	86 ± 66	215 ± 90	57 ± 14	0	187 ± 100	43 ± 25	100 ± 52
Chironomidae (14)	646 ± 33	1392 ± 83	646 ± 34	1249 ± 69	690 ± 34	559 ± 20	647 ± 21	703 ± 21	559 ± 34	833 ± 27	273 ± 12	632 ± 25	631 ± 20	660 ± 31
Ephemeroptera (1)	0	0	0	0	0	0	0	0	0	0	29 ± 29	0	0	0
Trichoptera (2)	0	0	0	14 ± 7	14 ± 7	29 ± 15	0	14 ± 7	0	0	14 ± 7	0	0	0

Appendix B: continued.

Site	Musk-16A	AML	BML	CML	IML	2ML	3ML	4ML	B-30	C-40	D-40	D-46	E-40
Turbellaria (1)	201 ± 63	0	72 ± 14	14 ± 14	0	43 ± 43	14 ± 14	0	29 ± 14	29 ± 29	14 ± 14	57 ± 38	1033
Oligochaeta (20)	6674 ± 218	1767 ± 35	1779 ± 54	8093 ± 338	2424 ± 62	1918 ± 59	2725 ± 62	6801 ± 247	2912 ± 82	5770 ± 192	4534 ± 144	4175 ± 149	1937 ± 92
Polychaeta (1)	0	0	0	0	0	0	0	0	0	0	0	0	0
Hirudinea (3)	0	0	0	0	0	0	0	0	0	0	0	0	43 ± 14
Gastropoda (4)	503 ± 88	0	28 ± 4	14 ± 4	0	65 ± 10	14 ± 4	14 ± 4	57 ± 6	43 ± 11	29 ± 7	71 ± 13	43 ± 11
Sphaeriidae (3)	445 ± 121	158 ± 53	173 ± 44	287 ± 58	215 ± 52	44 ± 7	215 ± 72	488 ± 142	1234 ± 369	158 ± 34	86 ± 29	244 ± 74	86 ± 29
Dreissena (1)	5626 ± 1730	14 ± 14	86 ± 66	0	14 ± 14	108 ± 108	187 ± 128	0	57 ± 38	57 ± 14	72 ± 29	0	0
Isopoda (1)	0	0	29 ± 14	0	0	0	0	0	14 ± 14	0	0	14 ± 14	215
Amphipoda (3)	14 ± 5	29 ± 10	100 ± 33	28 ± 5	29 ± 10	496 ± 154	301 ± 93	0	0	28 ± 5	57 ± 19	57 ± 19	947 ± 193
Ceratopogonidae (1)	0	0	0	43 ± 22	14 ± 7	0	0	0	0	0	14 ± 7	0	0
Chaoboridae (1)	57 ± 38	129 ± 43	86 ± 25	29 ± 14	72 ± 52	129 ± 43	115 ± 29	115 ± 14	86 ± 25	416 ± 63	100 ± 52	201 ± 76	43
Chironomidae (14)	401 ± 20	488 ± 28	746 ± 40	431 ± 13	1435 ± 86	818 ± 44	531 ± 28	660 ± 28	847 ± 51	301 ± 19	1234 ± 74	517 ± 37	861 ± 46
Ephemeroptera (1)	0	0	0	0	0	0	0	0	14 ± 14	0	0	0	0
Trichoptera (2)	43 ± 22	0	0	0	0	0	0	0	0	0	0	0	0

Appendix C: Sites and selected metrics that in the four groups resulting from the cluster analysis in Muskegon Lake, Michigan in fall 1999. Densities of taxa are in number of animals·m^{-2}. Cluster names reflect general position in the lake. The Trophic Condition Index (TCI) is based on oligochaetes from Milbrink (1983). See Table 1 for site locations.

Cluster	Sites	Depth (m)	TCI	N Taxa	Diversity	Total Benthos	Total Oligochaetes	*Aulodrilus* spp.	*A. pigueti*	*Limnodrilus hoffmeisteri*	*Quistadrilus multisetosus*
	Musk-11	8.9	1.94	10	0.96	10,393	8,987	217	136	106	296
South East	Musk-13	9.6	1.78	8	1.14	6,687	5,553	220	177	137	72
	Musk-14	8.6	1.57	12	1.21	11,161	9,094	864	834	70	620
	CML	10	1.93	10	0.89	0	8,094	215	158	301	129
	AML	16	1.38	6	1.42	2,583	1,765	215	72	100	144
	2ML	15	1.5	11	2.18	3,617	1,916	151	129	129	65
West Central	3ML.	21	1.28	9	1.69	4,105	2,727	761	617	43	258
	C-40	12.2	1.8	8	0.95	6,803	5,769	675	402	172	144
	D-40	12.2	1.66	8	1.3	6,143	4,535	875	675	144	115
	Musk-1	12.	1.48	6	1.04	4,650	3,803	1,607	359	72	14
South West	Musk-4	12.8	1.88	8	0.99	10,399	8,461	5,207	570	0	163
	1ML	11.5	1.11	7	1.66	4,205	2,425	847	531	14	14
	Musk-5	6.4	0.81	13	2.43	6,214	2,397	1,148	1,134	14	14
	Musk-6	4.1	0.78	11	2.44	5,612	2,512	1,292	1,220	29	14
Hartshorn	Musk-7	7.9	0.91	13	2.48	4,851	2,741	431	344	0	57
Anchorage	Musk-8	8.2	1.39	12	1.94	4,822	3,459	258	258	29	187
	Musk-10	7.4	1.03	11	2.3	5,454	2,669	459	445	14	187
	B-30	9.1	1.1	10	1.87	4,937	2,913	502	502	14	373

Appendix C: continued

Cluster	Sites	*Gammarus* sp.	Total Chironomidae	*Chironomus* sp.	*Coelotanypus concinnus*	*Procladius* sp.
	Musk-11	43	832	258	187	244
South East	Musk-13	0	631	244	43	273
	Musk-14	57	631	100	86	244
	CML	14	431	72	100	144
	AML	29	488	388	0	86
	2ML	474	818	624	43	108
West Central	3ML	287	531	388	14	86
	C-40	14	301	273	0	14
	D-40	57	1,234	1,048	14	115
	Musk-1	14	646	445	0	187
South West	Musk-4	1,206	646	474	0	43
	1ML	29	1,435	1,206	0	215
	Musk-5	244	1,249	14	976	144
	Musk-6	330	689	0	474	72
Hartshorn	Musk-7	29	560	57	230	100
Anchorage	Musk-8	57	646	230	144	158
	Musk-10	43	560	14	474	43
	B-30	0	847	14	718	29

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