CHANGES IN THE NEARSHORE AND OFFSHORE ZOOPLANKTON

COMMUNITIES OF SOUTHEASTERN LAKE MICHIGAN

by

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ABSTRACT

Zooplankton populations in southeastern Lake Michigan were analyzed across both space and time by examining nearshore to offshore collections on approximately a monthly basis from 1998 through 2000. Zooplankton density and biomass were significantly different among sites during all seasons, with differences more prevalent during spring and summer. Twice during the study, there was an increase in the proportion of small-bodied zooplankton. In fall 1998, there was a decrease in calanoid populations and subsequent replacement by smaller-bodied cyclopoids. Specifically, the number of *Diaptomus ashlandi* declined by over 50% between winter 1998 and winter 1999 at all sites. Changes in calanoid populations coincided with a strong year-class of alewives in 1998. A shift to smaller species of Cladocera also occurred at both of the deeper sites between 1999 and 2000. In summer 2000, the smaller *Bosmina longirostris* exhibited a two-fold increase in abundance relative to 1999, and *Daphnia galeata mendotae* decreased from over $2400 \cdot m^{-3}$ in summer 1999 to less than $200 \cdot m^{-3}$ in 2000. Both the low densities of *Daphnia* and the inshore-offshore patterns of cladocerans observed in this study were consistent with size-selective predation by fish. A comparison between 1998-2000 data with 1970s data showed significant decreases in zooplankton density and biomass in southeastern Lake Michigan. In summer and fall, zooplankton biomass was three to five times lower in the nearshore region during 1998-2000 relative to the 1970s and two to four times lower in the mid-depth region. Decreases were most likely due to reduced food availability caused by declines in both phosphorus concentrations and phytoplankton abundance nearshore. Predation and competition from exotic species may have also been responsible for long-term changes in zooplankton populations.

ACKNOWLEDGEMENTS

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INTRODUCTION

Zooplankton abundance and composition vary spatially in large lakes due to both abiotic (water temperature, currents, nutrients) and biotic (chlorophyll a, fish biomass) factors (Evans et al. 1980; Johannsson and O'Gorman 1991; Pinel-Alloul et al. 1999). Physical and chemical characteristics of the nearshore environment differ significantly from offshore regions (Scavia and Bennett 1980). It is important not only to understand both regions, but also to link nearshore and offshore zooplankton populations together. Previous studies of zooplankton in Lake Michigan have predominantly focused on either offshore (Wells 1970; Torke 1975; Makarewicz et al. 1995) or inshore communities (Evans et al. 1980). In order to gain a comprehensive understanding of how nearshore and offshore zooplankton populations vary together seasonally, it is necessary to sample both regions concurrently. This is the first study to analyze temporal changes in both nearshore and offshore zooplankton populations in Lake Michigan.

Zooplankton are an important link in the pelagic food web between primary production and fish populations. Therefore, it is critical to monitor seasonal and inter-annual changes in zooplankton populations in order to better understand and anticipate changes in the Lake Michigan ecosystem. Torke (1975) and Evans et al. (1980) found that zooplankton communities in Lake Michigan varied seasonally in response to temperature, food availability and predation. Little is known, however, about winter zooplankton assemblages in the Great Lakes because of the difficulty with sampling during ice cover and the dangerous weather conditions. Yet, understanding zooplankton populations during winter months is important since winter serves as a crucial time for copepod reproduction and recruitment (Torke 1975). Due to generally ice-free conditions and availability of a

large research vessel for the Episodic Events - Great Lakes Experiment (EEGLE) program in southern Lake Michigan between 1998 and 2000, it was possible to collect zooplankton from both nearshore and offshore regions of the lake during three consecutive winters. These winter data permitted a complete seasonal study of month-to-month variation within zooplankton populations in Lake Michigan.

Lake Michigan has undergone significant changes over the past 25 years. There have been reductions in phosphorus loading (Scavia et al. 1986), fluctuations in fish populations (Fleischer et al. 2000) and the invasion of nonindigenous invertebrates, including the zebra mussel, *Dreissena polymorpha* (Marsden et al. 1993) and the predatory cladoceran *Bythotrephes cederstroemi* (Evans 1988). Reduction in total phosphorus levels have caused major changes in the phytoplankton community of southeastern Lake Michigan (Chang and Rossmann 1988). Alewives (*Alosa pseudoharengus*) have been implicated in controlling large-bodied zooplankton in Lake Michigan (Wells 1970; Evans 1990). Zebra mussels have been hypothesized to have reduced zooplankton prey, including phytoplankton and microzooplankton, thereby competing with zooplankton for food (MacIsaac et al. 1991). *Bythotrephes* may be increasing predation pressure on summer zooplankton communities, resulting in a decrease in the biomass and diversity of cladoceran assemblages (Lehman and Caceres 1993).

The purpose of this research was to investigate seasonal patterns in zooplankton populations in southeastern Lake Michigan and to identify possible factors responsible for both short- and long-term changes. More specifically, this study consisted of three objectives: 1) to identify differences in zooplankton abundance and biomass between depth zones at different times of the year; 2) to analyze seasonal patterns in zooplankton

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community structure from 1998-2000; and 3) to investigate how zooplankton populations have changed since the 1970s using the extensive zooplankton data collected as part of the Cook Nuclear Plant monitoring program near the current study location (Evans et al. 1980; Evans 1990).

METHODS

Zooplankton analyzed for this study were collected from February 1998 through August 2000 in southeastern Lake Michigan. Samples were collected in February, March and May 1998 during the pilot phase of the EEGLE program, and at approximately monthly intervals beginning in September 1998. Collections were made at three sites along a nearshore to offshore transect near St. Joseph, Michigan (Fig. 1). The shallow site was 15 m in depth except in March and September 1998 when the shallow site was located at 10 m. The mid-depth site was 45 m in depth except in March 1998 when samples were collected at 30 m. The deep site was 80 m in depth except in February 1998 when the deep site was 110 m in depth. No collections were made from the deep site in May and November 1998 or in December 1999 due to rough lake conditions.

Two replicate samples of zooplankton were collected at each site with a 50-cm diameter, 2.5-m long, 153-µm mesh conical net equipped with an internal calibrated TSK flowmeter (Model 005WA200, KAHL Scientific Instrument Corporation, El Cajon, CA). The net was hauled vertically through the water column at a speed of 0.5 m· s^{-1} from approximately 2 m above the lake bottom to the surface. Zooplankton were narcotized with Alka-Seltzer and preserved with 2-4% sugar-formalin solution (Haney and Hall 1973). Epilimnetic temperatures were determined from temperature-depth profiles

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obtained at each station using a CTD (Sea-Bird Electronics, Inc., Bellevue, WA). Water was collected at each station with a 5-L Niskin bottle at a depth of 5 m for duplicate chlorophyll samples. Chlorophyll analysis was done fluorometrically after extraction with N,N-dimethylformamide according to the procedure defined in Speziale et al. (1984). Average precision (SE / $\overline{X}$) for replicate chlorophyll a analyses was 3%.

In the laboratory, subsamples of zooplankton were taken from a well-mixed total sample of 500 mL with a Stempel pipette. Enough subsamples of zooplankton were counted in a circular counting dish using a dissecting microscope at a magnification of 20 to 57 × until at least 600 animals were identified. All adult copepods and cladocerans were identified to species, immature copepodites to genus, and nauplii combined into one group using the keys of Wilson and Yeatman (1959) and Brooks (1959). Zooplankton counts from the subsamples were converted to individuals per cubic meter using information on volume subsampled and tow length. The precision (SE / $\overline{X}$) between replicate net tows for individuals per cubic meter averaged 7%.

To estimate zooplankton biomass, individual organisms were measured in length, and lengths converted to dry weights using published length-weight regressions (Culver et al. 1985; Malley et al. 1989). Total body length was measured with a video imaging system using Image-Pro Plus (Media Cybernetics, Silver Springs, MD), excluding caudal setae for copepods and shell spine for cladocerans. Average length was determined from measurements of 10 individual adult male and female copepods and 25 individual nauplii, copepodites and cladocerans. For each sampling time, length measurements were done for those taxa at the mid-depth site that contributed at least 5% to total density. Because length measurements from the mid-depth site were found to be representative of lengths

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from the shallow and deep sites, length measurements from the mid-depth site were applied to all other sites to calculate dry weight biomass for each sampling period. Default weights (Hawkins and Evans 1979) were used for rare taxa that were not measured.

Zooplankton abundance and biomass from each sampling date were compared between sites using ANOVA (SYSTAT 6.0, SPSS Inc., Chicago, IL). Data were also grouped by season in order to test for significant differences in zooplankton abundance and biomass across seasons using ANOVA. All data were log-transformed to obtain more normal distributions and p-values of 0.05 were considered significant for all tests. Seasons were defined based upon a combination of date and thermal structure: winter months included February and March (0 to 4°C); spring months included April, May and June (3 to 20°C); summer months included July, August and September (epilimnetic temperatures ranged from 16 to 25°C); and fall months included October, November and December (epilimnetic temperatures ranged from 7 to 14°C).

To document long-term changes in zooplankton between the 1970s and 1998-2000, zooplankton data from this study were compared to three separate analyses (Hawkins and Evans 1979; Evans et al. 1980; Evans 1990) completed from zooplankton collections in southeastern Lake Michigan (in the area labeled Evans study on Figure 1). Zooplankton data from the monitoring program in the 1970s were comparable to the current study because of the proximity of sampling locations and the similar sampling procedures. Zooplankton samples for Evans' work were analyzed from net tows of the full water column using a 50-cm, 156-μm mesh net. In addition, the dominance of a northward, longshore current in southeastern Lake Michigan acts to minimize differences in plankton distribution between the two regions (Beletsky and Schwab 2001).

An estimate of mean density of dominant copepod species and mean zooplankton biomass for spring (April–May), summer (July–August) and fall (October) were determined for individual years between 1972-1981 from graphs in Evans (1990) for the 30-45 m depth range. These numbers were then averaged to obtain mean spring, summer and fall values for the period 1972-1981 and standard errors were derived from seasonal means of each year. Seasonal means from the 1972-1981 period were compared against seasonal means at the mid-depth site from the 1998-2000 period. In addition, monthly zooplankton biomass values for 1975-1977 were estimated from graphs in Hawkins and Evans (1979) for the 10-20 m depth range (nearshore) and the 20-50 m depth range (mid-depth). Based on these data, mean zooplankton biomass was calculated for each month from April through December, and compared against mean biomass values at the shallow and mid-depth sites from 1998-2000. All data were log-transformed and analysis of variance was completed to compare both seasonal (Evans 1990) and monthly (Hawkins and Evans 1979) zooplankton data from the 1970s with the 1998-2000 results in order to test for significant differences between the two periods of time. Data from 1972-1981 (Evans 1990) covered a longer time period than the 1975-1977 analysis (Hawkins and Evans 1979), but did not include specific data on cladocerans or values that corresponded with the shallow site from the current study. Therefore, both sets of data were used for comparison with the current study. A comparison of mean zooplankton abundance and composition data for the months of April, July and October was done for stations in the 10-20 m depth range and 30-50 m depth range from 1973-1977 (Evans et al. 1980) with shallow and mid-depth sites from 1998-2000. Evans et al. (1980) presented two mean

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values for April based on warm (1973, 1974, 1976) and cold (1975, 1977) springs, therefore a calculated weighted average by number of years was used for April.

RESULTS

Nearshore versus offshore

The shallow, mid-depth and deep sites had very similar surface temperatures throughout most of the year with the exception of winter and spring (Fig. 2). Southern Lake Michigan began to stratify in late April-early May in all three years of the study and water temperature peaked during July (25 °C) or August (20 °C). In winter, temperatures at the shallow site were lower than both mid-depth and deep sites. Spring temperatures were higher at the shallow site relative to the two deeper sites with the exception of June 2000 when an upwelling event likely occurred.

Surface chlorophyll concentrations ranged from 0.6 to 5.7 $\mu g \cdot L^{-1}$ among all sites and fluctuations were greatest at the shallow site (Fig. 3). Chlorophyll concentrations peaked in March 1998, June 1999 and April 2000 at the shallow site and inshore-offshore differences were greatest during these months. Chlorophyll concentrations were very similar at the mid-depth and deep sites throughout the study period with the exception of summer 2000.

For all three sites, there were large monthly fluctuations in zooplankton concentration (Fig. 4) and biomass (Figs. 5a, 5b, 5c), with less severe variations in biomass. The shallow site had the largest fluctuations in concentration and biomass of zooplankton, ranging from 1,709 to 67,047 $\cdot m^{-3}$ and 3.33 to 136.53 mg $\cdot m^{-3}$, respectively. Zooplankton density and biomass peaked within years at the shallow site in May 1998,

December 1999 and April 2000. At the mid-depth site, zooplankton density and biomass ranged from 3,424 to 25,553· m^{-3} and from 9.26 to 62.06 mg· m^{-3}, respectively. Zooplankton density at the deep site ranged from 2,515 to 27,894· m^{-3} and biomass varied from 8.88 to 54.84 mg· m^{-3}, respectively. The ranges of both zooplankton density and biomass for the two deeper sites were similar and less than half the range seen at the shallow site. Zooplankton concentrations for both the mid-depth and deep sites reached their highest levels during 1999 and 2000 in July.

There were significant differences in either mean zooplankton density or biomass across sites for 14 of the 22 cruises from 1998 to 2000 (Table 1). No clear pattern among sites was obvious. Zooplankton density at the shallow site was significantly greater than at the mid-depth and deep sites in March 1998 and in comparison to the deep site in February 1999. In May 1998, December 1999 and April 2000, the density and biomass at the shallow site were significantly higher than at the mid-depth site. In October 1998, early April 1999, June 1999 and July 2000, zooplankton density and biomass were significantly greater at the mid-depth site relative to the shallow site. Zooplankton density at the mid-depth site was significantly higher than at the deep site in September and October 1998, September 1999 and April 2000. Zooplankton density at the deep site was significantly greater than the mid-depth site in March 1998 and April 1999, and both density and biomass at the deep site were significantly greater in June 1999 and August 2000.

Seasonal patterns and short-term changes

The crustacean zooplankton community of southeastern Lake Michigan was dominated by copepods in both numbers and biomass except in summer months when

cladoceran populations peaked (Figs. 5a, 5b, 5c). Twenty-three species of copepods and cladocerans were collected between 1998 and 2000 (Table 2). The dominant copepod taxa, which represented over 75% of copepod populations in all months, were *Diacyclops thomasi*, immature *Diacyclops thomasi* copepodites, *Diaptomus minutus*, *Diaptomus ashlandi*, immature *Diaptomus* spp. copepodites and nauplii. The two species, *Bosmina longirostris* and *Daphnia galeata mendotae*, made up over 90% of cladoceran populations at all times.

Seasonal patterns of zooplankton concentration and biomass were similar, and overall, winter values were low, spring numbers varied tremendously, summer estimates were high and fall values were moderate at all sites. Zooplankton abundance was significantly lower in winter relative to spring and summer. Winter zooplankton concentrations ranged from 2,515 to 8,921$\cdot$ m^{-3} and biomass varied between 8.88 to 33.55 mg$\cdot$ m^{-3}. Over-wintering adult copepods dominated the zooplankton community, including *D. thomasi* (13%), *D. minutus* (13%) and *D. ashlandi* (21%), as well as immature *D. thomasi* copepodites (21%) and *Diaptomus* spp. copepodites (10%). In spring, zooplankton concentrations varied from 1,710 to 67,047$\cdot$ m^{-3} and zooplankton biomass was between 3.33 to 136.53 mg$\cdot$ m^{-3}. Composition of zooplankton in spring was mostly made up of nauplii (23%), *Diaptomus* spp. copepodites (22%), *D. thomasi* copepodites (19%) and adult *D. thomasi* (16%). The density of zooplankton in summer was significantly higher in comparison to winter, spring and fall. Zooplankton biomass was also significantly higher in summer relative to spring and fall. Zooplankton concentrations in summer were between 6,212 to 27,895$\cdot$ m^{-3} and biomass ranged from 14.31 to 62.06 mg$\cdot$ m^{-3}. Summer zooplankton communities were primarily made up of *B. longirostris* (33%),

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Diaptomus spp. copepodites (21%), *D. thomasi* copepodites (16%) and *D. galeata mendotae* (6%). In fall, there were no significant differences in zooplankton abundance or biomass relative to winter or spring. Fall zooplankton concentrations varied from 5,278 to 24,908· m^{-3} and biomass values were between 10.37 and 81.73 mg· m^{-3}. Fall zooplankton assemblages consisted of a mixed community of *Diaptomus* spp. copepodites (38%), *D. thomasi* copepodites (27%) and *B. longirostris* (7%).

Zooplankton composition changed dramatically from 1998 to 2000 with major declines in some dominant species and a subsequent replacement by smaller species. For example, the relative abundance of the copepods *Diaptomus ashlandi, Diaptomus minutus* and *Diacyclops thomasi* changed substantially over the course of the 2½ year study. All three species are medium to small-sized copepods and of the three species, *D. ashlandi* is the largest (Table 3). The concentration of *D. ashlandi* was high for the first three months of the sampling period, and peaked in March 1998 at 2,849· m^{-3} at the shallow site, then decreased tremendously by fall 1998 and remained low until February 2000 (Fig. 6). The smallest calanoid, *D. minutus*, was low in abundance from February 1998 until July 1999, with concentrations less than 510· m^{-3} at all sites (Fig. 7). Nevertheless, *D. minutus* was the most abundant calanoid between September 1998 and June 2000, and reached its peak density of 7,488· m^{-3} at the shallow site in December 1999 (Fig. 7). The concentration of *Diacyclops thomasi* was low in winter 1998 with concentrations less than 360· m^{-3} at all sites, but then increased in 1999, reaching densities of 2,158· m^{-3} in March at the shallow site and 2,832· m^{-3} in June at the deep site (Fig. 8). In fall of 1998, *D. thomasi* remained at the same concentration or increased in abundance as the diaptomid population decreased. Within the copepods, there was a shift in dominance from calanoids to cyclopoids and then

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back to calanoids between 1998 and 2000 (Fig. 9). Even though there was a species shift within the copepods, the average dry weight of an adult copepod did not change greatly over the study period (Fig. 10).

Within the cladocerans, there was an increase in *Bosmina longirostris* (Fig. 11), and a decrease in *Daphnia galeata mendotae* at the mid-depth and deep sites between summer of 1999 and 2000 (Fig. 12). This change represented a major shift in the size structure of the cladoceran community (Table 3). *B. longirostris* was abundant between May and December, with peak densities in July for both 1999 (10,478· m^{-3}) and 2000 (9,987· m^{-3}) (Fig. 11). *B. longirostris* was typically more abundant at the shallow site than the two deeper sites, except in summer 2000 when the offshore counts were unusually high and exceeded those at the shallow site. Tremendous increases in abundance of *B. longirostris* were seen at both the mid-depth and deep sites, and specifically, there was a nine-fold increase in the density of *B. longirostris* at the deep site between July 1999 and July 2000.

D. galeata mendotae accounted for over 85% of the total *Daphnia* population density between July and December for all sites. The largest *Daphnia* species in Lake Michigan, *D. pulicaria* (Evans and Jude 1986), was found during spring and fall months at very low densities of less than 8· m^{-3}. The smallest *Daphnia* species in Lake Michigan, *D. retrocurva* (Evans and Jude 1986), was only found in September 1998 and August 2000, and concentrations were less than 22· m^{-3}. *D. galeata mendotae* was more abundant offshore in comparison to the shallow site, and reached a peak concentration of 2,500· m^{-3} in July 1999 at the deep site (Fig. 12). There was no peak in the concentration of *D. galeata mendotae* through the beginning of August 2000, with concentrations less than

170· m^{-3}. As a result of the decline in *D. galeata mendotae* and the increase in *B. longirostris*, the average dry weight of an individual cladoceran decreased tremendously between summer 1999 and 2000 at the deep site (Fig. 13). The mid-depth and deep sites had much higher average dry weight values in comparison to the shallow site in 1998 and 1999, but all three sites were very similar in 2000.

Comparison with the 1970s

Major differences in zooplankton composition and biomass were found between the years 1971-1982 and 1998-2000; however most pronounced differences were restricted to summer and fall. Only data from the mid-depth region were compared because they corresponded best with sites used by Evans (1990). At the mid-depth range, there was a significant decrease in mean zooplankton biomass between the two time periods for summer and fall, but not for spring (Table 4). For the three major adult copepod species identified, there was a significant decrease in the mean concentration of both *D. ashlandi* and *D. thomasi* in the fall. No significant differences were found for individual species in spring or summer.

Statistically significant reductions were also found in monthly estimates of zooplankton biomass between 1975-1977 and 1998-2000 (Table 5). Nearshore zooplankton biomass was lower by at least three-fold in July, September and October from 1998-2000 relative to 1975-1977. Zooplankton biomass for the mid-depth region was more than 50% lower in June, July, August, September and October from 1998-2000 compared to 1975-1977. Significant decreases in copepod concentrations accounted for most of the differences in biomass between the two time periods, and statistically

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significant differences were found for copepod biomass in the same months as total zooplankton biomass (Table 6). Statistically significant declines in cladoceran biomass only occurred in July and October nearshore and in October for the mid-depth area (Table 7).

Since Evans et al. (1980) published only the mean concentrations of zooplankton for the five-year period of their study, it was not possible to perform statistical analyses comparing their density data to those of the current study. However, general patterns of change were discernable by comparing the two data sets based on changes of large magnitude. A comparison of zooplankton composition and abundance between 1973-1977 and 1998-2000 indicated an overall decrease in zooplankton concentrations among all major taxa. The total number of zooplankton in April was similar between 1973-1977 and 1999-2000 for both the nearshore and mid-depth sites (Table 8). There were very few compositional differences in April between the two time periods. For July, current densities of zooplankton were 30% and 45% of those in the 1970s for nearshore and mid-depth regions, respectively (Table 9). In October, density of zooplankton decreased by nearly one-third for both regions between 1973-1977 and 1998-1999 (Table 10). Species composition in both July and October were very similar between the two periods of time for the nearshore and mid-depth areas, with the exception of cladocerans. The abundance of *Daphnia* spp. nearshore decreased from over $1,000 \cdot m^{-3}$ to zero in both July and October. Conversely, even though *B. longirostris* decreased in abundance at both sites, the relative percent composition of *B. longirostris* increased.

DISCUSSION

Differences across sites

Zooplankton populations often differ with distance from shore in large lakes, and results from this study showed significant differences in total density and biomass of zooplankton between shallow, mid-depth and deep sites during all seasons. Fluctuations in zooplankton concentration and biomass were greatest at the shallow site, and were significantly different from the mid-depth or deep site from 40 to 50% of the time. Specifically, differences were most prominent in spring and summer, when zooplankton concentrations at the shallow site were significantly different from one or both of the deeper sites 75% of the time compared to 33% of the time in winter. Although there were often differences in zooplankton concentrations between sites, the direction of these differences was not consistent throughout spring and summer. Evans et al. (1980) also found significant differences in zooplankton densities in the same region between depth zones of 5-10 m, 10-20 m, 20-30 m and 30-50 m for all April and all but one July collection between 1973-1977.

Potential factors that explain differences in zooplankton populations between the shallow site and the two deeper sites include influences of river inputs, food availability, temperature and predation. Within the years 1998, 1999 and 2000, chlorophyll concentrations varied four-fold at the shallow site, but there was no significant correlation between chlorophyll concentration and zooplankton density or biomass. Temperature appeared to influence patterns of zooplankton abundance, in that often warmer temperatures corresponded with higher densities of zooplankton. However, temperature alone cannot explain all of the patterns observed in this study. For example, in spring,

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when temperatures were higher nearshore, zooplankton densities were sometimes lower relative to the two deeper sites. More importantly, a test for correlation between zooplankton abundance and temperature was not significant. Previous studies showed that animals are not evenly distributed throughout the water column (Wells 1960; Vanderploeg et al. 1992), and differences in the proportion of epilimnion, metalimnion and hypolimnion may partially explain why zooplankton density and biomass vary between sites for the current study. Differences in community composition across sites were found for several species, including *D. minutus*, which is an epilimnetic species and was most abundant at the shallow site, and *D. sicilis*, which is a hypolimnetic species and was more abundant at the two deeper sites. Surprisingly, zooplankton concentration and biomass at the shallow site were similar to the mid-depth and deep sites from 40 to 50% of the time. In particular, there were few differences among sites in winter due to isothermal and well-mixed conditions in the lake.

Results of this study suggest that the mid-depth site may not adequately characterize offshore zooplankton populations. For 44% of the samples, zooplankton density at the mid-depth site was significantly different from the deep site. On several occasions, there was a two-fold difference in zooplankton concentration between the mid-depth and deep site. The majority (75%) of these differences occurred in spring and summer, and winter months made up only 12% of the total. I expected fewer differences between the mid-depth and deep site in comparison to the shallow site because both sites are deep and more than 15 km offshore. Although there were only 18 versus 22 cruise comparisons for the two deeper sites, two of the missing observations occurred in fall (when differences were less common) and two in May and July (when differences were

more common), so comparisons should not have been biased relative to shallow site comparisons.

Recent trends

Seasonal succession of zooplankton between 1998 and 2000 followed the same general pattern observed by Torke (1975) and Evans et al. (1980). However, there were unexpected changes within the zooplankton community that favored smaller-bodied species of both copepods and cladocerans during the current 2½ year period. These recent changes in the zooplankton community are all suggestive of size-selective vertebrate predation. Calanoid copepods dominated in the beginning of the study; however, following a peak in spring 1998, calanoids crashed and it took one year for the population to reach previous levels. Specifically, *D. ashlandi*, which has been the dominant crustacean zooplankton species of Lake Michigan over the past several decades (Torke 1975; Evans 1990; Makarewicz et al. 1995), declined in number more than any other species. Cyclopoids replaced calanoids in dominance beginning in the fall of 1998 and the recovery of the calanoid population began with an increase in the smaller-bodied *D. minutus* starting in summer 1999.

The crash of calanoids in fall of 1998 was concurrent with a major increase in both young-of-the-year and adult alewives, the dominant planktivorous fish in Lake Michigan (Fleischer et al. 2000) and important size-selective feeders (Wells 1970). Densities of both young-of-the-year and adult alewives were at least three times higher in 1998 compared to each of the previous five years (Fleischer et al. 2000). Wells (1970) showed that size-related changes in the zooplankton community of Lake Michigan were consistent with

selective predation by alewives between 1954 and 1966. An increase in alewife abundance was associated with a decrease in *Daphnia, Leptodora, Limnocalanus, Epischura*, and other large-bodied crustacean taxa and an increase in small-bodied zooplankton, specifically *B. longirostris* (Wells 1970).

Both the decrease in *Daphnia* populations during the summer of 2000 and the inshore-offshore patterns of cladocerans observed in this study are consistent with patterns of fish predation in Lake Michigan. Fish density is higher nearshore than offshore in Lake Michigan during summer (Brandt et al. 1991) and observations of smaller animals inshore have been linked to increased fish predation in nearshore waters (Hawkins and Evans 1979; Evans et al. 1980). The greater abundance of smaller species of cladocerans nearshore in summer is consistent with feeding patterns of alewife populations because alewife are planktivorous inshore and feed on mesozooplankton, but shift their feeding behavior in deep water to feed on *Mysis relicta* and *Diporeia* (Evans and Jude 1986). The tremendous decrease in *Daphnia* populations may have reduced competition with *B. longirostris*, and allowed the smaller-bodied species to increase in number.

An alternative explanation for the low abundance of *Daphnia* in 2000 may be invertebrate predation. However, prey selection and recent abundance patterns of *Bythotrephes*, the dominant invertebrate predator in the epilimnion of Lake Michigan (Lehman and Caceres 1993), argue against this hypothesis. *Bythotrephes* prey upon both small and large bodied zooplankton, especially cladocerans (Vanderploeg et al. 1993; Schulz and Yurista 1999). After the introduction of *Bythotrephes* to Harp Lake in 1993, there was a decrease in small species, including *B. longirostris*, and an increase in larger zooplankton, including *D. galeata mendotae* (Yan and Pawson 1997). It is possible that *D.*

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galeata mendotae can escape predation from *Bythotrephes* by its migratory behavior (Lehman and Caceres 1993). Densities of *Bythotrephes* in the St. Joseph region indicate that predation was not higher in July 1999 than in July 2000 (S. Pothoven, Great Lakes Environmental Research Laboratory, Muskegon, MI, personal communication). In addition, *Bythotrephes* have been in Lake Michigan since 1986, and such low numbers of *D. galeata mendotae* have not been reported before summer 2000 elsewhere (Makarewicz et al. 1995; Barbiero et al. 2001). The observed low densities of *D. galeata mendotae* offshore in summer 2000 and the concurrent increase in *B. longirostris*, was therefore more likely a function of vertebrate predation as opposed to invertebrate predation.

Appreciable inter-annual variation among species was expected based upon several previous studies on Lake Michigan zooplankton (Torke 1975; Evans 1990; Makarewicz et al. 1995). However, it was surprising to see that the decline in calanoid populations and the shift to a smaller species of zooplankton occurred over such a short period of time. Data were not collected from summer 1998 for this study and would have provided valuable information leading up to the crash in calanoids and additional data on *Daphnia* populations in order to compare with 1999 and 2000. The decline in *D. galeata mendotae* in 2000 only represents a one-year change in Lake Michigan and it is not known if it will continue in the future or if there was a downward trend beforehand.

Long-term changes

Over the past 25 years, Lake Michigan has undergone several changes that would potentially reduce the food base of the ecosystem (phosphorus reduction, zebra mussels) and increase predation pressures (*Bythotrephes*) for zooplankton. Not surprisingly, the

comparison of zooplankton populations of the 1970s and the late 1990s showed significant decreases in zooplankton biomass for both nearshore and mid-depth regions of southeastern Lake Michigan. Specifically, copepod and cladoceran biomass were lower during summer and fall in both regions of the lake.

Phosphorus loadings to Lake Michigan were substantially reduced after 1980, and consequently spring total phosphorus concentrations nearshore decreased by 40% between the 1970s and 1998-2000 (Madenjian et al. in press). In a comparison of a wide range of lakes of varying eutrophy, zooplankton biomass varied in direct proportion to total phosphorus concentration (Hanson and Peters 1984). In fact, total phosphorus concentration was found to be the strongest estimator of crustacean zooplankton biomass among the variables examined; including chlorophyll a, Secchi depth, mean depth or maximum depth (Hanson and Peters 1984). Thus a decrease in zooplankton is consistent with a decrease in phosphorus concentration.

In the nearshore region of Lake Michigan, chlorophyll concentrations decreased by more than 50% between the 1970s and 1998-2000 (Madenjian et al. in press), and likely contributed to the decline in zooplankton abundance and biomass between the two periods of time. Assuming no changes in algal food quality, a decrease in phytoplankton abundance (chlorophyll) could potentially result in lower zooplankton production. Zebra mussels in the nearshore areas may have been responsible for decreased chlorophyll concentrations as well since they filter phytoplankton out of the water column at a rapid rate (MacIsaac et al. 1992).

Top-down control from vertebrate predation does not appear to be a reasonable explanation for the long-term decrease in overall zooplankton number and biomass from

the 1970s to 1998-2000. Actually, alewives were more abundant between 1973-1981 compared to the years 1997 and 1999 (Fleischer et al. 2000). However, the number of alewives in 1998 exceeded all years between 1973-1981 with the exception of 1974 and 1981 (Fleischer et al. 2000). There were large fluctuations in alewife abundance during both periods of time, but alewives were more abundant overall between 1973-1981 than in 1998-2000.

The invasive species, *Bythotrephes*, has likely contributed to decreases in the density and biomass of cladocerans over the past 20 years as it was not present in Lake Michigan during the 1970s. *Bythotrephes* prey heavily upon cladocerans (Vanderploeg et al. 1993) and have remained relatively constant in number in southeast Lake Michigan since they were first found in 1986 (Pothoven et al. 2001).

The overall abundance, as well as, the diversity of *Daphnia* spp. decreased since the 1970s, when *D. retrocurva* was abundant (Evans and Jude 1986). The dominance by *D. galeata mendotae* was noted in previous studies that sampled zooplankton in Lake Michigan (Makarewicz et al. 1995); however this is the first seasonal study to show that the *Daphnia* community continues to be dominated by one species, *D. galeata mendotae*. It has been argued that *D. retrocurva* and *D. pulicaria* decreased in number during the 1980s due to invertebrate (Lehman 1991) or both vertebrate and invertebrate (Makarewicz et al. 1995) predation pressures. In addition, results from 1998-2000 show that there have been more recent changes in Lake Michigan since the early 1990s with the large increase in the abundance of *B. longirostris* and the decrease in *D. galeata mendotae* offshore.

Another important difference between zooplankton populations of southeastern Lake Michigan in the 1970s and 1998-2000 is the overall decrease in number of

zooplankton species. During the 1970s, Evans et al. (1980) found nine species of cyclopoids and twenty-seven cladoceran species. Only three cyclopoid species and twelve cladocerans were found in the collections from 1998-2000. The decrease in species diversity may be attributed in part to the fact that Evans et al. (1980) made zooplankton collections in shallower water (5-10 m) where there are a greater number of neritic, warm-water species associated with river mouths. Most of the species present in the 1970s collections that were not encountered in this study are found in more eutrophic areas, including *Cyclops vernalis, Alona affinis* and *Sida crystallina* (Balcer et al. 1984). Open-water species were similar between the two time periods even though relative abundances of zooplankton have changed in both nearshore and mid-depth regions of the lake. Certain neritic species have possibly been lost over the past 20 years due to decreases in phosphorus loading, lower primary productivity nearshore (Madenjian et al. in press) and possible removal of phytoplankton and microzooplankton by zebra mussels.

Conclusions

This study demonstrates the importance of simultaneous collections of inshore and offshore sites and seasonal coverage of zooplankton populations to deduce which factors are operating on short- and long-term changes. The frequency and magnitude of change are greater in nearshore zooplankton communities due to increased pressure from both top-down (e.g. vertebrate and invertebrate predation) and bottom-up (e.g. nutrients and phytoplankton) forces. Rapid fluctuations in zooplankton populations occurred from 1998-2000 due to vertebrate predation whereas slow, gradual nutrient changes led to decreases in zooplankton biomass and abundance over the past 20 years.

Table 1. Ratio of zooplankton density and biomass between sites for individual cruises from St. Joseph region in southeastern Lake Michigan, 1998-2000. Test of the variability between sites on each date using ANOVA (ns, not significant; *, $p < 0.05$; **, $p < 0.01$).

Year	Date	Density			Biomass		
		shallow:mid	shallow:deep	mid:deep	shallow:mid	shallow:deep	mid:deep
1998	Feb. 3	0.98^{ns}	1.83^{ns}	1.87^{ns}	1.16^{ns}	1.53^{ns}	1.32^{ns}
	Mar. 16	1.79^{**}	1.53^{**}	0.85^{*}	2.08^{**}	2.45^{**}	1.18^{ns}
	May 22	4.17^{*}	-	-	3.63^{*}	-	-
	Sept. 23	0.82^{ns}	1.28^{ns}	1.56^{*}	0.50^{*}	0.39^{**}	0.77^{ns}
	Oct. 28	0.72^{*}	1.78^{**}	2.48^{**}	0.59^{**}	0.85^{ns}	1.50^{*}
	Nov. 21	1.08^{ns}	-	-	0.84^{ns}	-	-
1999	Feb. 18	1.19^{ns}	1.45^{*}	1.22^{ns}	0.91^{ns}	1.35^{ns}	1.48^{*}
	Mar. 12	1.27^{ns}	1.16^{ns}	0.91^{ns}	1.28^{ns}	1.45^{ns}	1.13^{ns}
	Apr. 8	0.48^{**}	0.39^{**}	0.81^{ns}	0.40^{**}	0.38^{**}	0.95^{ns}
	Apr. 27	1.28^{ns}	0.67^{ns}	0.52^{*}	0.56^{ns}	0.39^{*}	0.71^{ns}
	June 5	0.45^{*}	0.22^{**}	0.48^{*}	0.34^{**}	0.14^{**}	0.40^{*}
	July 29	0.86^{ns}	2.05^{a}	2.39^{a}	0.52^{ns}	0.79^{a}	1.52^{a}
	Sept. 11	0.81^{**}	1.76^{**}	2.18^{**}	0.84^{ns}	0.63^{ns}	0.75^{ns}
	Oct. 20	1.89^{ns}	1.34^{ns}	0.71^{ns}	1.89^{ns}	0.83^{ns}	0.44^{ns}
	Dec. 14	1.76^{*}	-	-	1.75^{*}	-	-
2000	Feb. 21	0.77^{ns}	0.70^{ns}	0.91^{ns}	0.81^{ns}	0.90^{ns}	1.11^{ns}
	Mar. 11	0.78^{ns}	0.69^{ns}	0.89^{ns}	0.95^{ns}	0.87^{ns}	0.92^{ns}
	Apr. 11	2.80^{**}	1.69^{ns}	0.60^{*}	1.82^{*}	1.17^{ns}	0.64^{ns}
	May 16	0.82^{ns}	0.59^{ns}	0.72^{ns}	0.37^{*}	0.30^{**}	0.80^{ns}
	June 7	0.62^{ns}	0.79^{ns}	1.27^{ns}	0.74^{ns}	0.97^{ns}	1.32^{ns}
	July 10	0.52^{*}	0.37^{**}	0.70^{ns}	0.51^{*}	0.38^{**}	0.74^{ns}
	Aug. 10	0.94^{ns}	0.71^{*}	0.75^{*}	0.74^{*}	0.52^{**}	0.70^{*}

[a] only one replicate net tow for deep site

Table 2. Zooplankton taxa found in the St. Joseph region of southeastern Lake Michigan from 1998 to 2000.

Cyclopoida
  Tropocyclops prasinus mexicanus
  Mesocyclops edax
  Diacyclops thomasi

Calanoida
  Diaptomus minutus
  Diaptomus ashlandi
  Diaptomus oregonensis
  Diaptomus sicilis
  Eurytemora affinis
  Epischura lacustris
  Senecella calanoides
  Limnocalanus macrurus

Cladocera
  Bosmina longirostris
  Eubosmina coregoni
  Chydorus sphaericus
  Diaphanosoma leuchtenbergianum
  Ceriodaphnia quadrangula
  Daphnia retrocurva
  Daphnia galeata mendotae
  Daphnia pulicaria
  Polyphemus pediculus
  Cercopagis pengoi
  Bythotrephes cederstroemi
  Leptodora kindtii

Table 3. Average (± SD) lengths and dry weights of dominant zooplankton species in Lake Michigan with number of dates measured (N) and range of individual weights also provided.

Species	Length (mm)	Dry weight (µg)	Range of individual weights (µg)
Diacyclops thomasi			
Female	1.07 ± 0.07 (11)	4.77 ± 0.58 (11)	3.00 – 6.79
Male	0.88 ± 0.05 (11)	3.26 ± 0.33 (11)	2.15 – 4.25
Diaptomus minutus			
Female	0.98 ± 0.04 (9)	5.01 ± 0.74 (9)	2.31 – 7.29
Male	0.92 ± 0.03 (9)	3.89 ± 0.41 (9)	2.02 – 5.57
Diaptomus ashlandi			
Female	1.01 ± 0.05 (13)	5.91 ± 0.99 (13)	2.57 – 9.64
Male	0.94 ± 0.04 (13)	4.48 ± 0.75 (13)	1.97 – 8.62
Bosmina longirostris	0.33 ± 0.03 (9)	1.55 ± 0.39 (9)	0.52 – 5.18
Daphnia galeata mendotae	1.16 ± 0.11 (3)	9.72 ± 1.41 (3)	3.78 – 17.51

Table 4. Mean (± SE) density (no·m^{-3}) of the three major adult copepod species and total zooplankton biomass (mg·m^{-3}) at the 30-45 m depth range in 1972-1981 (Evans 1990) and the 45 m site in 1998-2000 for spring, summer and fall. ns = not significant.

| | Mean Density | | |
	1972-1981	1998-2000	p
Spring			
Diaptomus minutus	182 ± 42	619 ± 444	ns
Diaptomus ashlandi	929 ± 118	1034 ± 371	ns
Diacyclops thomasi	733 ± 137	1190 ± 456	ns
Total biomass	18 ± 1	27 ± 7	ns
Summer			
Diaptomus minutus	562 ± 99	929 ± 160	ns
Diaptomus ashlandi	1437 ± 210	755 ± 61	ns
Diacyclops thomasi	2758 ± 661	1684 ± 505	ns
Total biomass	77 ± 6	48 ± 14	<0.05
Fall			
Diaptomus minutus	198 ± 44	188 ± 7	ns
Diaptomus ashlandi	302 ± 41	48 ± 25	<0.01
Diacyclops thomasi	1150 ± 243	294 ± 285	<0.05
Total biomass	52 ± 5	16 ± 7	<0.01

Table 5. Monthly mean (± SE) biomass of zooplankton and total number of replicates (N) at nearshore (10-20m) and mid-depth (20-50m) sites from 1975-1977 taken from Hawkins and Evans (1979) and 1998-2000. Statistically significant values shown in bold (ANOVA, $p < 0.05$).

Month	Nearshore Biomass ($mg \cdot m^{-3}$)			Mid-depth Biomass ($mg \cdot m^{-3}$)		
	1975-1977	1998-2000	p	1975-1977	1998-2000	p
Apr.	32 ± 6 (3)	18 ± 11 (3)	0.21	21 ± 2 (3)	17 ± 3 (3)	0.30
May	13 ± 3 (3)	74 ± 62 (2)	0.30	34 ± 14 (3)	35 ± 2 (2)	0.72
June	66 ± 18 (3)	12 ± 9 (2)	0.08	**88 ± 16 (3)**	**19 ± 9 (2)**	**0.04**
July	**84 ± 10 (3)**	**27 ± 6 (2)**	**0.01**	**122 ± 10 (3)**	**51 ± 11 (2)**	**0.02**
Aug.	61 ± 20 (3)	21 (1)	0.33	**81 ± 5 (3)**	**29 (1)**	**0.01**
Sept.	**84 ± 26 (3)**	**16 ± 2 (2)**	**0.03**	**66 ± 7 (3)**	**25 ± 3 (2)**	**0.01**
Oct.	**76 ± 13 (3)**	**16 ± 2 (2)**	**0.01**	**76 ± 5 (3)**	**16 ± 7 (2)**	**0.02**
Nov.	76 (1)	10 (1)	-	87 (1)	7 (1)	-
Dec.	72 ± 2 (2)	82 (1)	0.17	50 ± 10 (2)	47 (1)	0.93

Table 6. Monthly mean (± SE) biomass of copepods and total number of replicates (N) at nearshore (10-20m) and mid-depth (20-50m) sites from 1975-1977 taken from Hawkins and Evans (1979) and 1998-2000. Statistically significant values shown in bold (ANOVA, $p < 0.05$).

	Nearshore Biomass ($mg \cdot m^{-3}$)			Mid-depth Biomass ($mg \cdot m^{-3}$)		
Month	1975-1977	1998-2000	p	1975-1977	1998-2000	p
Apr.	32 ± 6 (3)	18 ± 11 (3)	0.21	21 ± 2 (3)	17 ± 3 (3)	0.30
May	13 ± 3 (3)	74 ± 62 (2)	0.30	33 ± 13 (3)	35 ± 2 (2)	0.70
June	47 ± 8 (3)	11 ± 8 (2)	0.10	**67 ± 7 (3)**	**18 ± 9 (2)**	**0.04**
July	**54 ± 6 (3)**	**12 ± 7 (2)**	**0.04**	**90 ± 6 (3)**	**27 ± 7 (2)**	**0.01**
Aug.	41 ± 12 (3)	12 (1)	0.24	**62 ± 2 (3)**	**20 (1)**	**0.00**
Sept.	**56 ± 17 (3)**	**10 ± 5 (2)**	**0.05**	**50 ± 6 (3)**	**17 ± 2 (2)**	**0.01**
Oct.	**52 ± 4 (3)**	**14 ± 2 (2)**	**0.00**	**58 ± 1 (3)**	**16 ± 7 (2)**	**0.03**
Nov.	68 (1)	10 (1)	-	75 (1)	7 (1)	-
Dec.	65 ± 3 (2)	77 (1)	0.28	50 ± 10 (2)	45 (1)	0.86

Table 7. Monthly mean (± SE) biomass of cladocerans and total number of replicates (N) at nearshore (10-20m) and mid-depth (20-50m) sites from 1975-1977 taken from Hawkins and Evans (1979) and 1998-2000. Statistically significant values shown in bold (ANOVA, $p < 0.05$).

Month	Nearshore Biomass ($mg \cdot m^{-3}$)		p	Mid-depth Biomass ($mg \cdot m^{-3}$)		p
	1975-1977	1998-2000		1975-1977	1998-2000	
Apr.	0 (3)	0 (3)	-	0 (3)	0 (3)	-
May	0 (3)	1 ± 1 (2)	-	1 ± 1 (3)	0 (2)	0.22
June	20 ± 11 (3)	1 ± 1 (2)	0.27	21 ± 11 (3)	1 ± 1 (2)	0.15
July	**30 ± 5 (3)**	**15 ± 1 (2)**	**0.04**	32 ± 7 (3)	25 ± 3 (2)	0.60
Aug.	20 ± 8 (3)	9 (1)	0.54	19 ± 3 (3)	9 (1)	0.17
Sept.	28 ± 9 (3)	6 ± 3 (2)	0.09	16 ± 3 (3)	8 ± 5 (2)	0.23
Oct.	**24 ± 9 (3)**	**2 ± 1 (2)**	**0.01**	**18 ± 5 (3)**	**1 ± 1 (2)**	**0.02**
Nov.	8 (1)	0 (1)	-	12 (1)	0 (1)	-
Dec.	7 ± 2 (2)	5 (1)	0.59	0 (2)	2 (1)	-

Table 8. Mean density of major zooplankton taxa at nearshore (10-20m) and mid-depth (30-50m) sites for April 1973-1977 (Evans et al. 1980) and April 1999-2000. Standard error shown for 1999-2000 data.

Taxa	Nearshore (no·m^{-3})		Mid-depth (no·m^{-3})	
	1973-1977	1999-2000	1973-1977	1999-2000
Nauplii	6711	4370 ± 2229	2237	1218 ± 155
Cyclopoids C1-C5	427	794 ± 278	438	861 ± 162
Diacyclops C6	698	475 ± 126	1051	1765 ± 271
Diaptomus spp. C1-C5	785	840 ± 613	432	351 ± 152
Diaptomus spp. C6	1897	2026 ± 1376	1614	1051 ± 418
Bosmina sp.	31	21 ± 2	4	14 ± 12
Total Zooplankton	10708	8620 ± 4422	5912	5356 ± 390

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Table 9. Mean density of major zooplankton taxa at nearshore (10-20m) and mid-depth (30-50m) sites for July 1973-1977 (Evans et al. 1980) and July 1999-2000. Standard error shown for 1999-2000 data.

Taxa	Nearshore (no·m^{-3})		Mid-depth (no·m^{-3})	
	1973-1977	1999-2000	1973-1977	1999-2000
Nauplii	6402	632 ± 69	3210	802 ± 285
Cyclopoids C1-C5	6381	2565 ± 2505	9019	6127 ± 3240
Diacyclops C6	1170	931 ± 902	3174	1807 ± 383
Tropocyclops sp. C1-C6	494	721 ± 525	129	62 ± 2
Diaptomus spp. C1-C5	5950	1209 ± 373	10012	3375 ± 27
Diaptomus spp. C6	1952	485 ± 212	2410	1475 ± 408
Bosmina sp.	24301	8959 ± 1524	11790	7450 ± 2544
Daphnia spp.	1259	0 ± 0	2053	1270 ± 1226
Total Zooplankton	50495	16075 ± 5903	42718	22528 ± 3035

Table 10. Mean density of major zooplankton taxa at nearshore (10-20m) and mid-depth (30-50m) sites for October 1973-1977 (Evans et al. 1980) and October 1998-1999. Standard error shown for 1998-1999 data.

Taxa	Nearshore (no·m^{-3})		Mid-depth (no·m^{-3})	
	1973-1977	1998-1999	1973-1977	1998-1999
Nauplii	1380	542 ± 130	1095	542 ± 315
Cyclopoids C1-C5	7908	2798 ± 1351	9366	3907 ± 3064
Diacyclops C6	683	121 ± 24	871	294 ± 286
Tropocyclops sp. C1-C6	1432	630 ± 34	593	286 ± 101
Diaptomus spp. C1-C5	6530	3721 ± 2135	10903	3268 ± 299
Diaptomus spp. C6	415	288 ± 135	748	316 ± 35
Bosmina sp.	3442	1320 ± 109	300	344 ± 295
Daphnia spp.	2568	0 ± 0	2026	45 ± 23
Total Zooplankton	31483	10146 ± 753	27136	9430 ± 3670
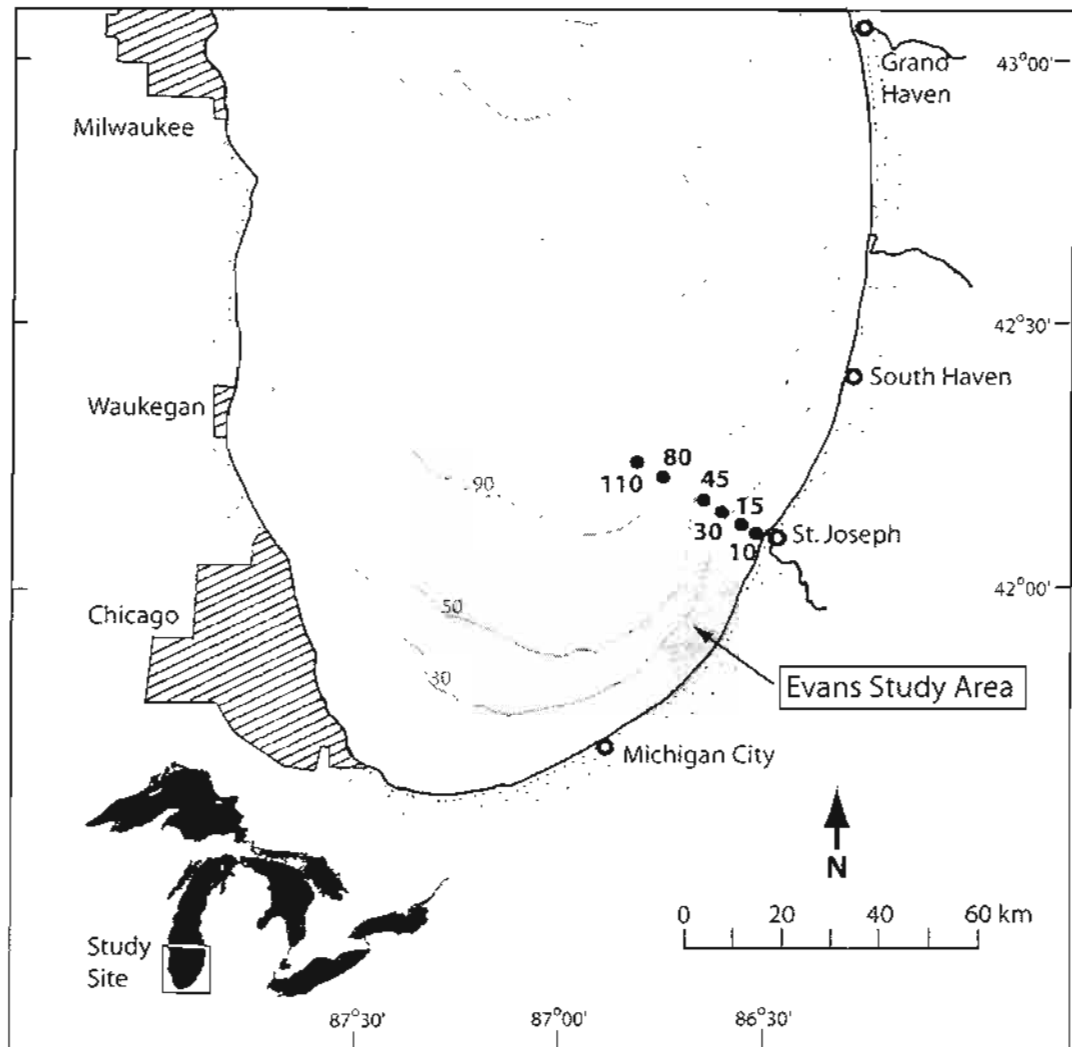
Figure 1. Location of sampling sites and depth contours in Lake Michigan. Evans study area for zooplankton collections in the 1970s represented by shaded box south of St. Joseph transect.
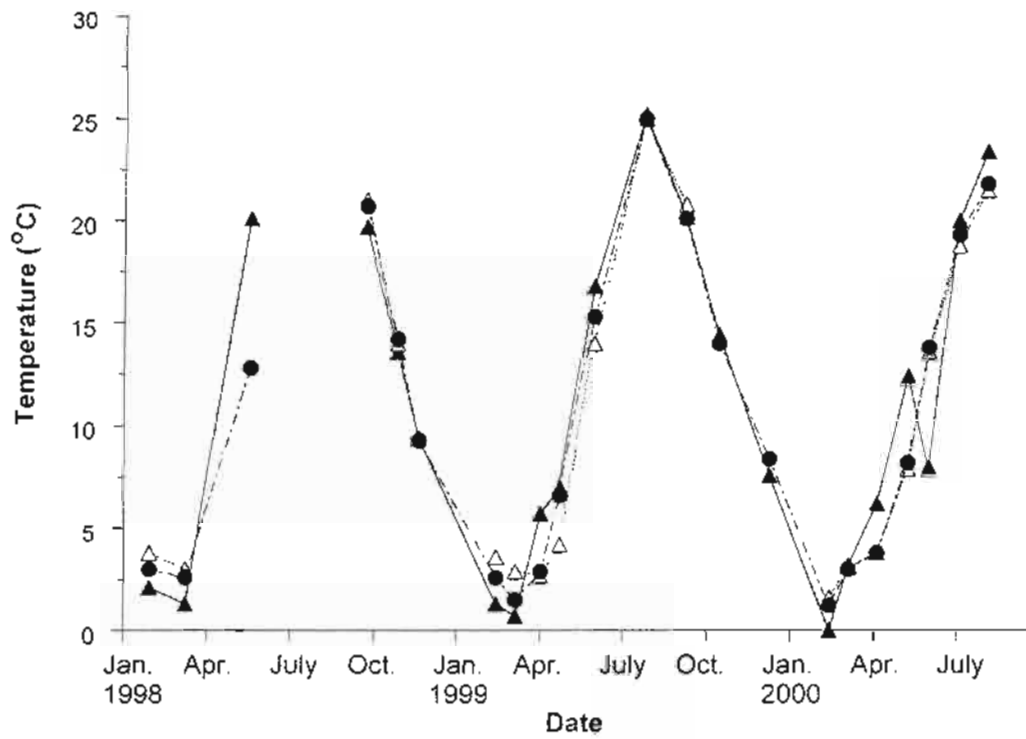
Figure 2. Water temperature at 5-m depth for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
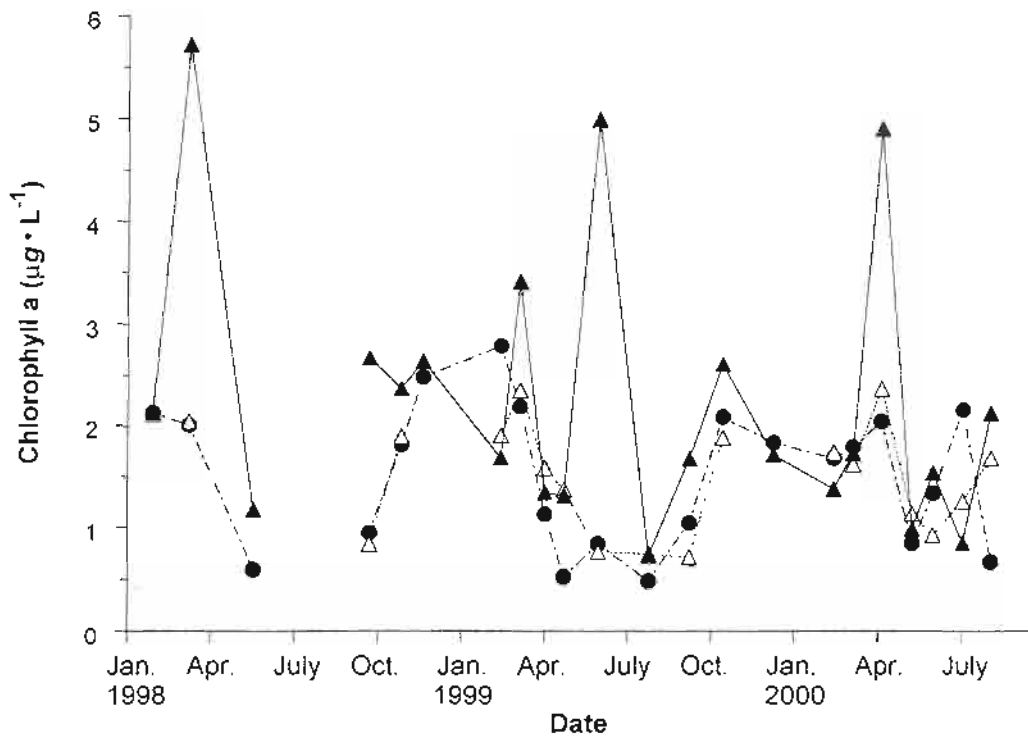
Figure 3. Mean chlorophyll *a* concentration at 5-m depth for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
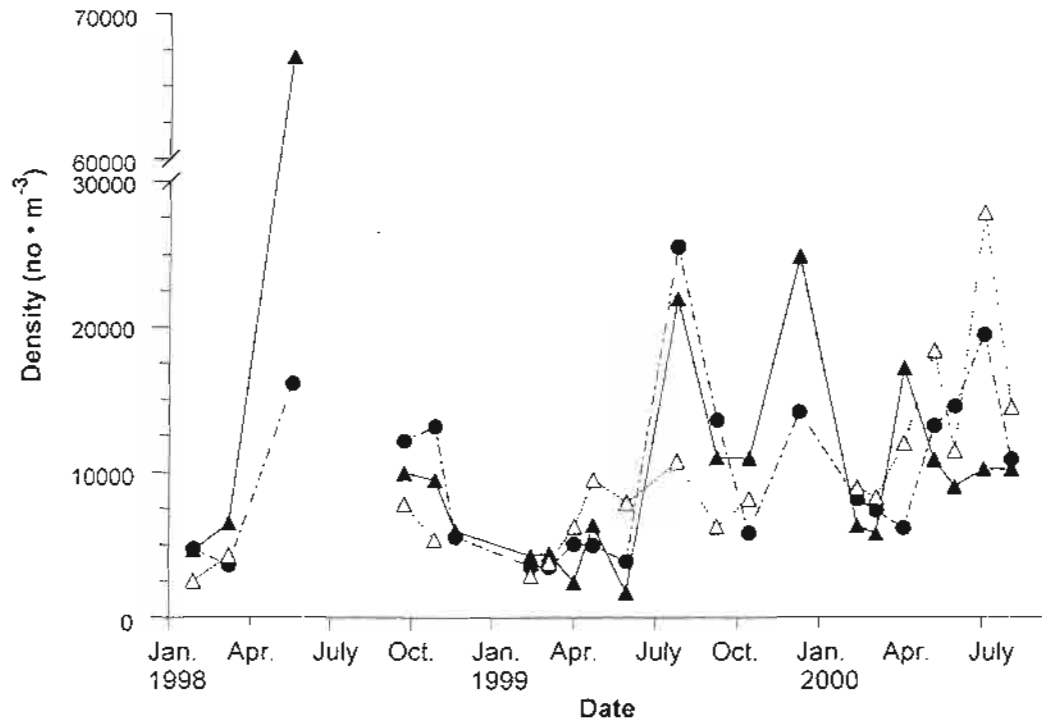
Figure 4. Mean density of total zooplankton for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
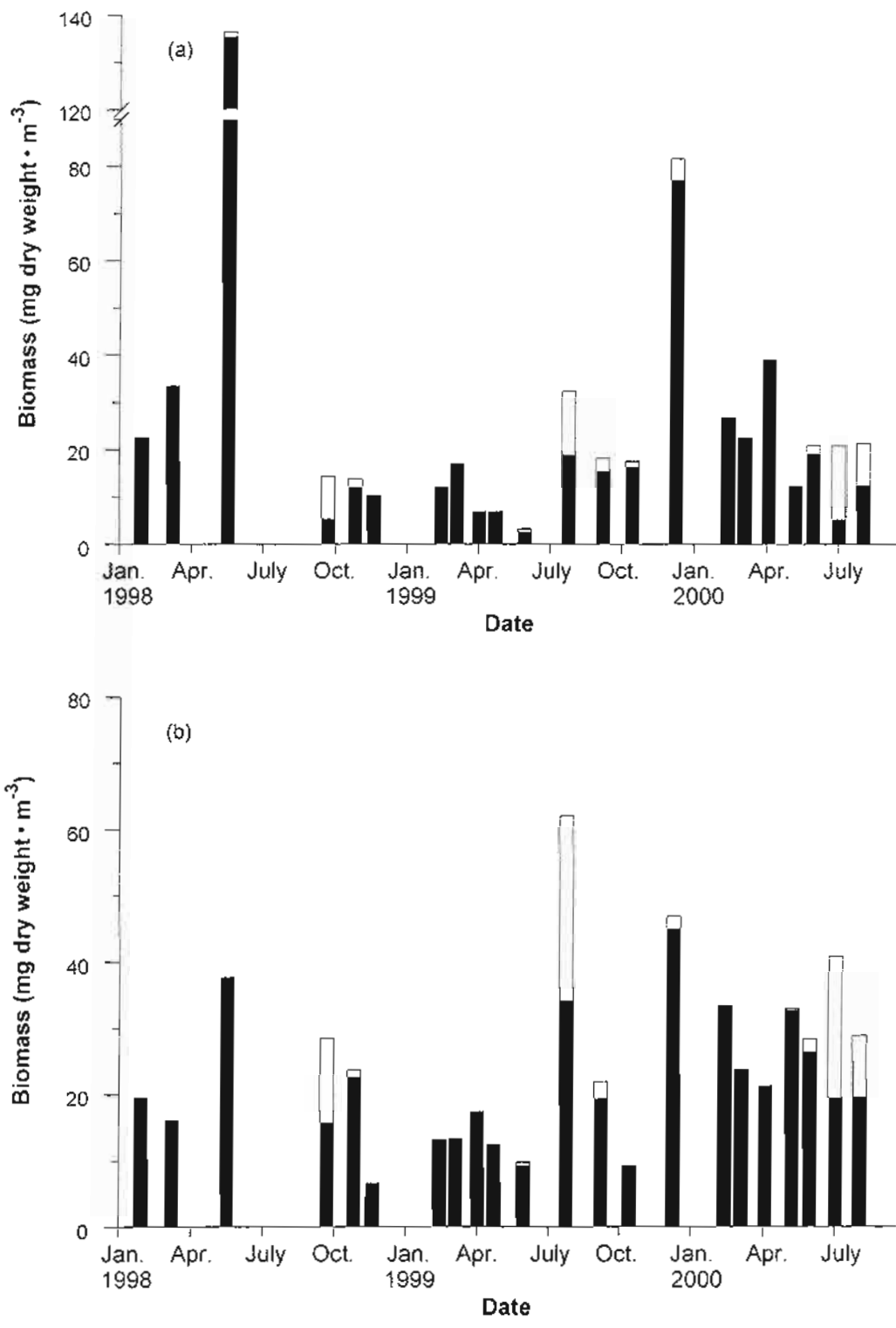
Figure 5. Mean biomass of total zooplankton for (a) shallow, (b) mid-depth and (c) deep sites in southeastern Lake Michigan. copepods (■), cladocerans (□).
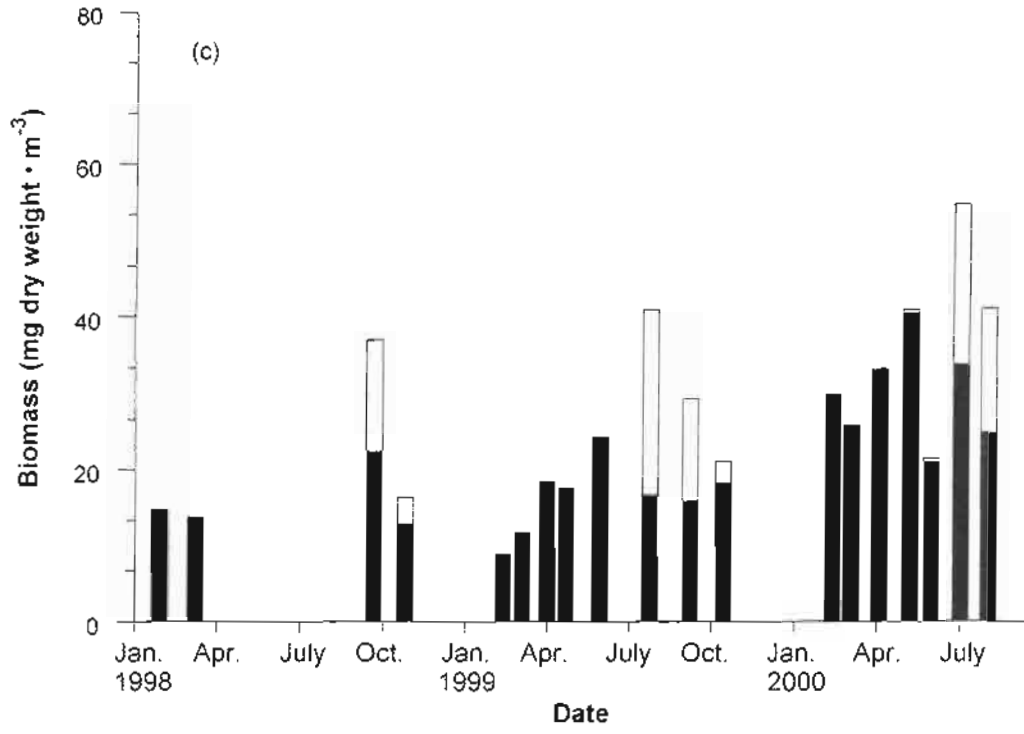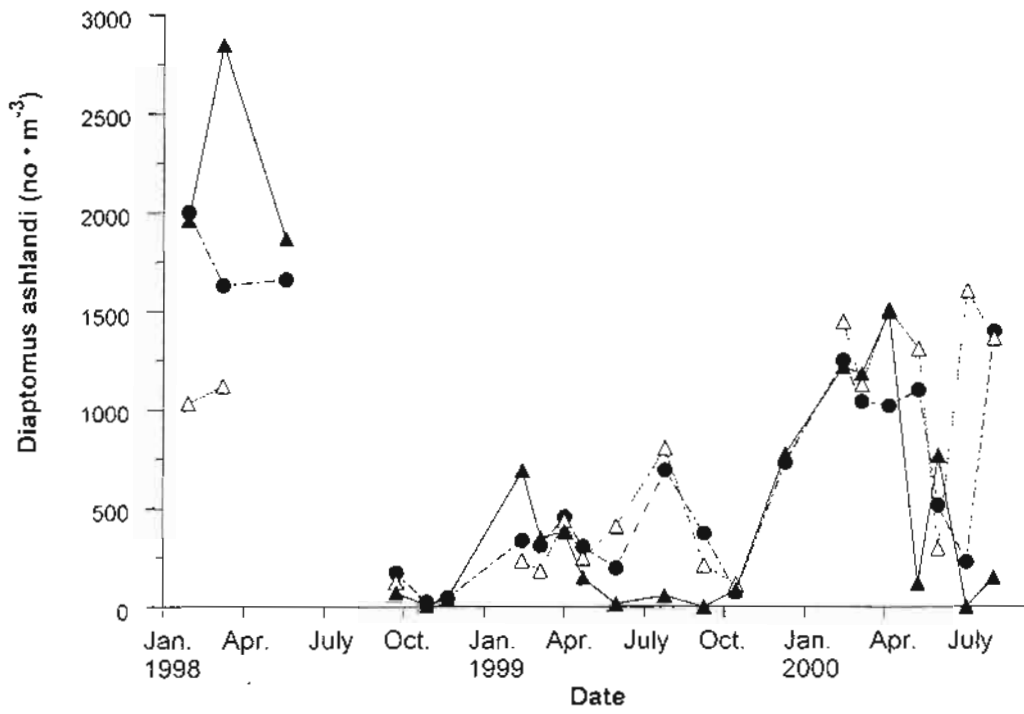
Figure 5. Continued

Figure 6. Mean density (no·m^{-3}) of adult *Diaptomus ashlandi* for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
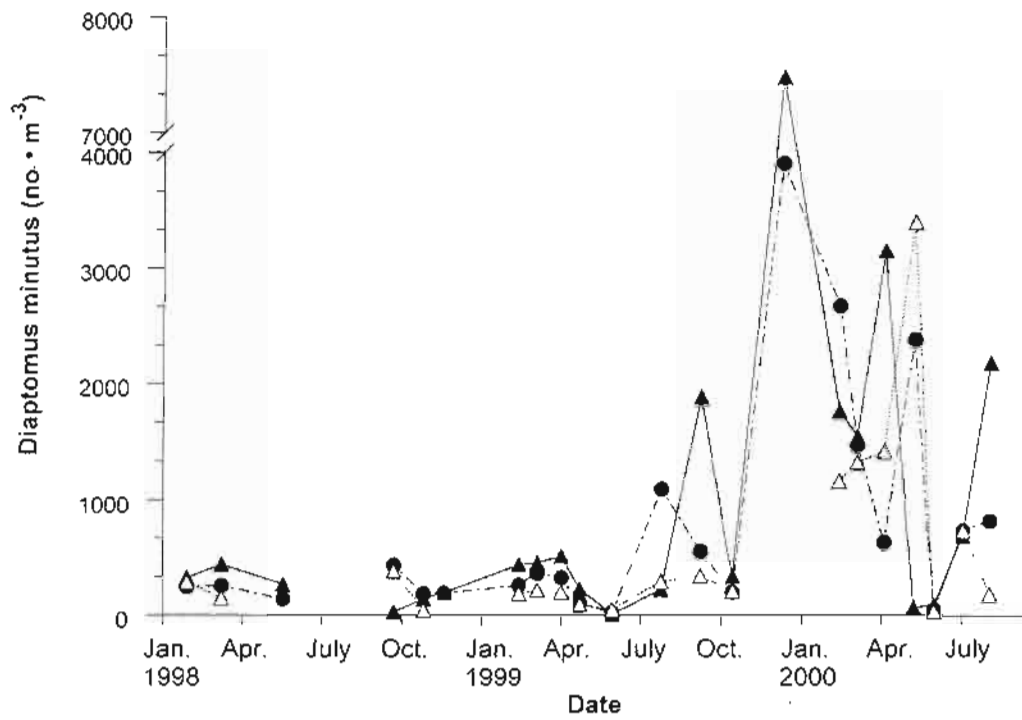
Figure 7. Mean density of adult *Diaptomus minutus* for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
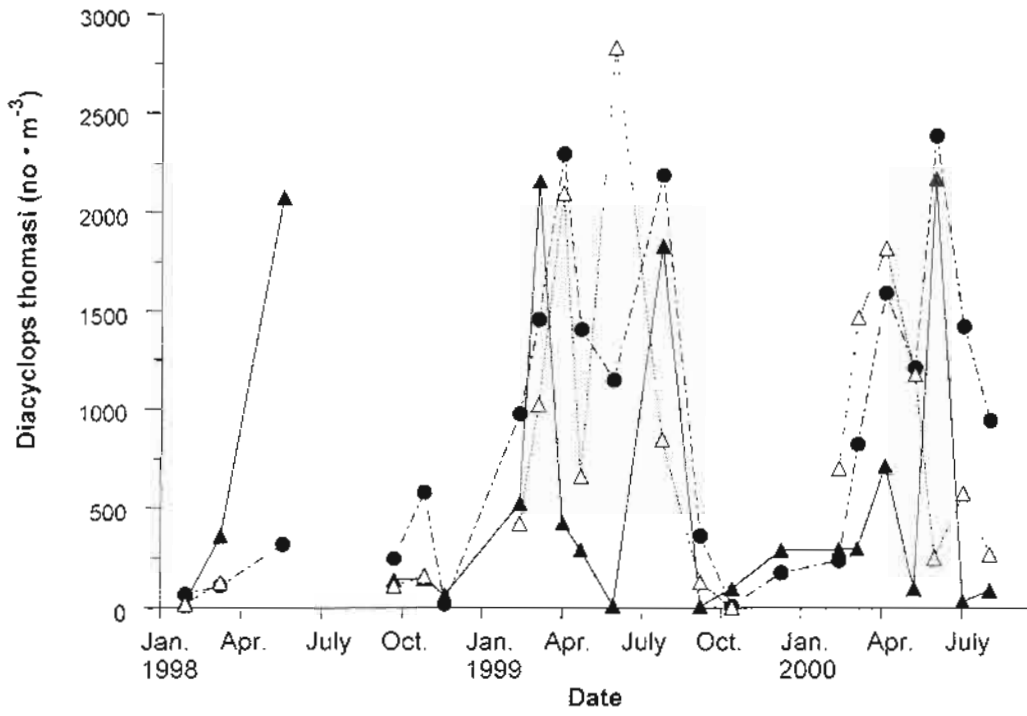
Figure 8. Mean density of adult *Diacyclops thomasi* for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
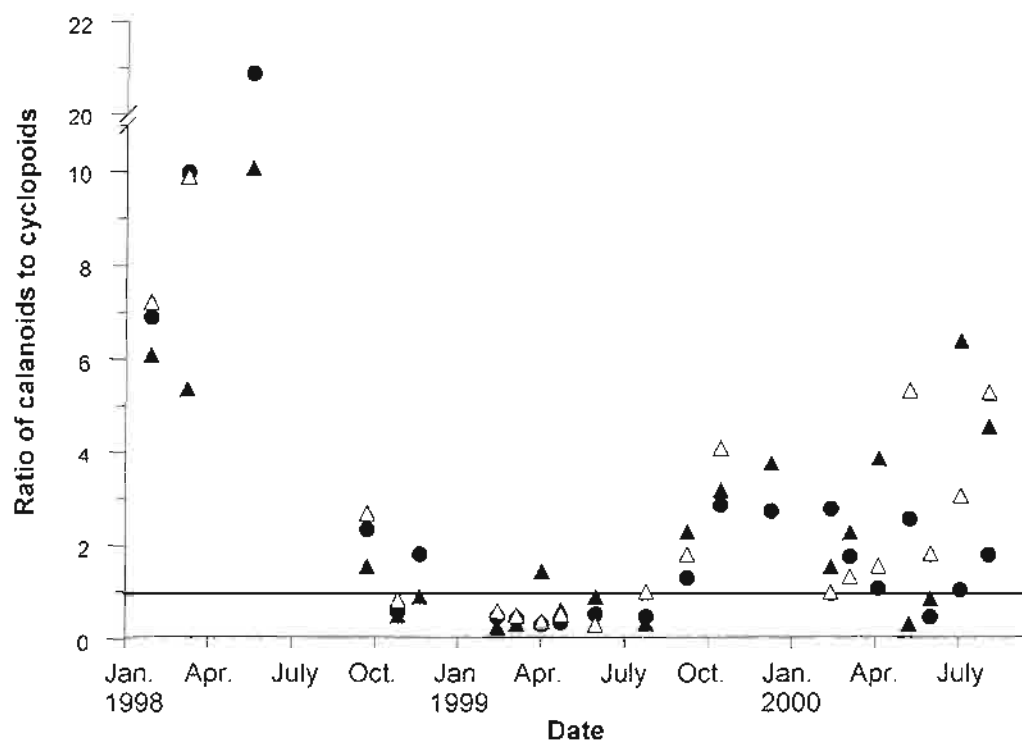
Figure 9. Ratio of calanoid abundance to cyclopoid abundance for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
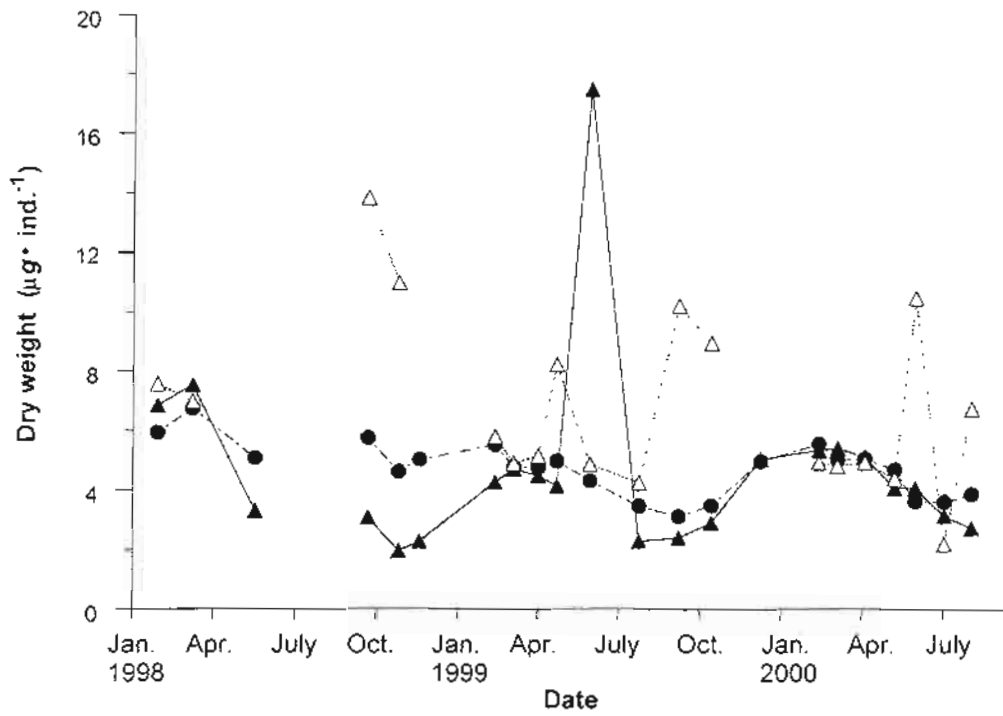
Figure 10. Mean dry weight of individual adult copepods for shallow (▲), mid-depth
(●) and deep (△) sites in southeastern Lake Michigan.

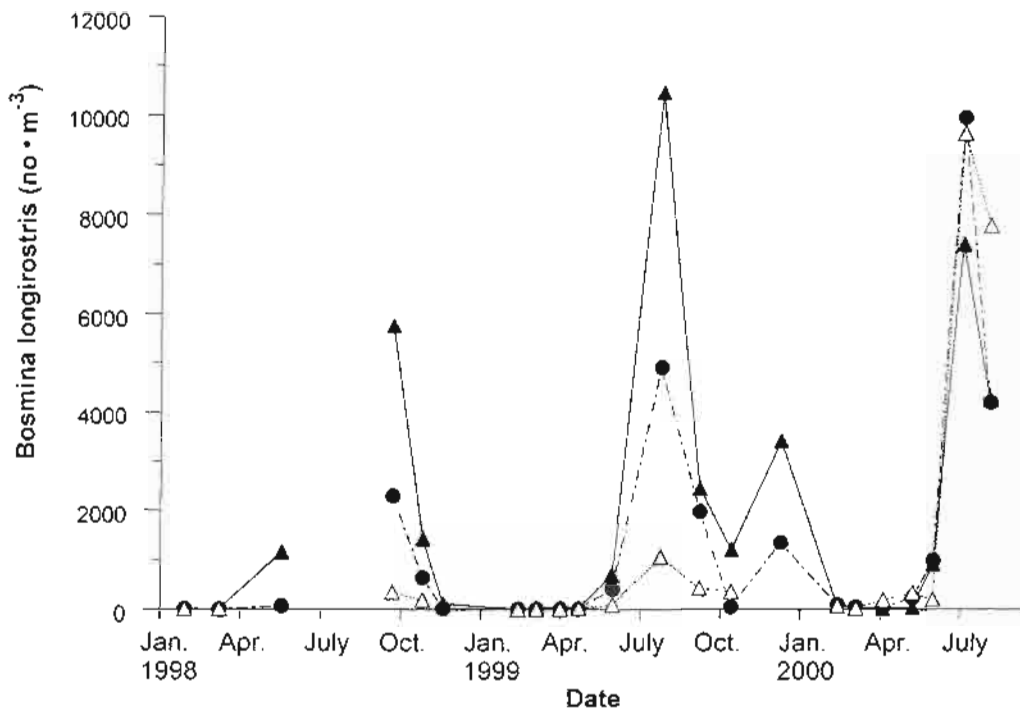Figure 11. Mean density of *Bosmina longirostris* for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.
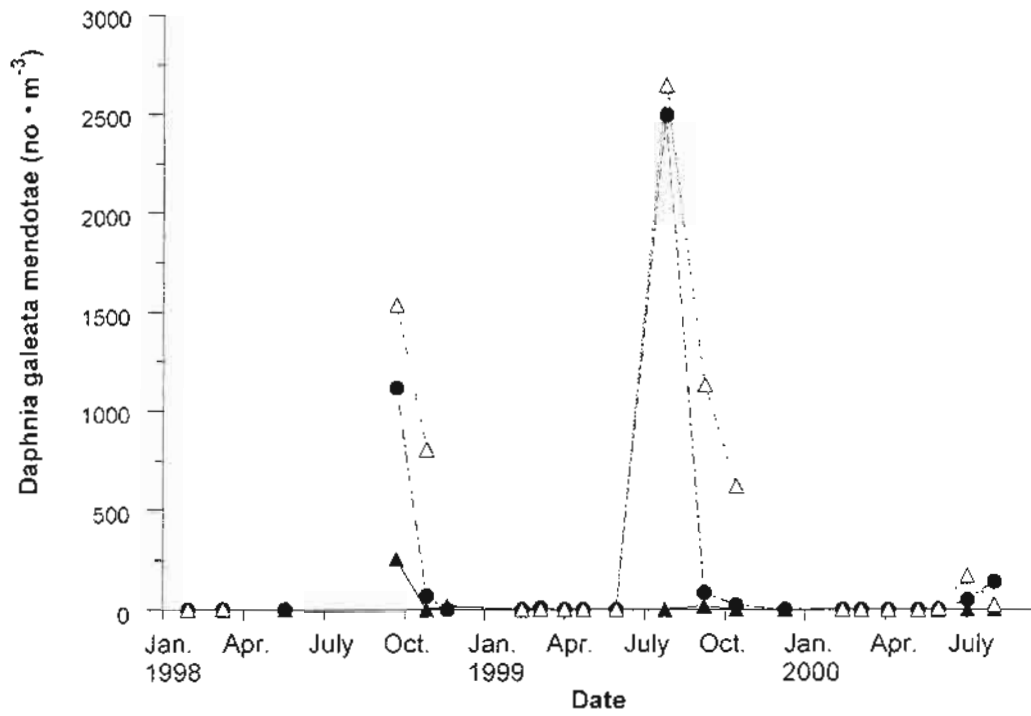
Figure 12. Mean density of *Daphnia galeata mendotae* for shallow (▲), mid-depth
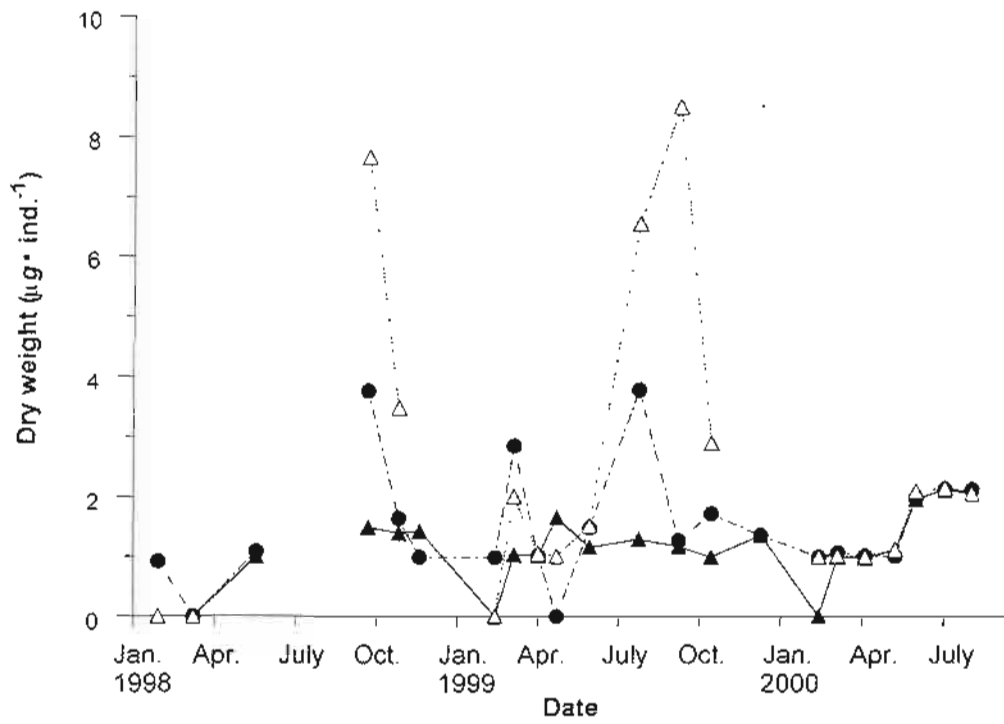(●) and deep (△) sites in southeastern Lake Michigan.

Figure 13. Mean dry weight of individual cladocerans for shallow (▲), mid-depth (●) and deep (△) sites in southeastern Lake Michigan.

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