LAKE MICHIGAN - Zooplankton

Mean Annual Abundance and Biomass of Zooplankton Groups

From 1983 to 1992, 7 1 species representing 38 genera from the Calanoida, Cladocera, Cyclopoida, Mysidacea, Rotifera, Mollusca and Harpacticoida comprised the offshore zooplankton community of Lake Michigan (Table 13). Twenty-one common species plus their juvenile stages accounted for 94.9% of the total biomass and 95.5% of the total abundance (Table 14). Yearly data on common spccics arc presented in Tables A13-A22 in the appendix. The Rotifera contained the largest number of spccics (34, Table 13) and accounted for the highest relative abundance (68.8%, Table 14). The Calanoida, Cyclopoida and the nauplius stage of the copepod represented 25.2% of the total zooplankton abundance (Table 14). The Calanoida (34.4%) followed by the Cladocera (27.7%) and the Cyclopoida (15.1%) contributed the most biomass to the zooplankton community, while the Rotifera represented only 5.6% of the zooplankton biomass over the ten-year period. Thcrc was a considerable difference in relative biomass between the 1983-87 and the 198X-92 periods. For example, Cladocera, Calanoida and Cyclopoida contributed 2 1. 1%, 40.8% and 2 1.1% of the biomass, respectively, from 1983 to 1988, while in the 1988 to 1992 period, their contributions were 35.8%, 28.6% and 8.7% (Table 15 and 16). Average density and biomass for 1983 - 1992 (spring and summer) was 91.3 organisms/L ± 6.7 (mean ± S.E.) and 48.0 µg/L ± 4.3 (mean ± S.E.) (Table 17). Biomass was considerably higher in the summer (X1.8 ± 8.5 µg/L) than in the spring (20.1±1.6 µg/L) (Table 18 and 19). In comparison to lakes worldwide, a mean biomass of 48 µg/L ranks in the range of biomass for oligotrophic and mesotrophic lakes (Schindler and Novcn 197 1)

Historical Trends in Abundance

Crustacean studies of the offshore waters of the Lake Michigan basin are few in number. Offshore crustacean zooplankton biomass data are available from 1976 (Bartone and Schelskc 1982) for northern Lake Michigan. No information is presented on sampling intensity or technique. A comparison with the average lakcwide 1984 and 1985 biomass data (Table 20) revealed that no significant difference in crustacean biomass existed between 1976 and 1984 and 1985. Another longer sequence of data from July and August collections are described by Scavia et al. (1986). Except for 1977, 1983 and 1984, zooplankton samples were primarily from an offshore station (40-m depth) west of Benton Harbor, MI. A comparison of the 1984 mean offshore lake-wide biomass data to Scavia's data from one station indicated good agreement (Fig. 1 8), thereby adding some confidence to comparisons bctwccn the data sets.

Within the 1983-92 data set, the 1986 and 1992 mean summer biomass were significantly higher ($P<0.05$, Tukey Test) than the 19X7-89 biomass. The high 1986 and 1992 zooplankton biomass do not appear to be significantly different from Scavia's et al.(1986) 1981 and possibly 1978 data (Fig. 18). From 1974 through 1989, there were no obvious trends in zooplankton biomass, except that a peak in biomass occurred every three to five years. After 1989, zooplankton biomass progressively increased to a peak in 1992 (Fig. 18).

Some time-trend patterns in biomass do emerge from the combined spring and summer data. The relative importance of' the Cladocera varied over the study period (Fig. 19). Relative biomass of Cladocera (spring and summer) was 45.3% in 1984, dccrcascd to approximately 20% from 1985-91 with a low of 8.5% in 1987, and increased dramatically to over 50 % of the total zooplankton biomass in 1991 and 1992. Summer Cladocera biomass varied even more decreasing from 41.7 μg/L in 1984 to a low of' 6.4 μg/L in 1987, and then peaking at 92.9 μg/L in 1991 (Table 18). An inverse correlation ($r= -0.83$) between Calanoida and Cladocera relative biomass was observed (Fig. 19). Relative biomass (spring and summer) of Cyclopoida decreased from 33% in 1986 to 5.5% in 1992 (Table 17). Rotifer relative biomass was low (<2%) through 1986 then it peaked at 15% in 1987, decreased steadily through 1990 and then increased again to a 1992 peak of about 20% of the total biomass (Fig. 19). Much of this later increase was due to *Asplanchna priodonta* in 199 1 and to *Kellicottia longispina* and *Polyarthra vulgaris* in 1992 (Table A21 and A22, Appendix).

Geographical Distribution of Zooplankton Groups

The geographical pattern of' total zooplankton biomass in Lake Michigan varied little over the study period (Fig. 20), with the exception of summer of 1992. Biomass was slightly higher in the summer at the deeper, open water stations. A peak at Station 11 in the southern basin in the summer of 1992 was due to a bloom of *Daphnia galeata mendotac* (25 organisms/L).

Geographical patterns of selected zooplankton groups in Lake Michigan are presented in Figures 21 and 22. Stations 77, 64, 57 and 6, all nearer shore or in shallower waters, were sampled only in 1984. Within the offshore and deep water areas (Stations 47, 41, 34, 27, 23, 18, 1 1), there were no significant differences between stations in Calanoida, Cyclopoida, Cladocera or Copepoda nauplii biomass. Calanoida biomass was generally lower, but not significantly, at the sites nearer shore or shallow water areas (Stations 77, 64, 6) with the exception of Station 57. The lack of significance is related to the low number of samples taken at these sites - one in 1984. Cyclopoida, Calanoida and the Copepoda nauplius biomass were significantly lower at Station 6 compared to the deep water Stations (Fig. 21 and 22). Cladocera biomass north of Station 34 was less variable than south of' Station 34 (Fig. 21). The greatest average Cladocera biomass was observed at the southern stations 37, 23 and 11, although the greatest annual variability was at these stations also. Rotifera biomass increased from south to north reaching a peak at Station 41 and decreased northward (Fig. 22).

Historical Changes in Species Composition

Ro tifera

Rotifer studies reported in the literature are primarily from the nearshore region of the lake. The abundance of rotifers in Lake Michigan has generally decreased from the nearshore into the offshore (Gannon et al. 1982, Stemberger and Evans 1984) although the species composition of nearshore and offshore populations has been similar.

Common rotifer species in the open waters of Lake Michigan during 1983- 1992 included Keratella cochlearis and Polyarthra vulgaris, two species that were also reported as dominant or common in the offshore waters in 1930s (Ahlstrom 1936), and in the nearshore waters in 1926-27 (Eddy 1927), 1962 (Williams 1966), 1970 (Johnson 1972) and 1977 (Gannon 1982). Kellicottia longispina was common in 1927, 1977 and 1983-1992. Since 1977, but not before, Kellicottia crassa and Conochilus unicornig (a colonial rotifer) also have been common.

Although the species of rotifers present in Lake Michigan has been consistent historically, their relative abundance has not. The three most abundant rotifer species during the period 1983- 1987, P. vulparis, K. cochlearis, and Synchaeta sp. (Table 15), were also among the four most abundant species during the period 1988- 1992 (Table 16). However, during the latter five years, the abundance of these species was over 2.6 times that of the former period, and the most abundant species during 1988-1992, C. unicornis, was 15.2 times more abundant than during the previous five years (Fig. 23). Ploesoma truncatum also became quite common during 1988- 1992, following a sporadic presence during 1983- 1987 (Fig. 23).

Crustacea

Although no intensive zooplankton studies of the offshore waters of the entire lake basin have taken place, some offshore studies of Lake Michigan zooplankton do exist. Wells (1960, 1970) sampled Crustacea with a number 2 (366μm) net on four dates in June, July and August in 1954, 1966 and 1968 from the offshore region off Grand Haven, Michigan. On six dates (March 1969 to January 1970), Gannon (1975) collected crustaceans with a 64-μm mesh net from the offshore and inshore of Lake Michigan along a cross-lake transect from Milwaukee to Ludington. In September of 1973, northern Lake Michigan was sampled with a 250-μm mesh net (Schelske et al. 1976). Also, Stemberger and Evans (1984) provided abundance data (76-μm net) for a few zooplankters from offshore waters of the southeastern Lake Michigan area in 1979.

The data of Wells (1960, 1970) and Schelske et al. (1976) are useful **but** have to be used with caution. A 366-μm and a 250-μm net are probably quantitative for larger crustaceans but certainly would not be for smaller crustaceans such as Chydorus sphaericus, Bosmina longirostris, Eubosmina coregoni, Ceriodaphnia spp., Tropocyclops prasinus and copepods (Makarewicz and Likens 1979).

The zooplankton populations in Lake Michigan underwent striking size-related changes between 1954 and 1966 (Wells 1970). Species that declined sharply were the largest cladocerans (Leptodora kindtii, Daphnia galeata mendotae and D. retrocurva), the largest calanoid copepods (Limnocalanus macrurus, Epischura lacustris and Diaptomus sicilis) and the largest cyclopoid copepod (Mesocyclops edax). Medium-sized or small species (D. longiremis, H. gibberum, Polyphemus pediculus, Bosmina longirostris, Ceriodaphnia, sp., Cyclops bicuspidatus, Cyclops vernalis, Diaptomus ashlandi) increased in number, probably in response to selective alewife predation on the larger organisms. After the alewife dieback, M. edax and D. galeata mendotae were still rare in 1968 when the composition of the zooplankton community shifted back toward one similar to 1954 (Wells 1970).

In northern Lake Michigan during September of 1973, predominant species were Daphnia galeata mendotae, D. retrocurva, Limnocalanus macrurus, Diaptomus oregonensis, Eubosmina coregoni and Diaptomus sicilis. Cyclopoid copepods were a minor component of the fauna captured by a 250 μm net in 1973 (Schelske et al. 1976).

Cladocera

The changing nature of the zooplankton community of Lake Michigan (e.g., Scavia et al. 1986, Lehman 199 1, Evans 1992) was evident by differences between our data for 1983 and that of earlier surveys (Table 2 1) . D. galeata mendotae and D. retrocurva were the prominent daphnids in the 1954 study of Wells (1960). During the 1960's, D. galeata mendotae were rare, but D. retrocurva remained common with variable abundance. By 1983, D. galeata mendotae were again common, and they have remained so through 1992. D. retrocurva abundances were variable during 1983-1986, but then they became very rare in 1987 and subsequent years. In 1991 and 1992, D. galeata mendotae abundance greatly increased while D. retrocurva were absent. The variation in abundance of another large cladoceran, Leptodora kindtii, was similar to that of D. retrocurva: about equally abundant in 1954 and 1983-1986, reduced abundance in the 1960s, and absent since 1989.

Most interesting is the appearance of' the large daphnid D. pulicaria in the offshore region in the 1980's (Table 21). Evans (1985) reported that this species was first observed in Lake Michigan in 1978. Abundance remained low in southeastern Lake Michigan until 1982. In 1983, they dominated the summer Daphnia community both at the offshore stations of this study and at a station southwest of Grand Haven, Michigan. During 1984-1986, D. pulicaria were much less abundant than D. galeata mendotae, and by 1987, they had disappeared from the lake except for a few that were observed in 1990 (Table 21).

Another large cladoceran species was first identified in Lake Michigan in 1986, Bythotrephes cederstroemi. This organism preys on other zooplankton species, and it has been consistently present in summer zooplankton collections from 1987 through 1992.

Smaller daphnids have also exhibited highly variable abundances year to year. The large increases in numbers of Bosmina longirostris and Eubosmina coregoni in 1983, compared to 1968, are probably due to smaller meshed nets being used for the 1983-1992 collections. From 1983-1992, B. longirostris was usually much more abundant than E. coregoni, with unusually large abundances in 1987 and 1990. Far fewer were collected in 199 1 and 1992. E. coregoni, however, were rare or absent in 1987- 1988 and again in 199 l- 1992.

In general, cladoceran diversity and equitability were greater during 1984 to 1986 than in later years (Table 22). More species were present with more similar biomass during the early 1980's, coincident with lowest predation pressure on zooplankton from the alewife (Fig. 24).

After 1986, B. cederstroemi became established, alewife populations were larger than during 1983-1985, and large herbivorous cladocerans such as H. pibberum. Leptodora kindtii, D. retrocurva and D. pulicaria became rare or absent. By 1991 and 1992, only three cladoccra species were observed: the predator B. cederstroemi, the large D. galeata mendotac and the diminutive B. longirostris.

Cladocera biomass was lowest in 1987 (2.2 µg/l) compared to the 10 year average (25.1 µg/l). In 1991 and 1992, however, 97.8 µg/l and 78.6 µg/l of cladoccran biomass, respectively, were observed due to the overwhelmingly dominant numbers of D. galcata mendotae.

Copepoda

Cyclons bicuspidatus was the dominant cyclopoid copcpod during the 1983-92 period (Table 14 and 23). It reached its highest abundance in the mid-80s, decreased between 1987-1989, and increased to levels comparable to 1966 during 1990 to 1992.

Fewer Mesocyclops cdax were found in August of 1983-87 than in 1954, another period of low alewife predation. However, abundance of this species had obviously increased since the 1960's, when they were not reported, and in the mid- 1980s they appeared to bc approaching levels similar to those observed in 1954. For cxamplc, abundance of M. edax in early October of 1983 reached a level comparable to 1954 (151 organisms/m’, mean station abundance). However after 1985, abundance of M. cdax decreased until 1990 when it was not observed (Table 23).

Tropocyclops prasinus mexicanus was not observed in the early works of Wells (1970). The large mesh net used in the earlier study undoubtedly missed this small cyclopoid.

Diaptomus ashlandi was the dominant calanoid copcpod during 1983-1992. Its abundance was consistent year-to-year for the entire period 1983- 1992 at levels 10 to 100 times than those reported for 1954, 1960 or 196X. In general, howcvcr, the abundance of calanoids in 1992 is generally greater than 1954 and 1966 and perhaps more comparable to 1968 (Table 23). Diaptomus minutus appeared to have decreased abundance relative to 1968 from 1983-1985, and again from 1988 to 1990. During 1991-1992 its abundance was similar to that in 1968. D. oregonensis abundance in the 1980s remained similar to 1954, 66 and 68 although there was a clear decline from 1985 to 1991, and a rcsurgcncc in 1992. August abundance of‘ D. sicilis and Enischura lacustris was generally higher in the 1980s than in the 1960s. Abundance of

Limnocalanus macrurus in the 1980s was variable, but more similar to the reduced numbers observed in 1966.

GENERAL DISCUSSION

1983-1986: Alewife Predation

The large cladocerans, calanoid copepods and cyclopoid copepods which were observed by Wells (1970) to have decreased sharply in Lake Michigan between 1954 and 1966 had increased in abundance again by 1983- 1985 to densities similar to or greater than those of August 1954. In addition, a new large cladoceran, Daphnia pulicaria, had become well established in the offshore waters by 1983. The resurgence of larger zooplankton in Lake Michigan in the early 1980's to abundances reminiscent of those in 1954 were correlated with the sharp decline in the abundance of the planktivorous alewife (Alosa pseudoharengus) in 1982 and 1983 (Jude and Tesar 1985; Scavia et al. 1986). Both 1954 and 1983-1985 were periods of relaxed alewife predation. The 1983 lakewide catch of adult alewifes was only 31% of that of 1982 and only 12% of the 198 1 catch (Figure 24). The relaxation of alewife predation pressure played an important role allowing the establishment of Bythotrephes cedcrstrocmi in the offshore waters of Lake Michigan in 1986. As Lake Ontario, Bythotrephes appeared during a period of relaxation of alewife predation but disappeared after alewife abundance increased the following year (Makarewicz 1990).

1986-1992: Bythotrephes Control or a Complex of Factors?

Wells (1970) observed that large-bodied D. galeata mendotae were lost during periods of strong alewife planktivory and that only the smaller D. retrocurva persisted when planktivorous fish increased in abundance. Daphnid species compositions in 1986 and 1987 were exactly opposite to this pattern: D. retrocurva became rare and D. galeata mendotae became abundant. Considering this, and considering that the remaining D. pulicaria increased in size and only small individuals were taken, Lehman (1991) and Lehman and Caceres (1993) argued that the daphnid composition was consistent with invertebrate, rather than vertebrate predation.

Also, some of the changes in species composition observed in this study could be due to indirect effects of Bythotrephes predation. For example, the loss of the predaceous Leptodora from Lake Michigan by Bythotrephes predation may have triggered further changes, including increased abundances of Bosmina and the colonial rotifer Conochilus, both of which are important prey items for Leptodora (Branstrator and Lehman) . Since 1986 and the introduction of Bythotrephes, abundance of Conochilus has increased dramatically (Fig. 23). However, abundance of Bosmina longirostris, which did increase considerably for one year in 1987 after the establishment of Bythotrephes, has decreased to abundances similar to those observed in 1950s and 1960s when abundances of Leptodora kindtii were high (Table 21) which suggests control by another species. With the absence and lack of predation from Leptodora in the late 1980s and early 1990s, the decrease in B. longirostris and Eubosmina coregoni could be due to predation by other plankton feeders in the late 1980s and/or by interf'crence competition (Vanni 1986) resulting from the domination of the plankton community by Daphnia galeata mendotae in Lake Michigan in the early 1990s.

Our lake-wide data not only support the contention that major changes in the Daphnia community occurred after the invasion of B. cederstroemi in 1986 but also that changes occurred in the abundance of several other species of Cladocera and one Cyclopoida. Subsequent to the establishment of B. cederstroemi in 1986, the relatively large, perhaps less mobile, herbivorous Cladocera (D. pulicaria, D. retrocurva, Leptodors kindtii, Holopedium gibberum) and the large cyclopoid M. edax decreased, abundance of the small Cladocera Bosmina longirostris was variable but increased (until 199 1) compared to abundance in 1986 and the mean length of the Cladocera community dropped sharply from about 1.5mm to less than 0.5mm in one year from 1986 to 1987 (Fig. 25) suggesting the resurgence of a size-selective predator. Sprules et al (1990) argued that since abundance of Bosmina increased and that of Daphnia decreased while Bythotrephes cederstroemi abundance increased, predation by planktivorous fish was likely rather than by an invertebrate such as Bythotrephes. Not all large zooplankton species were reduced in number after 1987, however. The large calanoid Epischura lacustris had generally increased in abundance, and the abundances of the relatively large Diantomus minutus (mean length = 0.90 mm), D. sicilis and D. ashlandi (mean length= 0.92 mm) were greater than those reported for 1954. The persistent occurrence of larger copepods in the presence of planktivorous fish does not necessarily invalidate a hypothesis of planktivorous fish predation af'f'ccting zooplankton species composition. It depends on the type of fish planktivory (i.e. obligate). For example, Rudstam et al (1993) found little effect of planktivory by cisco and perch on calanoid copepods in Lake Mendota, Wisconsin, even though Daphnia were removed.

A major change in the species composition of Lake Michigan zooplankton was evident by 1990. By 1990 populations of other predaceous zooplankton such as the cladoccran Leptodora and the cyclopoid Mesocyclops edax were not observed in our lake-wide plankton samples. Abundances of smaller herbivorous Cladocera (Bosmina longirostris and Eubosmina coregoni) were variable through the 1980's, but they, too, sharply declined during 1991-1992. While there were 10 species of cladocerans in 1985, there were only three left by 1991, and in 1992 a single species (D. galeata mendotae) accounted for over 95% of the Cladocera abundance. Most of the herbivorous copepod species that were present during 19X3-1985 remained abundant during 1991-1992. Is it possible that Bvthotrenhes is the sole cause of all the compositional changes in the pelagic zooplankton community of Lake Michigan observed, especially after 1990 when major changes in zooplankton composition occur while Bvthotrenhes abundance is considerably lower than in 1989? We can not answer that question directly. However, has the abundance of other planktivorous organisms in the pelagic region of Lake Michigan increased?

Both alewife and the bloater chub (Coregonus hoyi) populations increased in 1987 over abundance levels of the previous year (Fig. 26). Adult alewife (over 1 year old) abundance in 1987 was 83% of the alewife population in 198 1, a relatively high abundance year. Furthermore, young of the year alewife were at the highest abundance in five years in 1987 (Table 23). Similarly, abundance of adult bloaters Coregonus hoyi (>1 year) were exceptionally high between 1987-1989 and 1992 (Fig. 20) but not young-of-the-year.

Not only do alewife feed on B. cederstroemi (Keilty 1990), but it is likely that the adult bloater will take B. cederstrocmi since they readily feed on Mysis and Leptodora (Wells and Beeton 1963). In Lake Michigan, bloaters less than 20mm in size fed selectively on cyclopoid copepods and above 35mm on Daphnia (Warren and Lehman 1988). switch to a benthic habitat and prey after one year among the pelagic zooplankton (Crowder and Crawford 1984). Dorazio et al. (1987) argued that changes in zooplankton composition and behavior observed in 1985 probably resulted from increased predation by visually oriented planktivorous fish such as the bloater. Without stomach and gut content analysis from alewife, bloater and Bvthotrenhes from each year, the best that can be argued is that these planktivores either consecutively, starting with Bvthotrenhes, or simultaneously depressed cladocerans populations starting in 1987 and had a continued grazing pressure on cladocerans and some cyclopoids. It is possible that one or more predators other than Bvthotrenhes cederstroemi have been affecting the composition and abundance of zooplankton in Lake Michigan.

More recent data are needed on stomach content of bloaters from Lake Michigan. Even though the adult bloater population increased by a factor of 33% from 1986 to 1987, bloater are dismissed as the cause of the change in composition of the Danhnia populations because bloater were reported as changing from a pelagic to a benthic mode of feeding due to competition for food from alewife (Crowder and Crawford 1984). However, before the alewife presence, bloaters had been reported as pelagic zooplanktivores until age 3+, when they then began to switch to a bottom habitat and to benthic prey. Species of zooplankton present in bloater stomachs prior to alewife introduction include Bosmina longirostris, Holonedium gibberum, Danhnia retrocurva, Danhnia galeata mendotae, Cyclops bicuspidatus, etc., (Wells and Beeton 1963)- all zooplankton species whose abundance is changing in Lake Michigan . It is possible that with a depressed alewife population, the f'ceding behavior of adult bloater in Lake Michigan has changed.

A major question is what allows Daphnia galeata mendotae to increase in abundance in the face of a highly successful predator that has successfully eliminated several species of Cladocera? We do not have an answer to this. However, a similar situation was recently described in Lake Mendota (Rudstam et al. 1993). Three species of Danhnia were present in Lake Mendota: Danhnia pulicaria, Daphnia galeata mendotae, and Danhnia retrocurva. In the face of planktivory by a coregonid, the larger Daphnia nulicaria abundance was reduced, while the smaller Danhnia, galeata mendotae abundance was marginally affected. The interyear changes in daphnid composition were explained by a combination of factors including differential planktivory, structure of the habitat and the physiological ecology of the dominant planktivore interacting with the competitive ability of the two species at different levels and temperature.

Food web model predictions based on functional or size-grouped components of Lake Michigan suggest that increased Bythotrephes abundance will cause lake Michigan's plankton to return to a community similar to that of the 1970s with Diantomus- dominated zooplankton assemblage (Scavia et al 1988). Such a change in zooplankton composition has occurred but not necessarily due solely to Bvthotrenhes predation. Our data clearly demonstrate that the composition and abundance of the calanoid community after 1987 are not unlike that of 1960s

(Table 21) and that the calanoids are now the dominant crustacean group as compared to the cladocerans in the early 1980s (Table 23). However, the species diversity and evenness of the Cladocera community in the early 1990s is unlike anything that has been previously reported for Lake Michigan. Cladocera dominance is centered in one species, Daphnia galeata mendotae, and only three species of Cladocera were observed in the lake in 199 1 and 1992.

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