# THE CRUSTACEAN ZOOPLANKTON OF THE SOUTHERN NEARSHORE ZONE Ó THE CENTRAL BASIN OF LAKE ERIE IN 1978 AND 1979: <br> INDICATIONS OF TROPHIC STATUS 

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The crustacean zooplankton community of the southern nearshore zone of the Central Basin was investigated as part of a two-year intensive limnological surveillance of Lake Erie conducted by the United Strtes and Canada. Thirty stations were sampled in 1978 in an area approximately 155 km long and up to 5 km from shore between Vermilion and Ashtabula, Ohio. Six stations were sampled in 1979. Four sampling cruises were conducted each year from April or May through October.

Sampling methods differed between 1978 and 1979 in terms of depth of tows, net mesh widths ( 243 and 64 microns), number of stations sampled, number of samples per station, and sampling dates. The samples collected in 1979 from one meter above the bottom with a 64 micron mesh net provided greater abundance estimates than those collected in 1978 from two meters above the bottom with a 243 micron mesh net. Zooplankton abundance was highly variable between stations and at individual stations during each cruise, indicating a patchy zooplankton distribution; however, definite seasonal patterns in the abundance of the individual species and the total zooplankton were observable.

Thirty-two crustacean taxa were identified in 1978, including 17 species of Cladocera, six Cyclopoida, seven Calanoida, one Harpacticoida, and the order Ostracoda. In 1979, 22 species were encountered, including 11 cladocerans, four cyclopoids, six calanoids, and one ostracod. The smaller number of taxa seen in 1979 probably resulted from sampling at only six stations, only one of which was close to shore, thereby eliminating semiplanktonic or tychoplanktonic species. Highest crustacean abundances were encountered during the June, July, and October cruises, and the lowest abundances were found in April, May, and August. In 1979 the nauplii usually constituted the most abundant group and the majority of the crustaceans. The Cladocera were more numerous in July, however, at four of the six stations. In descending order of abundance, the major species during the four 1979 cruises were Daphnia galeata mendotae, D. retrocurva, Eubosmina coregoni, Chydorus sphaericus, Eubosmina with pseudomucro, Cyclops bicuspidatus thomasi, Bosmina sp., Tropocyclops prasinus mexicanus, Mesocyclops edax, Diaptomus ashlandi, and $D$ oregonensis. All of the species reported as occurring in the middle of the Central Basin in 1967 and 1968 were encountered in the nearshore zone in 1978 and 1979.

In order to evaluate whether or not major changes have taken place in the crustacean zooplankton composition of the Central Basin over the past 30 years, the present results were compared with previous Central Basin studies. Comparison of these studies was complicated by the different sampling areas; different sampling methods, apparatus, and mesh sizes; varying sampling dates; and taxonomic uncertainties. No one species has consistently been the predominant species in all studies, probably due largely to these variables, although several cladocerans and copepods have remained numerically important in the lake since at least 1928. Some species appear to have disappeared or to have increased or decreased in relative abundance, and this may be related to an increase in the eutrophication of the lake.

A trophic index based on the ratio of the abundance of calanoid copepods to the abundance of cyclopoid copepods plus cladocerans was applied to this
and several earlier studies of Lake Erie. No difference in this ratio between the present and previous studies was detectable. Compared to values obtained in parts of the upper Great Lakes, however, the ratio indicates a relatively eutrophic status for all three basins of Lake Erie. Further investigation of the effectiveness of this ratio in measuring the trophic status of lakes is necessary, especially with regard to the effects of the inclusion or exclusion of naupliar stages of copepods and the dates of sample collection.

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## INTRODUCTION

The crustacean zooplankton community of the St. Lawrence Great Lakes forms an essential component of the food base for fishes (Wilson 1960), and its species structure provides an indication of the trophic status of the lakes (Gannon and Stemberger 1978). More fundamentally, knowledge of this community is important to understanding the inter-relations between the biotic and abiotic components of these large lake ecosystems.

Although detailed studies of the crustacean zooplankton community of Lake Erie date back at least to 1928 (Fish 1929), the composition and dynamics of the community are not well documented. All of the studies have been conducted on limited areas of one or more of the three basins, have employed a variety of sampling devices and methods, have been conducted during varying months of the year for varying durations, and have often been beset with a lack of taxonomic certainty. Yet probably the main factor precluding a detailed history of zooplankton composition and abundance in Lake Erie has been the lack of continuing studies in specific areas of the lake over the years.

The few investigations of the southern nearshore zone (defined for this report as less than 5 km offshore) of the Central Basin have been conducted during the past 30 years by Davis (1954, 1962) and Czaika (1978). A few other Central Basin studies, primarily by Davis (1968, 1969) and Patalas (1972), characterized the crustacean zooplankton of the open lake and included few if any nearshore stations. In this study, estimates of total crustacean zooplankton abundance and individual species contributions are presented and are related to the past and present trophic status of Lake Erie.

This study formed part of a two-year intensive surveillance program conducted by the United States and Canada in which the major physical, chemical, and biological components of the water column and sediments of Lake Erie were measured. The program conformed to a planning study performed by the Center for Lake Erie Area Research (CLEAR) (Herdendorf 1978), which reflected the general objectives of the Surveillance Subcommittee, Great Lakes Water Quality Board, International Joint Commission. The objectives of the surveillance plan, as stated by Herdendorf (1978), were (1) to search for, monitor, and quantify violations of the existing Agreement objectives, the IJC recommended objectives, and jurisdictional standards, criteria and objectives; (2) to monitor local and whole lake response to abatement measures and to identify emerging problems; (3) to determine the cause-effect relationship between water quality and inputs in order to develop the appropriate remedial-preventative actions and predictions of the rate and extent of local and whole lake responses to alternative abatement proposals. With consideration of key issues specific to Lake Erie, the surveillance plan additionally focussed on (1) determining the long-term trophic state of Lake Erie and determining to what degree remedial measures have effected improvements; and (2) assessing the presence, distribution, and impact of toxic substances.

In addition to this report, other reports on the southern nearshore zone of the Central Basin assess the physical and chemical components (Richards 1981), the bacteriology (E. [Stanford] McMahon, in preparation), the phytoplankton (P. A. Kline, in preparation), and the zoobenthos (Krieger 1981). Additional reports are being produced for the nearshore zones of the Eastern and Western Basins and the open lake of all three basins.

The sampling stations were located in an area approximately 155 km long from northwest of Vermilion, Ohio, to east of Ashtabula, Ohio, at distances as much as 5 km from shore (Figure 1 ). The exact location and the rationale for the selection of each station are provided by Herdendorf (1978). Stations were generally clustered around river mouths and harbors. Station depths at the time of sampling ranged from about 5 to 15 m .

During the four cruises in 1978, 30 stations were sampled throughout the study area, representing areas both within and outside of harbors. During the four 1979 cruises, six stations were sampled, and none of these was within harbors (Figure 1).


Figure 1. Map of the study area, showing stations sampled in 1978 and 1979.

## METHODS

Sampling methods differed between 1978 and 1979 in ways which directly affected the data. Both years the zooplankton was sampled with a 0.5 m diameter cone net with a detachable straining bucket. In 1978, vertical tows at a constant rate were made beginning at two meters from the bottom. In 1979, vertical tows were made from one meter off the bottom. In July, August, and October 1979, at stations with a depth of over 11 m , an additional tow was made beginning at 10 m . The samples were obtained between 0700 and 1630 hours local time during four cruises each year. The sampling dates are shown in Table 1.

In 1978, a net with mesh openings of 243 microns was used, thereby retaining only the larger immature and adult crustacean zooplankters. In 1979, the 243 micron mesh net was employed except in October to obtain samples for comparison with the 1978 samples. Most samples in 1979 were obtained with a net having 64 micron mesh openings in order to ensure collection of all of the life stages of the crustacean zooplankters.

In 1978, a single sample was taken at most of the 30 stations each cruise, although duplicate samples were obtained at a few of the stations. The duplicated stations varied from cruise to cruise. In 1979, only six stations were sampled for zooplankton (Figure 1). During the April, July, and August 1979 cruises, one 64 micron sample was collected with the 243 micron net, and a second sample was collected with the 64 micron net. Duplicate samples were collected with each net at two of the stations each cruise. During the July, August, and October 1979 cruises, one 64 micron sample (or duplicates) was obtained at each station on each of three consecutive days.

The volume of water strained during each tow was measured with a calibrated General Oceanics digital flowmeter attached to the net bridle. After each tow the net was thoroughly backwashed with a stream of water to rinse all zooplankters into the straining bucket. Each sample was poured into a 500 ml bottle, and about 15 ml of carbonated water were added to anesthetize the zooplankters. After several minutes the sample was preserved with 25 ml of $37 \%$ formalin, yielding approximately $2 \%$ formalin in the sample.

In the laboratory, samples with few zooplankters were concentrated to a workable volume. $A \quad 1.13 \mathrm{ml}$ or 2.32 ml aliquot was withdrawn from the thoroughly mixed sample with a calibrated Hensen-Stempel pipet and was placed in a Ward's zooplankton counting wheel for identification and enumeration of the specimens. A minimum of 200 non-naupliar crustaceans was enumerated, with additional aliquots taken as necessary. Duplicate aliquots were enumerated from $5.2 \%$ of the 1978 samples, and $7.5 \%$ of the 1978 samples were obtained in duplicate. Duplicate aliquots were omitted from the 1979 sample analysis, but approximately $33 \%$ of the 1979 samples were obtained in duplicate.

Cladocerans and adult copepod crustaceans were identified to species and sexed when possible. The systematics of the cladoceran family Bosminidae is unsettled, and variant forms occur in the Great Lakes (Watson 1974, Gannon and Stemberger 1978). Thus, bosminid specimens were identified as Bosmina sp. (with mucrones, probably B. longirostris), Eubosmina coregoni (without mucrones or pseudomucrones), and Eubosmina with pseudomucrones. There was often a gradation in the form and extent of development of the pseudomucrones

Table 1. Dates encompassed by the sampling cruises in 1978 and 1979.

in the specimens of a given sample. Sources for identification included Brooks (1957), Czaika and Robertson (1968), Deevey and Deevey (1971), Edmondson (1959), Pennak (1978), and Torke (1974). The samples are on deposit at Heidelberg College.

Zooplankton densities were calculated as:
Number per $\mathrm{m}^{3}=\frac{\mathrm{N}[\mathrm{V}(\mathrm{d}) / \mathrm{V}(\mathrm{a})]}{\mathrm{Q}}$
where

$$
\begin{aligned}
\mathrm{N} & =\text { total zooplankters in aliquot } \\
\mathrm{V}(\mathrm{~d}) & =\text { total sample volume (ml) } \\
\mathrm{V}(\mathrm{a}) & =\text { combined volume of aliquots }(\mathrm{ml}) \\
Q & =\text { quantity of water strained }\left(\mathrm{m}^{3}\right) .
\end{aligned}
$$

A detailed analysis of the 1978 samples was reported previously (Krieger 1980). Because the 243 micron mesh size employed in obtaining those samples allowed a large proportion of the crustaceans to pass through the net (see below), the data should be considered to be qualitative; estimates of zooplankton numbers made from these samples are too low, particularly for samples obtained when a large proportion of the crustaceans consisted of small immature forms.

Analyses of variance, t-tests, regressions, and correlations were performed using the package Minitab (Ryan et al. 1980).

## RESULTS AND DISCUSSION

Detailed data on the species enumerated from each sample collected in 1978 and 1979 are provided in several appendices available under separate cover.

## Environmental and Analytical Influences on the Data

The data obtained from duplicate samples and duplicate aliquots from the 1978 cruises were compared to determine the amount of field (environmental and equipment) and analytical (subsampling) variation. Selected data are presented in Table 2. A t-test revealed a highly significant difference $[t(9,6)=27.42, p<.01]$ in the agreement between duplicate sample densities and duplicate aliquot densities. Estimates of total crustacean zooplankton density were less variable between aliquots (mean similarity of estimates $=$ 0.92 ) than between samples (mean similarity $=0.74$ ). The high similarity of the aliquots indicates that the samples were thoroughly mixed prior to subsampling. The lower similarity between replicate samples is expected from the general patchiness of zooplankton distributions in lakes (Wetzel 19'75).

In contrast to total density (Table 2), there was essentially no difference in the extent of variation between replicate aliquots and replicate samples for total taxa, taxa shared, and percent Cladocera. In these instances, the variation of both aliquots and samples would have been reduced by counting more than 200 non-nauplii, although this would have represented a compromise in terms of increased time for analysis.

Similarly, the 1979 data from 243 micron mesh tows were analyzed to determine the amount of variation between replicate samples (Table 3). The range of similarities between duplicate samples for total abundance was very similar to the 1978 range, with a mean similarity of 0.77 .

Duplicate samples obtained with the 64 micron mesh net for three consecutive days were analyzed to determine whether total zooplankton abundance differed between days. F ratios obtained by oneway analyses of variance (Table 4) indicated that there was a significant difference in total abundance between days in only one of six sample sets, and in the abundance of cladocerans (water fleas) in two of the six sets. Thus, it appears that, in general, temporal changes in crustacean zooplankton dynamics cannot be detected within a three-day time interval, at least not without increasing the number of samples obtained each day (i.e., increasing precision). Nevertheless, as the 1978 data showed (Figure 2), zooplankton dynamics can be observed over a 15 day period even by sampling only once at many widely spaced stations.

Paired tows from the 10 m depth and from one meter above the bottom were accomplished on eight occasions in 1979 at three stations (Table 5). For six of the eight sample pairs, the "bottom" tow yielded a greater estimate of total zooplankton abundance, as would be expected if the zooplankters are distributed throughout the water column. The two pairs in which the 10 m tow yielded a greater estimate were at two stations where "bottom" tows produced greater estimates on other dates. Samples were collected at about the same

Table 2. Similarities (s) between duplicate samples ( $R$ ) and duplicate aliquots (A) of the crustacean zooplankton in 1978. Rotiod are the suallex number divided by the larger number.

time of day each day. From these results, it appears that considerable variation in the abundance estimates can arise from the sampling process itself, perhaps being affected by such factors as the amount of drift of the sampling craft during the tow, causing an oblique tow which is taken at a

Table 3. Comparison of total crustacean zooplankton estimates (No./m3) from duplicate samples collected in 1979 with a 243 micron mesh net.

| Station | Date | Sample 1 | Sample 2 | Similarity |
| :---: | :---: | :---: | :---: | :---: |
| 59 | 790830 | 1813 | 3260 | .56 |
| 69 | 790723 | 25479 | 32260 | .79 |
| 72 | 790827 | 1481 | 1145 | .77 |
| 96 | 790417 | 4219 | 5325 | .79 |
| 111 | 790714 | 18399 | 15126 | .82 |
| 139 | 790411 | 4663 | 5212 | .89 |

Table 4. Estimates of total crustacean zooplankton and total cladoceran abundance (No./cu.m.) from duplicate samples obtained on three consecutive dates in 1979 with a 64 micron mesh net. F ratios derived by one-way analyses of variance were either highly significant ( $p<.01, * *$ ), significant ( $p<.05, *$ ) or not significant.

| Total Zooplankton |  |  |  |  | Total Cladocera |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Station | Dates |  |  | F Ratio | Dates |  |  | F Ratio |
| 59 | 790830 | 798031 | 790901 | 8.89 | 790830 | 790831 | 790901 | 7.33 |
|  | 30629 | 26780 | 52671 |  | 5328 | 5091 | 8086 |  |
|  | 24196 | 35920 | 45349 |  | 4535 | 6318 | 7112 |  |
| 69 | 790723 | 790724 | 790725 |  | 790723 | 790724 | 790725 |  |
|  | 66325 | 52872 | 52755 | 0.89 | 37372 | 32044 | 22867 | 12.52* |
|  | 94722 | 68677 | 74584 |  | 41814 | 27109 | 26313 |  |
| 69 | 791016 | 791017 | 791018 |  | 791016 | 791017 | 791018 |  |
|  | 54007 | 67941 | 53643 | 0.51 | 14266 | 20551 | 20007 | 0.04 |
|  | 65098 | 52986 | 53137 |  | 19959 | 15646 | 15775 |  |
| 72 | 790827 | 790828 | 790829 |  | 790827 | 790828 | 790829 |  |
|  | 14175 | 22094 | 24608 | 3.62 | 2011 | 3417 | 1098 | 66.90** |
|  | 14209 | 24823 | 16430 |  | 2091 | 3875 | 753 |  |
| 111. | 790714 | 790715 | 790716 |  | 790714 | 790715 | 790716 |  |
|  | 193013 | 96690 | 97621 | 49.45** | 16355 | 22784 | 33086 | 5.54 |
|  | 174596 | 110798 | 90519 |  | 15142 | 36208 | 33120 |  |
| 139 | 791002 | 791003 | 791004 |  | 791002 | 791003 | 791004 |  |
|  | 151766 | 124200 | 138563 | 0.17 | 51503 | 29239 | 29396 | 0.39 |
|  | 84458 | 72934 | 96712 |  | 21239 | 20710 | 30911 |  |






Figure 2. Total zooplankton density ( $\mathrm{No} . / \mathrm{m}^{3}$ ) at each stations during each cruise in 1978, estimated with a 243 micron mesh net. Densities include all crustaceans and the large rotifers of the genus Asplanchna. Hashed bars indicate the higher density of two duplicate samples, and the solid bars beneath indicate the lower density. Asterisk indicates no sample was obtained.
shallower depth than the apparent sampling depth; the extent of rolling of the sampling craft during the tow, again influencing the effective depth of sampling; whether or not the plankton net opens immediately upon beginning the tow; and the natural horizontal patchiness of zooplankton distribution, as two successive hauls are never at exactly the same location in the water column due to drifting of the craft and lake currents.

In April, July, and August 1979, paired tows were accomplished once at each of the six stations, one tow employing a 243 micron mesh net, and the other a 64 micron mesh net. Total zooplankton, cladoceran, and cyclopoid copepod abundance (number per $\mathrm{m}^{3}$ ) as estimated by each net is shown in Table 6. Except for the samples obtained at station 96 in July, every pair of samples showed much larger abundance estimates in all three categories for the 64 micron mesh than for the 243 micron mesh. Mesh width (pore size) has been shown to directly affect filtration efficiency (Tranter and Smith 1968): A mesh width of 0.27 mm ( 270 microns) and a porosity of 0.44 demonstrated a $97 \%$ filtration efficiency, whereas a mesh width of 0.06 mm and 0.26 porosity demonstrated an $88 \%$ efficiency. It is also known, and was often very apparent during our study, that nets with smaller mesh widths clog more readily than those with larger mesh widths, and in this way filtration efficiency is further reduced in nets with smaller mesh widths.

Despite the reduced efficiency of the 64 micron mesh net, the data in Table 6 indicate that a much larger number of crustaceans was retained in that net than in the 243 micron net. Nauplii present in the 64 micron samples but absent in the 243 micron samples account for much of the difference in total zooplankton estimates. Similarly, the much less numerous young copepodid stages of the copepods were retained in the 64 micron net but usually escaped through the 243 micron net. However, the cladocerans were generally larger, and most should have been retained by both mesh sizes. As Table 6 shows, the 243 micron mesh estimates for cladocerans were also much lower than the 64 micron mesh estimates, even in July, when many of the cladocerans were large daphnias measuring well over 0.5 mm in height and over 1.0 mm in length. The greater filtration efficiency of the 243 micron net was expected to increase the estimates of those samples relative to the 64 micron samples. Thus, it seems possible that many of the larger crustaceans also were forced through the larger openings of the 243 micron net. Other factors which could have influenced the sample estimates, such as tow speed, filtering area, and depth of tow, were constant between the two mesh sizes. Different flowmeters were used on the two nets, and each was factory calibrated; therefore, erroneous readings should not have occurred. Because the 64 micron mesh net was known to retain all life stages of the crustacean zooplankters, despite its greater tendency to clog, and assuming that both flowmeters were accurate, the 64 micron mesh estimates are probably more correct than are the 243 micron mesh estimates. This smaller mesh size should be used in all future studies of the crustacean zooplankton of the Great Lakes. Few, if any, published studies of Lake Erie crustaceans have employed a mesh size greater than 119 microns (see Table 16).

Table 5. Comparison of total crustacean zooplankton abundance estimates ( $\mathrm{No} . / \mathrm{m}^{3}$ ) from samples obtained with a 64 micron mesh net at depths of 10 m and 1 m from the bottom.

|  |  | Date | Actual <br> Depth (m) | 10 m <br> Tow | "bottom" <br> Tow |
| :---: | :---: | :---: | :---: | :---: | :---: |

[^0]
## Abundance Patterns at 30 Stations in 1978

(243 Micron Mesh Samples)
Thirty-two crustacean taxa were identified from the Central Basin nearshore zone in 1978 and included 17 species of Cladocera, 14 species of Copepoda (six Cyclopoida, seven Calanoida, one Harpacticoida), and the order Ostracoda (not identified further) (Tables 7 - 10).

Zooplankton densities, as estimated by the 243 micron mesh net, varied greatly from station to station during each sampling period, but even more so at each station between sampling periods (Figure 2). In June 1978 some zooplankton densities were more than ten times higher than those recorded in May and October. The highest densities encountered (164,000/m3) were in June at stations 80 and 114. However, the stations with the highest zooplankton densities were different for each sampling period.

The lowest densities were found during the August-September cruise. At that time densities were severely depressed in and around Cleveland Harbor, with as few as 341 crustaceans $/ \mathrm{m}^{3}$ (Figure 2). A slight depression in total density in this vicinity was also apparent in May and October 1978.

The total densities obtained during each sampling period were strongly affected by the seasonal dynamics of the zooplankton community. During May a general increase in total abundance was apparent from west to east (Figure 2), and a gradual decline in numbers was reflected in August-September and October, again from west to east, which was the progressive direction of the cruises. Indeed, each set of histograms in Figure 2 continues at the approximate density at which the preceding set ends. Thus, differences in the crustacean densities between longitudinal areas of the basin probably are expressions more of temporal changes than instantaneous spatial differences.

Table 6. Comparison of the abundance ( $\mathrm{No} . / \mathrm{m}^{3}$ ) estimates of total crustacean zooplankton, total cladocerans, and total cyclopoid copepods (excluding nauplii) provided by paired samples, one employing a cone net with 243 micron mesh openings, the other a cone net with 64 micron mesh openings.

| Station | Date | Total Zooplankton 64243 |  | Total Cladocera |  | Total | Cyclopoida |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | 64 | 243 |  | 243 |
| 59 | 790423 | 52020 | 3425 | 2871 | 633 | 2134 | 406 |
|  | 790723 | 61947 | 29311 | 45645 | 28122 | 5356 | 1020 |
|  | 790830 | 30626 | 1813 | 5327 | 1256 | 2683 | 137 |
| 69 | 790423 | 32057 | 1600 | 1083 | 565 | 1118 | 208 |
|  | 790723 | 66325 | 25479 | 37372 | 22727 | 11293 | 2674 |
|  | 790830 | 18549 | 4563 | 2915 | 3192 | 1255 | 67 |
| 72 | 790421 | 21648 | 2111 | 1162 | 229 | 1419 | 734 |
|  | 790720 | 77472 | 20292 | 50100 | 15586 | 10264 | 4156 |
|  | 790827 | 14174 | 1481 | 2010 | 578 | 2060 | 219 |
| 96 | 790417 | 33405 | 4219 | 1524 | 518 | 6741 | 1800 |
|  | 790717 | 45140 | 49347 | 37495 | 41057 | 5734 | 6316 |
|  | 790824 | 21835 | 504 | 1329 | 276 | 4506 | 5 |
| 111 | 790414 | 27686 | 4477 | 897 | 230 | 4783 | 1987 |
|  | 790714 | 193015 | 18399 | 16355 | 7964 | 32063 | 10002 |
|  | 790821 | 49983 | 7576 | 9302 | 4074 | 7060 | 471 |
| 139 | 790411 | 39426 | 4663 | 225 | 119 | 6038 | 2855 |
|  | 790711 | 163078 | 21313 | 44249 | 17510 | 27477 | 3602 |
|  | 790818 | 18454 | 731 | 1915 | 576 | 1711 | 50 |

The number of taxa encountered was similar for the western, central, and eastern areas of the Central Basin nearshore zone during each sampling period. The harbors revealed a possible reduction in species richness when compared to open stations except in August-September, when both areas possessed the same number of taxa. The inshore stations consistently revealed more taxa than the offshore stations, due largely to the presence shoreward of several semiplanktonic or tychoplanktonic species which do not occur in the open lake.

Seasonal changes in the abundance of each crustacean group (Cladocera, Calanoida, Cyclopoida) followed a similar pattern in most parts of the study area, with lowest densities in May and October, and peak densities in June. The changes correspond very well with the historical density fluctuations demonstrated by Watson (1974). Likewise, Davis (1968, 1969), who sampled the open lake in July and October 1967 and January 1968, noted much greater densities of all groups in July. Britt et al. (1973) sampled the Western

Table 7. Mean densities (No. $/ \mathrm{m}^{3}$ ) of crustacean zooplankton taxa during May 1978. Means were computed using all replicates and subsamples. Station areas are Lorain-Vermilion ( $L-V$ ), Cleveland (CLEV), Fairport Harbor-Ashtabula ( $\mathrm{FH}-\mathrm{A}$ ) ; harbor, open; inshore (IN), offshore (OFF).

|  | L-V | CLEV | FH-A | HARBOR | OPEN | IN | OFF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| OSTRACODA | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CLADOCERA |  |  |  |  |  |  |  |
| Alona guttata Sars | 5 | 0 | 0 | 0 | 2 | 0 | 5 |
| Alona quadrangularis O.F. Müller | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ceriodaphnia lacustris Birge | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| Ceriodaphnia reticulata (Jurine) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Chydorus sphaericus (O.F. Muller) | 10 | 38 | 210 | 18 | 125 | 46 | 180 |
| Daphnia ambigua Scourfield | 2 | 47 | 6 | 46 | 4 | 27 | 0 |
| Daphnia galeata mendotae Birge | 22 | 27 | 5 | 24 | 9 | 19 | 15 |
| Daphnia parvula Fordyce | 73 | 15 | 0 | 36 | 24 | 19 | 49 |
| Daphnia retrocurva Forbes | 1,115 | 918 | 836 | 478 | 1,199 | 901 | 1,061 |
| Diaphanosoma leuchtenbergiana Fischer | 0 | 18 | 5 | 0 | 12 | 11. | 0 |
| Bosminidae | 1,665 | 3,437 | 5,586 | 1,976 | 4.483 | 2,704 | 5,642 |
| Holopedium gibberum Zaddach | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ilyocryptus spinifer Herrick | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Leptodora kindtii (Focke) | 13 | 23 | 5 | 2 | 20 | 10 | 21 |
| Leydigia quadrangularis (Leydig) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

COPEPODA

## HARPACTICOIDA

| Canthocamptus sp. | 25 | 5 | 0 | 5 | 12 | 13 | 2 |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |

## CYCLOPOIDA

immature Cyclopoida
Cyclops bicuspidatus thomasi S.A. Forbes
Cyclops Scutifer Sars
Cyclops vernalis Fischer
Eucyclops speratus (Lilljeborg)
Mesocyclops edax (S.A. Forbes)
Tropocyclops prasinus mexicanus Kiefer

| 790 | 4,086 | 7,526 |
| ---: | ---: | ---: |
| 548 | 469 | 2,177 |
| 0 | 0 | 3 |
| 111 | 86 | 181 |
| 3 | 0 | 6 |
| 12 | 73 | 114 |
| 0 | 0 | 0 |

2.229
820
0
154
9
82
0

| 5,291 | 3,312 | 6,275 |
| ---: | ---: | ---: |
| 1,217 | 815 | 1,666 |
| 2 | 2 | 0 |
| 112 | 96 | 193 |
| 0 | 4 | 0 |
| 60 | 52 | 103 |
| 0 | 0 | 0 |

CALANOIDA

| 1mmature Calanoida <br> Dlaptomus ashlandi Marsh |  |
| :---: | :---: |
|  |  |
|  | Diaptomus minutus Lilljeborg |
|  | Diaptomus oregonensis Lilljeborg |
|  | Diaptomus sicilis S. A. Forbes |
|  | Diaptomus siciloides Lilljeborg |
|  | Epischura lacustris S. A. Forbes |
|  | Eurytemora affinis (Poppe) |


| 2,134 | 1,196 | 820 | 1,093 |
| ---: | ---: | ---: | ---: |
| 160 | 29 | 157 | 81 |
| 37 | 19 | 89 | 13 |
| 16 | 1 | 0 | 1 |
| 0 | 0 | 3 | 0 |
| 5 | 6 | 0 | 6 |
| 0 | 0 | 0 | 0 |
| 350 | 372 | 9 | 563 |
|  |  |  |  |
| 7,118 | 11,065 | 25,699 | 8,325 |

1,500
131
67
8
2
2
0
72

18,284

| 1,172 | 1,773 |
| ---: | ---: |
| 81 | 188 |
| 32 | 87 |
| 3 | 10 |
| 2 | 0 |
| 1 | 10 |
| 0 | 0 |
| 76 | 162 |
|  |  |
| 11,464 | 22,337 |

Mean Total Individuals Per $\mathrm{m}^{3}$
,

Table 8. Mean densities (No. $/ \mathrm{m}^{3}$ ) of crustacean zooplankton taxa during June 1978. Means were computed using all replicates and subsamples. Station areas are Lorain-Vermilion (L-V), Cleveland (CLEV), Fairport Harbor-Ashtabula (FH-A); harbor, open; inshore (IN), offshore (OFF).

|  | $\mathrm{L}-\mathrm{V}$ | CLEV | FH-A | HARBOR | OPEN | IN | OFF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| OSTRACODA | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| CLADOCERA |  |  |  |  |  |  |  |
| Alona guttata Sars | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Alona quadrangularis O.F. Muller | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ceriodaphnia lacustris Birge | 26 | 29 | 28 | 33 | 24 | 28 | 26 |
| Ceriodaphnia recticulata (Jurine) | 0 | 0 | 55 | 0 | 29 | 13 | 33 |
| Chydorus sphaericus (O.F. Mưller) | 67 | 0 | 10 | 29 | 24 | 16 | 52 |
| Daphnia ambigua Scourfield | 0 | 0 | 29 | 0 | 15 | 0 | 35 |
| Daphnia galeata mendotae Birge | 60 | 274 | 492 | 247 | 292 | 347 | 90 |
| Daphnia parvula Fordyce | 57 | 0 | 0 | 52 | 0 | 26 | 0 |
| Daphnia retrocurva Forbes | 24,126 | 53,738 | 54,011 | 50,867 | 40,054 | 47,859 | 33,816 |
| Diaphanosoma leuchtenbergiana Fischer | 332 | 517 | 1,303 | 713 | 720 | 745 | 647 |
| Bosminidae | 4,113 | 6,416 | 3,558 | 5,077 | 4,479 | 4,242 | 5,873 |
| Holopedium gibberum Zaddach | 0 | 21 | 31 | 9 | 22 | 14 | 26 |
| Ilyocryptus spinifer Herrick | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Leptodora kindtii (Focke) | 192 | 124 | 209 | 213 | 154 | 210 | 85 |
| Leydigia guadrangularis (Leydig) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

COPEPODA

## HARPACTICOIDA

Canthocamptus sp.
CYCLOPOIDA

| immature Cyclopoida | 9,256 | 13,862 | 10,032 | 11,089 | 11,028 | 11,811 | 9,071 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Cyclops bicuspidatus thomasi S.A. Forbes | 3,630 | 3,047 | 2,279 | 2,363 | 3,338 | 2,993 | 2,966 |
| Cyclops scutifer Sars | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cyclops vernalis Fischer | 1,556 | 123 | 77 | 182 | 813 | 412 | 1,036 |
| Eucyclops speratus (Lillueborg) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mesocyclops edax (S.A. Forbes) | 282 | 617 | 1,034 | 512 | 719 | 756 | 353 |
| Tropocyclops prasinus mexicanus Kiefer | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

CALANOIDA

| immature Calanoida | 2,721 | 1,017 | 1,897 | 786 | 2,496 | 1,087 | 3,936 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Diaptomus ashlandi Marsh | 268 | 136 | 161 | 101 | 238 | 129 | 344 |
| Diaptomus minutus Lilljeborg | 203 | 198 | 1,853 | 378 | 962 | 722 | 827 |
| Diaptomus oregonensis Lilljeborg | 364 | 254 | 1,975 | 612 | 1,007 | 817 | 988 |
| Diaptomus sicilis S.A. Forbes | 19 | 15 | 19 | 0 | 28 | 19 | 15 |
| Diaptomus siciloides Lilljeborg | 330 | 617 | 1,746 | 635 | 1,046 | 837 | 1,055 |
| Epischura lacustris S.A. Forbes | 38 | 0 | 147 | 9 | 91 | 68 | 45 |
| Eurytemora affinis (Poppe) | 453 | 128 | 545 | 194 | 478 | 252 | 695 |
| Total Individuals per m ${ }^{3}$ | 48,093 | 81,324 | 81,501 | 74,136 | 68,142 | 73,496 | 62,014 |

In 1978, the high June densities of Cladocera were maintained in the August samples in the western area of the basin, but not in the other areas, whereas the Cyclopoida gradually declined between June and October in all areas. The Calanoida demonstrated minimum densities in May and August, with a slight recovery in some areas in October. Britt et al. (1973) found minimum densities of Calanoida in June 1961 followed by a gradual increase in density throughout the sampling season.

Table 9. Mean densities ( $N o . / \mathrm{m}^{3}$ ) of crustacean zooplankton taxa during August-September 1978. Means were computed using all replicates and subsamples. Station areas are Lorain-Vermilion ( $\mathrm{I}-\mathrm{V}$ ), Cleveland (CLEV), Fairport Harbor-Ashtabula (FH-A); harbor, open; inshore (IN), offshore (OFF).


CLADOCERA


| 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 122 | 10 | 6 | 26 | 51 | 52 | 17 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9,191 | 215 | 1,599 | 1,551 | 4,382 | 2,259 | 6,583 |
| 12 | 0 | 0 | 11 | 0 | 5 | 0 |
| 9,744 | 814 | 379 | 1,322 | 4,382 | 2,325 | 6,127 |
| 5,927 | 195 | 673 | 1,086 | 2,571 | 2,214 | 1,706 |
| 8,173 | 2,311 | 3,843 | 2,131 | 5,901 | 4,298 | 5,566 |
| 275 | 80 | 31 | 16 | 174 | 58 | 289 |
| 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| 200 | 10 | 94 | 114 | 90 | 107 | 76 |
| 0 | 0 | 3 | 3 | 0 | 2 | 0 |

COPEPODA

## HARPACTICOIDA

Canthocamptus sp.
CYCLOPOIDA
immature Cyclopoida

| Cyclops bicuspidatus thomasi |
| :--- |
| Cyclops |
| Scutifer Sars |
| Cyclops | Forbes

Eucyclops speratus (Lilljeborg)
Mesocyclops edax (S.A. Forbes)
Tropocyclops prasinus mexicanus Kiefer

| 2,872 | 248 | 996 | 908 | 1,518 | 1,200 | 1,622 |
| ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 116 | 5 | 83 | 18 | 92 | 76 | 44 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 103 | 15 | 9 | 30 | 44 | 20 | 90 |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2,574 | 28 | 328 | 489 | 1,118 | 785 | 1,238 |
| 0 | 0 | 7 | 0 | 4 | 3 | 0 |

## CALANOLDA

| immature Calanoida | 2,055 | 132 | 295 | 375 | 973 | 732 | 885 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Diaptomus ashlandi Marsh | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diaptomus minutus Lilljeborg | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diaptomus oregonensis Lilljeborg | 1,290 | 21 | 363 | 402 | 594 | 588 | 374 |
| Diaptomus sicilis S. A. Forbes | 23 | 0 | 0 | 0 | 11 | 10 | 0 |
| Diaptomus siciloides Lilljeborg | 104 | 10 | 45 | 4 | 75 | 60 | 28 |
| Epischura lacustris S. A. Forbes | 0 | 0 | 3 | 3 | 0 | 2 | 0 |
| Eurytemora affinis (Poppe) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| n Total Individuals per m ${ }^{3}$ | 42,855 | 4,474 | 8,891 | 8,534 | 22,299 | 15,074 | 24,739 |

The relative contribution of each crustacean group in the large mesh 1978 samples varied with the sampling period (Figure 3). These samples undoubtedly would have revealed somewhat different group ratios had the nauplii and smaller immature stages been retained. In May the Cladocera were present in relatively low numbers, but in June, August-September, and October they comprised the predominant group in all areas, becoming most important in June and August. The cyclopoid copepods were relatively most abundant in May in

Table 10. Mean densities (No. $/ \mathrm{m}^{3}$ ) of crustacean zooplankton taxa during October 1978 . Means wexe computed using all replicates and subsamples. Station areas are Torain-Vermilion (L-v), Cleveland (CLEV), Fairport Harbor-Ashtabula (FH-A); harbor, open; inshore (IN), offshore (OFF).

|  | $\mathrm{L}-\mathrm{V}$ | CLEV | FH-A | HARBOR | OPEN | IN | OFF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| OSTRACODA | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

## CLADOCERA

| Alona guttata Sars | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Alona quadrangularis O.F. Muller | 3 | 1 | 0 | 1 | 2 | 2 | 0 |
| Ceriodaphnia lacustris Birge | 0 | 8 | 21 | 10 | 9 | 12 | 3 |
| Ceriodaphnia reticulata (Jurine) | 0 | 0 | 15 | 0 | 7 | 5 | 4 |
| Chydorus sphaericus (O.F. Muller) | 574 | 380 | 48 | 178 | 439 | 314 | 416 |
| Daphnia ambigua Scourfield | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Daphnia galeata mendotae Birge | 390 | 95 | 20 | 41 | 256 | 156 | 232 |
| Daphnia parvula Fordyce | 3 | 0 | 0 | 3 | 0 | 1 | 0 |
| Daphnia retrocurva Forbes | 1,372 | 923 | 519 | 671 | 1,120 | 815 | 1,252 |
| Diaphanosoma leuchtenbergiana Fischer | 457 | 129 | 53 | 163 | 262 | 140 | 395 |
| Bosminidae | 2,647 | 2,186 | 2,452 | 2,244 | 2,546 | 2,279 | 2,754 |
| Holopedium gibberum Zaddach | 5 | 4 | 6 | 0 | 8 | 7 | 2 |
| Ilyocryptus spinifer Herrick | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Leptodora kindtii (Focke) | 163 | 34 | 42 | 82 | 86 | 70 | 113 |
| Leydigia guadrangularis (Leydig) | 0 | 1 | 6 | 6 | 0 | 3 | 0 |

COPEPODA

## HARPACTICOIDA

Canthocamptus sp .
$6 \quad 0 \quad 0$
$6 \quad 0$
0
6
CYCLOPOIDA

| immature Cyclopoida | 1,216 | 496 | 247 | 467 | 804 | 462 | . 1,119 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Cyclops bicuspidatus thomasi S.A. Forbes | 688 | 97 | 13 | 215 | 334 | 179 | 509 |
| Cyclops scutifer Sars | 0 | 0 | 2 | 0 | 1 | 1 | 0 |
| Cyclops vernalis Fischer | 442 | 6 | 9 | 70 | 223 | 117 | 273 |
| Eucyclops speratus (Lilljeborg) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mesocyclops edax (S.A. Forbes) | 424 | 111 | 8 | 73 | 260 | 125 | 331 |
| Tropocyclops prasinus mexicanus Kiefer | 0 | 0 | 2 | 0 | 1 | 1 | 0 |

CALANOIDA

| immature Calanoida | 1,408 | 1,025 | 774 | 1,025 | 1,124 | 989 | 1,283 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Diaptomus ashlandi Marsh | 3 | 0 | 0 | 0 | 2 | 2 | 0 |
| Diaptomus minutus Lilljeborg | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diaptomus oregonensis Lilljeborg | 1,321 | 505 | 36 | 553 | 722 | 551 | 881 |
| Diaptomus sicilis S.A. Forbes | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Diaptomus siciloides Lilljeborg | 416 | 63 | 4 | 79 | 229 | 136 | 256 |
| Epischura lacustris S.A. Forbes | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Eurytemora affinis (Poppe) | 24 | 2 | 48 | 48 | 12 | 28 | 18 |
| Total Individuals per m ${ }^{3}$ | 12,101 | 6,421 | 4,370 | 6,070 | 8,873 | 6,634 | 10.341 |

most areas but showed no distinct pattern during the remainder of the season. The calanoid copepods also presented an unclear pattern, but their contribution appeared to be least in most areas in June and August, when their numbers were especially reduced in the Cleveland area.


Figure 3. Percent of zooplankton abundance contributed by major crustacean groups during all cruises in 1978 (top) and during the May, June, August-September, and October 1978 cruises (bottom), estimated with a 243 micron mesh net. The "Other" category includes large rotifers of the genus Asplanchna, which were consistently retained in the net, as well as harpacticoid copepods and ostracods.

Comparison of Abundances between 1978 and 1979
( 243 Micron Mesh Samples)
Of the 30 stations sampled in 1978 , only three were again sampled in 1979. Table 11 provides a comparison of the numbers per $\mathrm{m}^{3}$ of cladocerans, cyclopoids, and calanoids computed from 243 micron mesh samples obtained each year at the stations. These data represent only the relative numbers each year, as the naupliar and smaller immature copepodid and cladoceran stages were not retained in the samples.

The sampling dates for the stations each cruise were from three to 13 days apart. These differences in sampling dates make comparison of stations within a single cruise of questionable value because of the continual seasonal shifts in abundances noted above. Furthermore, because only a single sample was obtained at each station on most dates, the degree of variability of sample estimates and hence an accurate measure of the similarity of the three stations is not available. On occasions when replicate samples were obtained at a station, the variability was large; thus, the average abundances of crustaceans at the stations probably would have been more similar than were the one-sample estimates in Table 11.

At only one station on one cruise were the sampling dates similar in 1978 and 1979. Therefore, it is impossible to compare in detail the similarity of seasonal abundances between the two years. In general, June and July appear to be the months of peak zooplankton abundance in the Central Basin nearshore zone. In April and early May, calanoid copepods outnumbered cladocerans and cyclopoid copepods, and in late May through October the cladocerans were the most abundant group, especially in June and July.

## Abundance Patterns at Six Stations in 1979 <br> (64 Micron Mesh Samples)

Twenty-two crustacean zooplankton species were encountered in the 64 micron mesh samples in 1979, including 11 cladocerans, 4 cyclopoids, 6 calanoids, and one ostracod. Total zooplankton abundance in April averaged $34,370 / \mathrm{m}^{3}$. In July the average abundance was $92,030 / \mathrm{m}^{3}$ with the largest sample estimate for the study of $193,000 / \mathrm{m}^{3}$. By August the average abundance at the six stations had decreased to only $23,890 / \mathrm{m}^{3}$, but in October an average of 99,960 crustacean zooplankters $/ \mathrm{m}^{3}$ with a maximum of $185,000 / \mathrm{m}^{3}$ was obtained. By comparison, Czaika (1978), in samples obtained near Cleveland Harbor in 1973 and 1974, found a maximum mean abundance in June of $158,000 / \mathrm{m}^{3}$, and the second highest mean abundance in August of $110,000 / \mathrm{m}^{3}$, whereas her lowest numbers were in November-December, with $27,600 / \mathrm{m}^{3}$, followed in April with $47,300 / \mathrm{m}^{3}$. Figure 4 presents the mean number per $\mathrm{m}^{3} \pm$ one standard error of each major group. Samples were collected only one day at each station in April, but on three days during the remaining cruises.

The nauplii (cyclopoid and calanoid) constituted the largest group of crustaceans throughout the year except in samples obtained in July at the four westernmost stations, where the nauplii were outnumbered by the cladocera. The nauplii usually comprised well over half of the total zooplankton except in October, when they nevertheless were the most abundant group.

Table 11. Comparison of the numbers per $\mathrm{m}^{3}$ of cladocerans, cyclopoids, and calanoids computed from 243 micron mesh samples obtained each year at three stations.


Station 111

|  | 28 May | 24 Jun | 6 Sep | 17 Oct | 14 Apr | 14 Jul | 21 Aug |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Cladocera | 17935 | 17167 | 1440 | 2629 | 230 | 7964 | 4074 |
| Cyclopoida 30422 | 5129 | 191 | 100 | 1987 | 10002 | 471 |  |
| Calanoida | 1135 | 4292 | 99 | 800 | 2259 | 432 | 3030 |
| Total 49492 | 26588 | 1730 | 3529 | 4477 | 18399 | 7576 |  |

Station 139

|  | 31 May | 27 Jun | 9 Sep | 11 Apr | 11 Jul | 18 Aug |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| Cladocera | 5250 | 64623 | 9386 | 119 | 17510 | 576 |
| Cyclopoida | 2788 | 14914 | 2805 | 2855 | 3602 | 50 |
| Calanoida | 398 | 9717 | 972 | 1689 | 200 | 104 |
| Total | 8436 | 89254 | 13163 | 4663 | 21313 | 731 |

The presence of large numbers of nauplii throughout the four cruises indicates a continuous production of new copepods during that period, although the species probably varied. The cruises showing the greatest productivity were in April and October, except at the two easternmost stations, where the most nauplii occurred in July and October (Figure 4).

As in the 243 micron samples, non-naupliar calanoids outnumbered the cladocerans in April but were themselves outnumbered by non-naupliar cyclopoids at three of the six stations during that month. In July and October the calanoids were much less abundant than either the cyclopoids or the cladocerans, but in August the three groups were present in approximately equal proportions. The total abundance of calanoids appeared to remain about


Figure 4. Mean number per cubic meter + one standard error of each major crustacean zooplankton group at six stations during each cruise in 1979.
the same throughout all four cruises except at the easternmost station in october, when unusually high numbers were encountered.

The non-naupliar cyclopoid copepods usually maintained intermediate abundances between the cladocerans and the calanoids throughout the sampling year. Their numbers were somewhat higher at the three easternmost stations during all cruises. They demonstrated two peaks, the first in July and the second, usually larger one in October.

The Cladocera increased sharply in abundance from the least numerous group in April to the most abundant group in July. Their numbers declined again by August but during that cruise were somewhat higher than the April abundances. A second peak was encountered in October which was somewhat smaller or about the same as the July peak.

In each group, the species contributing most to the abundance of the group changed throughout the sampling season. The more abundant species, and their ecological implications, are discussed below.

Cladocera. The abundance of each species at each station during each cruise is presented in Table 12. The two most abundant species, as in 1978, were Daphnia retrocurva and I. galeata mendotae (Figure 5), which had attained approximately equal abundances in July. Both species were generally absent in April. In October a second increase in abundance was noted for both species, although $D$. galeata was less abundant and was even absent at two of the stations at that time.

In the 1978 ( 243 micron) samples, D. retrocurva had completely dominated the crustaceans in June, whereas D. galeata did not reach high densities until the August cruise. Both species were found to be less abundant in May and October 1978 than in June and August 1978.

Previous studies throughout Lake Erie have presented similar but slightly varying abundance patterns for these two daphrid species. Britt et al. (1973) reported that in the shallow Western Basin in 1969 D. galeata mendotae ". . . was the dominant cladoceran species, becoming abundant at the end of July and continuing so through the end of the summer. D. retrocurva was always present too, but showed two obvious pulses, one in early July and the other at the end of August and continuing into September." Davis (1969) found in his open lake samples that these two species formed most of the cladoceran biomass and that D. galeata was the more abundant. He found both species in relatively small numbers in October, and in still smaller numbers in January. Davis (1968) noted for his July 1967 samples that D. galeata occurred in similar abundances in all three basins, whereas D. retrocurva occurred sporadically except in the Western Basin, where it exceeded D. galeata at five of the eight stations. However, he reported (Davis 1962) that D. retrocurva was ". . . the most common daphnid in the Cleveland Harbor area of the Central Basin in 1957."

Males of $D$. retrocurva were often encountered in the June 1978 samples throughout the Central Basin nearshore zone, less commonly in October, and infrequently in May and August. In 1979, by contrast, males were encountered infrequently and only in October. A few males of D. galeata were found in May

Table 12. Abundance (No. $/ \mathrm{m}^{3}$ 土 one standard error) of cladoceran species at each station during each cruise in 1979 .

| STATION |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| TAXON | CRUISE | 59 | 69 |  | 72 |  | 96 |  | 111 |  |  | 139 |  |
| Bosmina sp. | AFR | 39 | 89 |  | 37 |  | 98 |  | 149 |  |  | 135 |  |
|  | AUG | $37 \pm 21$ | 0 |  | 23 | $\pm 13$ | 0 |  | $15 \pm$ | $\pm$ | 15 | 3 | $\pm 3$ |
|  | OCT | $1861 \pm 786$ | 1667 | $\pm 179$ | 713 | $\pm 40$ | 3763 | $\pm 972$ | $347 \pm$ | $\pm$ | 244 | 188 | $\pm 95$ |
| $\frac{\text { Eubosmina }}{\text { Coregoni }}$ | APR | 1047 | 550 |  | 166 |  | 344 |  | 262 |  |  | 0 |  |
|  | JUL | $1591 \pm 970$ | 991 | $\pm 121$ | 2651 | $\pm 728$ | 485 | $\pm 53$ | $596=$ | $\pm$ | 137 | 119 | $\pm 119$ |
|  | AUG | $1872 \pm 287$ | 1619 | $\pm 340$ | 465 | $\pm 99$ | 374 | $\pm 77$ | 269 | $\pm$ | 147 | 167 | $\pm 70$ |
|  | OCT | $21340 \pm 2741$ | 10360 | $\pm 2008$ | 15708 | $\pm 1507$ | 13626 | $\pm 1749$ | $2410 \pm$ | $\pm$ | 489 | $2674 \pm$ | $\pm 339$ |
| Eubosmina with |  |  |  |  |  |  |  |  |  |  |  |  |  |
| pseudomucro | APR | 0 | 0 |  | 387 |  | 344 |  | 411 |  |  | 90 |  |
|  | JUL | $660 \pm 39$ | 1544 | $\pm 310$ | 2972 | $\pm 1044$ | 1472 | $\pm 652$ | $708 \pm$ | $\pm$ | 371 | 357 | $\pm 357$ |
|  | AUG | $3151 \pm 651$ | 2954 | $\pm 914$ | 1252 | $\pm 516$ | 1156 | $\pm 169$ | 2431 | $\pm$ | 1050 | 613 | $\pm 283$ |
|  | OCT | $73 \pm 73$ | 375 | $\pm 156$ | 823 | $\pm 417$ | 1428 | $\pm 213$ | $1978=$ | $\pm$ | 641 | 13681 | $\pm 2044$ |
| Diaphanosoma | JUL | 0 |  | $\pm \quad 59$ |  | $\pm 141$ | 0 |  | 164 | $\pm$ | 106 | 247 | $\pm 141$ |
| leuchtenbergiana | AUG | $231 \pm 83$ | 129 | $\pm 39$ | 125 | $\pm 56$ | 46 | $\pm 12$ | 489 | $\pm$ | 428 | 13 | $\pm 13$ |
|  | OCT | $404 \pm 225$ | 239 | $\pm \quad 26$ | 457 | $\pm 155$ | 316 | $\pm 169$ | 446 | $\pm$ | 165 | 2561 | $\pm 1048$ |
| $\frac{\text { Holopedium }}{\text { gibberum }}$ | AUG | $12 \pm 12$ |  | $\pm \quad 17$ | 0 |  | 0 |  | 0 |  |  | 0 |  |
|  | OCT | $95 \pm 95$ | 0 |  | 0 |  | 0 |  | 0 |  |  | 752 | $\pm 277$ |
| Chydorus <br> sphaericus | APR | 1668 | 373 |  | 498 |  | 738 |  | 75 |  |  | 0 |  |
|  | JUL | $776 \pm 621$ |  | $\pm 35$ | 0 |  | 0 |  | $307=$ | $\pm$ | 239 | 169 | $\pm 169$ |
|  | AUG | $386 \pm 88$ |  | $\pm 14$ | 62 | $\pm 15$ |  | $\pm 19$ | $700 \pm$ | $\pm$ | 207 | 80 | $\pm 45$ |
|  | OCT | $8454 \pm 2458$ | 4798 | $\pm 1363$ | 15536 | $\pm 3270$ | 15638 | $\pm 4169$ | 12965 | $\pm$ | 5151 | $8513=$ | $\pm 3126$ |
| $\frac{\text { Leptodora }}{\text { kindtii }}$ | ㅇ. JUL | $194 \pm 39$ | 256 | $\pm 129$ |  | $\pm 81$ |  | $\pm 59$ | 273 | $\pm$ | 136 | 853 | $\pm 549$ |
|  | ¢ AUG | $60 \pm 32$ |  | $\pm 19$ |  | $\pm 20$ |  | $\pm 11$ | $53 \pm$ | $\pm$ | 33 |  | $\pm 8$ |
|  | ¢ OCT | 0 |  | $\pm 48$ | 0 |  | 0 |  | 0 |  |  | 0 |  |
|  | $\sigma^{\circ} \mathrm{OCT}$ | $73 \pm 73$ | 0 |  | 0 |  | 0 |  | 0 |  |  | 0 |  |
| $\frac{\text { Daphnia }}{\text { retrocurva }}$ | $\bigcirc \mathrm{F}$ APR | 39 | 0 |  | 0 |  | 0 |  | 0 |  |  | 0 |  |
|  | ㅇ JUL | $13934 \pm 5861$ | 12459 | $\pm 3215$ | 10218 | $\pm 810$ | 27617 | $\pm 7556$ | $13936=$ | $\pm$ | 4363 | $13407=$ | $\pm 1834$ |
|  | ¢ AUG | $368 \pm 157$ | 137 | $\pm 51$ |  | $\pm 92$ |  | $\pm 34$ | 686 | $\pm$ | 498 | 151 | $\pm 127$ |
|  | $\bigcirc$ OCT | $3394 \pm 1124$ | 620 | $\pm 209$ | 1511 | $\pm 285$ |  | $\pm 481$ | $1082 \pm$ | $\pm$ | 488 | 5795 | $\pm 4144$ |
|  | $\bigcirc$ OCT | $232 \pm 127$ |  | $\pm 43$ | 315 | $\pm 198$ |  | $\pm 64$ | 0 |  |  | 0 |  |
| Daphnia galeata mendotae | ¢ JUL | $16147 \pm 4813$ | 15416 | $\pm 5026$ | 31749 | $\pm 2728$ | 17673 | $\pm 7670$ | 8090 | $\pm$ | 797 | 21141 | $\pm 6551$ |
|  | $\bigcirc$ AUG | $49 \pm 12$ | 0 |  |  | $\pm \quad 27$ | 0 |  | 37 | $\pm$ | 37 | 26 | $\pm 21$ |
|  | 9 OCT | $168 \pm 86$ |  | $\pm 44$ | 253 | $\pm 154$ | 0 |  | 0 |  |  | 2362 | $\pm 1729$ |
| Daphnia parvula | $\bigcirc \mathrm{APR}$ | 78 | 71 |  | 74 |  | 0 |  | 0 |  |  | 0 |  |
| $\frac{\text { Ceriodaphria }}{\text { lacustris }}$ | 7 OCT | 0 | 0 |  | 0 |  | 0 |  | 51 |  | 51 | 86 | $\pm 86$ |



Figure 5. Mean number per cubic meter $\pm$ one standard error of Daphnia retrocurva and $D$. galeata mendotae at six stations during each cruise in 1979.
and October 1978 but none were found in the 1979 samples. Previous investigators have not recorded the occurrence of male cladocerans.

Species of Bosmina and Eubosmina were major contributors to the Cladocera throughout the $1 \overline{979 \text { sampling period (Figure 6), as they were in 1978, although }}$ their abundance never approached that of the daphnids. They were the most numerous cladocerans in October both years. Bosmina was present in relatively low numbers in April and August 1979 and was entirely absent from the samples in July. It was collected in greatest numbers in October 1979. Eubosmina coregoni was present every cruise, showing a continual increase in abundance from April through October. Eubosmina coregoni attained about five times the abundance of Bosmina. Intermediate forms of Eubosmina (some of which may actually be cyclomorphic forms of Bosmina; see Kerfoot 1980) showed an increase similar to that of E. coregoni, although their abundance was declining during the October cruise.

Davis (1969) reported that the Bosminidae, along with Chydorus sphaericus, were the important crustacean zooplankters in October and January in the open lake. He reported (Davis 1968) a maximum of 238,000 bosminids $/ \mathrm{m}^{3}$ in the Western Basin in July, with an average of $92,000 / \mathrm{m}^{3}$, whereas in his open lake samples from the Central and Eastern basins in October (Davis 1969) they were considerably less numerous than in the October 1979 samples.

Of the remaining cladoceran species, only Chydorus sphaericus contributed over 10,000 individuals $/ \mathrm{m}^{3}$ during the 1979 sampling period (Table 12). It showed inconsistent but relatively low abundances at the six stations except in October, when it reached peak abundances of about 5,000 to $15,000 / \mathrm{m}^{3}$ (Figure 6). In 1978 Chydorus was present in all areas of the Central Basin nearshore zone during all cruises, and it also demonstrated an October peak as in 1979. Thus, this species along with the bosminids comprised the predominant cladocerans in Lake Erie during the fall. Britt et al. (1973) stated that Chydorus was the predominant cladoceran in the Western Basin in late August 1961. Davis (1968) reported it to be present in very low numbers in the Central Basin in July 1967 and to be apparently absent in the Eastern Basin. He later found it to be common and actively reproducing in the Central Basin in October 1967 (Davis 1969). Earlier counts have shown densities of Chydorus as high as $24,000 / \mathrm{m}^{3}$ in October $196^{r}$ in the Cleveland vicinity (Davis 1962), an abundance very similar to that encountered in 1979 at the three stations nearest Cleveland (Figure 6), and 8,500/m in October 1967 near the center of the Central Basin (Davis 1969). Vorce in 1882 (cited by Davis 1969) reported the species to be common in Lake Erie.

Cyclopoida. Immature cyclopoid copepods were present throughout the 1979 sampling period. Relatively low numbers were encountered in April and August, and the greatest abundances were recorded in october (except in July at the easternmost station), when densities approached $31,000 / \mathrm{m}^{3}$ (Figure 7). It was possible to identify the larger stages of the immature cyclopoid copepods to species (Table 13). Immature specimens of three of the four species were found during each cruise. Immature Tropocyclops prasinus mexicanus were observed during all except the April cruise.

Of the four cyclopoid species identified in 1979, Cyclops bicuspidatus thomasi occurred in the greatest numbers, with a maximum abundance of up to


Figure 6. Mean number per cublc meter $\pm$ one standard error of Bosmina sp., Eubosmina spp. and Chydorus sphaericus at six stations during each cruise in 1979.


Figure 7. Mean number per cubic meter $\pm$ one standard error of immature Cyclopoida and immature Calanoida at six stations during each cruise in 1979.

Table 13. Species of immature copepods identified at each station each cruise in 1979. $P$ indicates that the species was present; $U$ indicates that species were not identified for the samples.

| TAXON | CRUISE | 59 | 69 | STATION |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | 72 | 96 | 111 | 139 |
| Cyclops | APR | U | P | P | P | P | P |
| bicuspidatus | JUL, | U | P | P | P | P | P |
| thomasi | AUG | P | P | P | P | P | P |
|  | OCT | P | P | P | P | P | P |
| Cyclops | APR | U |  |  | P | P | P |
| vernalis | JUL | U | P | P | P | P | P |
|  | AUG | P |  | P | P | P | P |
|  | OCT | P | P | P | P | P | P |
| Mesocyclops | APR | P | P |  |  | P |  |
| edax | JUL | U | P | P | P | P | P |
|  | AUG | P | P | P | P | P | P |
|  | OCT | P | P | P | P | P | P |
| Tropocyclops | APR | U |  |  |  |  |  |
| prasinus | JUL | U | P |  |  | P | P |
| mexicanus | AUG |  | P | P | P | P | P |
|  | OCT | P | P | P | P | P | P |
| Diaptomus spp. | APR | U |  | P | P | P | P |
|  | JUL | U | P | P | P | P | P |
|  | AUG | P | P | P | P | P | P |
|  | OCT | P | P | P | P | P | P |
| $\frac{\text { Eurytemora }}{\text { affinis }}$ | APR | U |  |  | P | P | P |
|  | JUL. | U |  |  |  |  | P |
|  | AUG | P |  | P |  | P | P |
|  | ОСт | P | P | P | P | P | P |

5,000 adults $/ \mathrm{m}^{3}$ in July (Table 14). A somewhat lower abundance was encountered in April, and adults of this species were uncommon in August and October. Mesocyclops edax also was most abundant in July (less so than C. bicuspidatus), was entirely absent in April, and occurred infrequently in August and October. Tropocyclops prasinus mexicanus was generally absent in April 1979 but the number of adults increased each cruise to a maximum in October. Cyclops vernalis was the least abundant adult cyclopoid, being generally absent in April and present in minimal numbers during the other cruises. This species was not found in the samples from the easternmost station.

The ratio of adult males to adult females of each cyclopoid species

Table 14. Abundance ( $N . . / \mathrm{m}^{3} \pm$ one standard error) of nauplii and cyclopoid copepods at each station during each cruise in 1979 .

STATION

| TAXON | CRUISE | 59 | 69 | 72 | 96 | 111 | 139 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Nauplii | APR | 42747 | 28223 | 17205 | 22878 | 19801 | 30641 |
|  | JUL | $11644 \pm 1397$ | $17664 \pm 2936$ | $19771 \pm 3008$ | $19412 \pm 11281$ | $80910 \pm 29999$ | $65827 \pm 9902$ |
|  | AUG | $23962 \pm 5599$ | $16942 \pm 1827$ | $10706 \pm 845$ | $12972 \pm 1071$ | $15121 \pm 4505$ | $7866 \pm 3135$ |
|  | OCT | $20127 \pm 404$ | $29500 \pm 3747$ | $47763 \pm 4100$ | $76993 \pm 8481$ | $26531 \pm 5224$ | $55342 \pm 628$ |
| Inmature | APR. | 1862 | 763 | 885 | 3100 | 2055 | 2659 |
|  | JUL | $5162 \pm 272$ | $5489 \pm 747$ | $7881 \pm 813$ | $6514 \pm 3738$ | $13575 \pm 3355$ | $29322 \pm 1913$ |
|  | AUG | $3095 \pm 440$ | $1034 \pm 60$ | $3222 \pm 811$ | $3899 \pm 118$ | $5344 \pm 908$ | $1369 \pm 296$ |
|  | OCT | $14260 \pm 1158$ | $8745 \pm 467$ | $15304 \pm 983$ | $30955 \pm 10756$ | $20778 \pm 5476$ | $18422 \pm 1901$ |
| Cyclops | $\% \mathrm{APR}$ | 78 | 124 | 313 | 1870* | 1532* | 2433* |
| bicuspidatus | ¢ APR | 194 | 195 | 221 | 1771 | 1196 | 946* |
| thomasi | ㅇ JUL | $388 \pm 388$ | $782 \pm 535$ | $1211 \pm 250$ * | $545 \pm 248 *$ | $2582 \pm 1455 *$ | $1057 \pm 451$ * |
|  | O* JUL | $388 \pm 388$ | $912 \pm 471$ | $244 \pm 244$ | $147 \pm 147$ | $2440 \pm 1836$ | $166 \pm 83$ |
|  | $\bigcirc$ AUG | $49 \pm 49$ | 0 | $30 \pm 30^{*}$ | 0 | 0 | 0 |
|  | O RUG | $24 \pm 24$ | 0 | $30 \pm 30$ | 0 | $90 \pm 68$ | 0 |
|  | $\bigcirc$ OCT | $86 \pm 86$ | $37 \pm 37$ | $76 \pm 76$ | 0 | 0 | 0 |
|  | ${ }^{\circ} \mathrm{OCT}$ | $73 \pm 73$ | 0 | $44 \pm 44$ | 0 | 0 | $289 \pm 177$ |
| Cyclops vernalis | ¢ ${ }^{\text {a }}$ APR | 0 | 18 | 0 | 0 | 0 | 0 |
|  | $\bigcirc$ ¢ JUL | 0 | 0 | 0 | 0 | $47 \pm 47 *$ | 0 |
|  | $\sigma$ JUL | $272 \pm 39$ | 0 | 0 | $131 \pm 131$ | $147 \pm 77$ | 0 |
|  | 우 AUG | $37 \pm 21$ | 0 | $31 \pm 31$ | 0 | 0 | 0 |
|  | ${ }^{*}$ AUG | $51 \pm 25$ | 0 | $198 \pm 198$ | $25 \pm 13$ | $37 \pm 37$ | 0 |
|  |  | $245 \pm 150$ | 0 | $76 \pm 76$ | 0 | $51 \pm 51$ | 0 |
|  | $\bigcirc$ OCT | $73 \pm 73$ | $86 \pm 44$ | $457 \pm 155$ | $245 \pm 122$ | $353 \pm 221$ | 0 |
| Mesocyclops | \% JUL | $349 \pm 116$ | $68 \pm 68$ | $563 \pm 79 *$ | $913 \pm 632 *$ | $195 \pm 34$ | $200 \pm 105$ |
| edax | O* JUL | $621 \pm 621$ | $199 \pm 11$ | $965 \pm 366$ | $1190 \pm 446$ | $579 \pm 188$ | $1234 \pm 305$ |
|  | $\sigma$ AUG | 0 | 0 | $15 \pm 15$ | $11 \pm 11$ | 0 | $15 \pm 15$ |
|  | $\bigcirc \mathrm{OCT}$ | 0 | 0 | 0 | $246 \pm 246$ | $151 \pm 88$ | $86 \pm 86$ |
|  | $O^{\circ} \mathrm{OCT}$ | $86 \pm 86$ | 0 | $76 \pm 76$ | $246 \pm 246$ | $151 \pm 88$ | $792 \pm 510$ |
| Tropocyclops | 9 APR | 0 | 18 |  |  |  |  |
| prasinus | ¢ JUL | 0 | $199 \pm 11$ | $81 \pm 81$ | $66 \pm$ 66 | $182 \pm 182^{*}$ | 0 |
| mexicanus | $0^{\circ}$ JUL | 0 | $35 \pm 35$ | ${ }^{0} 8^{\circ}+6^{*}$ | $120 \pm$ <br> $400 \pm$ <br> $163 *$ | $131 \pm 80$ | $54 \pm 17 *$ |
|  | \% AUG | $291 \pm 158$ | $251 \pm$ $145 \pm 29$ | $118 \pm 26 *$ $133 \pm 28$ | $404 \pm 145$ | re9 $\pm 41$ | $156 \pm 114$ |
|  | $\bigcirc$ AUG | $377 \pm 218$ $1055 \pm 470$ | $145 \pm 19$ $311 \pm 14$ | 133 $887 \pm 447 *$ | $186 \pm 10{ }^{*}$ | $331 \pm 156$ * | $290 \pm 177 *$ |
|  | $\circ$ $\circ$ $\circ$ | $\begin{aligned} 1055 & \pm 470 \\ 633 & \pm 395\end{aligned}$ | $311 \pm 5$ | $430 \pm 160$ | $379 \pm 223$ | $474 \pm 172$ | $782 \pm 544$ |

* Ovigerous females present.
varied considerably from station to station and from cruise to cruise (Table 14). Ovigerous (egg-bearing) females of C. bicuspidatus were observed in the April, July, and August samples, but only at the four easternmost stations. Ovigerous females of $\mathbb{M}$. edax occurred in July at two Cleveland area stations, and ovigerous Tropocyclops were observed in July, August, and October, but not at the westernmost station. Only one ovigerous female of $\underline{C}$. vernalis was seen, in July near Fairport Harbor.

Within the limitations of the cruise dates, the periods of maximum abundance of Cyclops bicuspidatus and M. edax agree with earlier studies. Davis (1968) reported a mean density of C. bicuspidatus in July 1967 in the middle of the Central Basin of 5,950 adults $/ \mathrm{m}^{3}$ with a maximum of $11,900 / \mathrm{m}^{3}$ 。 He reported (Davis 1962) a June 1957 maximum of $20,400 / \mathrm{m}^{3}$ in the Cleveland Harbor area. Davis (1968) found that M. edax was distinctly less abundant than C. bicuspidatus in July 1967, as was true in the present study, and reported a maximum abundance of $5,730 / \mathrm{m}^{3}$, as compared to a maximum of 4,138 in July 1979 in the Cleveland Harbor area (station 96). Davis (1962) reported a similar August 1957 maximum for this species of $4,300 / \mathrm{m}^{3}$ in the Cleveland Harbor area.

The data of Britt et al. (1973) show that C. vernalis was generally more abundant than M. edax in the Western Basin in 1961. However, Davis (1962) found C. vernalis only in October 1956 in his Cleveland Harbor area study, and in 1967-1 $\overline{968}$ (Davis 1968, 1969) he found only very small numbers of C. vernalis in the Central Basin, which corresponds to the present results for the nearshore zone.

Calanoida. Immature calanoid copepods were present in minimal numbers in April 1979 but during July, August, and October maintained relatively high numbers, with a very large abundance $\left(15,800 / \mathrm{m}^{3}\right)$ in October at the easternmost station (Figure 7). They were usually much less abundant than the immature cyclopoids. Five of the six calanoid species found in 1979 belonged to the genus Diaptomus. Adults were present in low numbers during every cruise, although a few samples yielded over $1,500 / \mathrm{m}^{3}$ (Table 15). Immature diaptomids were found in the samples every cruise at every station (Table 13), but D. oregonensis was the only species for which adults were found during all four cruises. It occurred only sporadically in April and July, and never attained large numbers except at the easternmost station in October.

Adult Diaptomus siciloides were found in July, August, and October 1979, but always sporadically and in small numbers. Both D. ashlandi and D. sicilis were found in April at all stations and in July were represented by females at a single station. D. ashlandi in April attained the largest abundance of all the diaptomid species. Adult $\underline{D}$. minutus were seen only in the April samples.

The period of greatest diaptomid reproduction appeared to be in April, as ovigerous females of three of the five species were observed only at that time (Table 15). Ovigerous females of $D$. oregonensis were seen in the August and October samples, and no ovigerous females of D. siciloides were observed.

The only other calanoid species observed in the 1979 samples was Eurytemora affinis. Immature Eurytemora were observed sporadically in the April, July, and August samples but consistently in the October samples (Table

Table 15. Abundance ( $\mathrm{No} . / \mathrm{m}^{3} \pm$ one standard error) of calanoid copepod species at each station during each cruise in 1979 .

| STATION |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| TAXON | CRUISE |  | 59 | 69 | 72 |  | 96 |  | 111 |  |  | 139 |  |
| Immature |  | APR | 504 | 195 | 129 |  | 197 |  | 0 |  |  | 180 |  |
|  |  | JUL | $1048 \pm 349$ | $1208 \pm 392$ | $2969 \pm$ | $\pm 1035$ | $1522 \pm$ | $\pm 225$ | 3856 | $\pm$ |  | 3591 | $\pm 1809$ |
|  |  | AUG | $2576 \pm 716$ | $845 \pm 253$ | $3483 \pm$ | + 1424 | $1112 \pm$ | $\pm 95$ | 4475 | $\pm$ | 560 | 903 | $\pm 178$ |
|  |  | OCT | $1604 \pm 449$ | $1385 \pm 301$ | $3482 \pm$ | + 299 | $4808 \pm$ | $\pm 1251$ | 5651 | $\pm 1$ | 723 | 15857 | $\pm 1947$ |
| Diaptomus | 9 | APR | 1086 | 249 | 369* |  | 344* |  | 486 |  |  | 586* |  |
| ashlandi. |  | APR | 776 | 479 | 443 |  | 836 |  | 486 |  |  | 1036 |  |
|  | $\bigcirc$ | JUL | 0 | 0 | 0 |  | 0 |  | 0 |  |  | $119 \pm 119$ |  |
| $\frac{\text { Diaptomus }}{\text { minutus }}$ | 앙 | APR | 1009 | 107 | 332* |  | 148* |  | 187* |  |  | 90 |  |
|  |  | APR | 543 | 479 | 203 |  | 295 |  | 448 |  |  | 225 |  |
| $\frac{\text { Diaptomus }}{\text { oregonensis }}$ |  | APR | 78 | 0 | 55 |  | 0 |  | 37 |  |  | 0 |  |
|  |  | APR | 39 | 0 | 18 |  | 0 |  | 75 |  |  | 45 |  |
|  |  | JUL | 0 | 0 | $486 \pm 282$ |  | $359 \pm 188$ |  | $364 \pm 364$ |  |  | 0 |  |
|  |  | JUL | 0 | 0 | $723 \pm 238$ |  | $207 \pm 123$ |  | $108 \pm 55$ |  |  | 0 |  |
|  |  | AUG | 0 | $21 \pm 21$ | $31 \pm 16 *$ |  | $48 \pm 16$ |  | $53 \pm 33^{*}$ |  |  | 0 |  |
|  |  | AUG | 510 | $21 \pm 21$ | $109 \pm 87$ |  | 650 |  | $59 \pm 41$ |  |  | $7 \pm 7$ |  |
|  | 9 | OCT |  | $37 \pm 37$ | $106 \pm$$76 \pm$ | 10676 |  |  | $25 \pm$$50 \pm$ |  | 25 | $\begin{aligned} 696 & \pm 571 * \\ 2174 & \pm 1683 \end{aligned}$ |  |
|  |  | OCT | $73 \pm 73$ | $48 \pm 48$ |  |  | $123 \pm$ | $\pm 123$ |  |  | $50$ |  |  |
| $\frac{\text { Diaptomus }}{\text { sicilis }}$ |  | $A P R$ | 78 | 71 | 184* |  | 49* |  | 75* |  |  | 135* |  |
|  |  | $A P R$ | 155 | 53 | 129 |  | 344 |  | 411 |  |  | 225 |  |
|  | ¢ | JUS | 0 | 0 | $81 \pm$ | 81 | 0 |  | 0 |  |  | 0 |  |
| $\frac{\text { Diaptomus }}{\text { siciloides }}$ |  | Jut. | $\begin{aligned} & 78 \pm 78 \\ & 12 \pm 12 \end{aligned}$ | 0 | 0 |  | 0 |  | $47 \pm 47$ |  |  | $119 \pm 119$ |  |
|  | 9 | AUG |  | 0 | $8 \pm 8$ |  | 0 |  | 0 |  |  | 0 |  |
|  |  | AUG | 0 | 0 |  |  | 0 |  | $\begin{array}{rr}13 & \pm \\ 0\end{array}$ |  | 13 | 0 |  |
|  | ¢ | OCT | 0 | 0 | $97 \pm 49$$195 \pm 135$ |  | 0 |  |  |  | 0 |  |  |
|  |  | OCT |  | 0 |  |  | 0 |  | 0 |  |  | 0 |  |
| Eurytemora |  | JUL | 0 | 0 | $80 \pm 80$ |  | 0 |  | 0 |  |  | 0 |  |
| affinis |  | OCT | 0 | 0 | $44 \pm$ | $\pm 44$ | $123 \pm$ | $\pm 123$ | 0 |  |  | 0 |  |
|  |  | OCT | 0 | 0 |  | $\pm \quad 76$ | $64 \pm 64$ |  |  |  |  | $177 \pm 141$ |  |

* Ovigerous females present.
13), and adults were found occasionally in small numbers in July and October (Table 15). No egg-bearing females were observed.

Previous reports on the calanoid copepods compare favorably with the present results. Britt et al. (1973) found that mature and immature calanoids were most numerous in late August 1961, although peak abundance in 1979 appeared to occur from July through October. Davis (1968) found a July 1967 maximum of $D$. oregonensis of $1,640 / \mathrm{m}^{3}$ at a station in the middle of the Central Basin, With an average of only $700 / \mathrm{m}^{3}$. He reported (Davis 1962) as many as $2,700 / \mathrm{m}^{3}$ in the Cleveland Harbor area in September 1957.

Davis (1968) found that $D$. siciloides was more abundant than D. oregonensis at several open-lake Central Basin stations in July 1967 and obtained a maximum abundance there of $1,570 / \mathrm{m}^{3}$ at two stations, as opposed to a lake-wide maximum of $6,470 / \mathrm{m}^{3}$ in the Island Region. In the present study, the average October abundance of D. siciloides was slightly greater than that of D. oregonensis at one station.

Although we found D. minutus only in April 1979 and in May and June 1978, Britt et al. (1973) found it in June and July in the Western Basin in numbers fewer than $100 / \mathrm{m}^{3}$, and Davis $(1968,1969$ ) only rarely recorded the species in the western Central Basin, in July and January.

Both Davis (1968, 1969) and Britt et al. (1973) found only the five diaptomid species reported in the present study. Diaptomus pallidus Herrick, though not found in these studies, has been reported from Lake Erie (Watson 1974), most recently from the Eastern Basin in 1976 but previously only from the Central Basin (Cap 1979).

In this study, D. ashlandi was found in April and July 1979 and in May, June, and October $\overline{1978}$. The studies by Britt et al. (1973) and Davis (1962, 1968, 1969) described similar abundances and temporal patterns. D. sicilis was infrequently found in all of these studies.

The euryhaline calanoid E. affinis was first recorded in the Great Lakes system in 1959 from Lake Ontario and has subsequently invaded the other Great Lakes (Watson 1974). It was first reported in Lake Erie in 1962 in the Western Basin (Faber and Jermolajev 1966). Davis (1968, 1969) found adult E. affinis in July and October. In the present study, adults were found throughout the nearshore zone in May, June, and October 1978 and July and October 1979, being absent entirely in August both years.

The calanoid Epischura lacustris was found in low numbers in June and August 1978 but did not appear in our 1979 samples. This species has been reported previously in low numbers at sporadic locations (Britt et al. 1973; Davis 1962, 1968, 1969).

Trophic Status of the Nearshore Zone
All except two of the crustacean zooplankton species listed by Watson (1974) as occurring in Lake Erie, as well as all those reported by Davis (1968, 1969) for the middle of the Central Basin, were recorded in the present study. Watson (1974) also listed the calanoids Limnocalanus macrurus, usually found in cold, deep water, and Diaptomus pallidus. Britt et al. (1973), who
sampled the shallow Western Basin, also reported $L$. macrurus, as well as the cladocerans Daphnia pulex and Eurycerus lamellatus, neither of which was found in the present study.

Several cladoceran species appeared rarely in the 1978 samples from the Central Basin nearshore zone which have not often been reported for Lake Erie. One of these, Ilyocryptus spinifer, was previously found in the Islands Region in 1960 and 1962 (Bradshaw 1964). Leydigia quadrangularis apparently has not been reported earlier from Lake Erie. These two species appear to be characteristically benthic (Pennak 1978) or tychoplanktonic and probably only occasionally venture into or become suspended in the water column.

In order to evaluate whether or not major changes have occurred in the crustacean zooplankton composition of the Central Basin since the beginning of detailed studies, the present results were compared with earlier investigations. Table 16 summarizes nine major studies which have been conducted on the crustacean zooplankton of Lake Erie from 1928 to 1979 and lists in descending order the most abundant species encountered in each study. Comparison of the studies is difficult because different areas of the lake and often different stations within areas were sampled, sampling methods and mesh sizes varied, and sampling dates were often considerably different. As demonstrated above, the month of sampling may have an important influence on which species are encountered, and of those encountered which ones are abundant. Taxonomic uncertainties in most of the analyses further complicate attempts at comparison.

With the many variables involved, the overall similarity of the predominant species in many of the investigations is remarkable. No one species has consistently been the most abundant species in all studies, probably due largely to these variables. Daphnia galeata mendotae, often referred to earlier by various synonyms (see Cap 1980), has been among the most important crustaceans since the 1928 study of Fish and associates (1929) and has ranged from the most abundant species to the eighth most abundant species. Daphnia retrocurva has ranked among the three most abundant species at least since 1950-1951 (Davis 1954), although it was not abundant in Fish's study. Cyclops bicuspidatus has been an important species in most studies except in 1928, whereas M. edax has been shown to be abundant from 1928 to the present. Both of these cyclopoids have consistently been relatively less abundant in the Western Basin than in the Central and Eastern Basins. Diaptomus ashlandi, whose appearance in the samples is very seasonal, has occasionally been encountered in relative abundance from the 1928 study to the present time.

Changes in the relative abundance of several species seem to have occurred since 1928, and these may relate to changes in the trophic status of the lake. Gannon and Stemberger (1978) have noted that because most crustacean zooplankton species occur in a wide variety of lake types, their utility as indicators of the trophic status of lakes is limited to conditions of extreme oligotrophy or eutrophy. They emphasize, however, that the relative abundance of species can serve as a sensitive indicator of subtle differences in physicochemical characteristics. Such factors as toxic substances, eutrophication, and imbalance between planktivorous and piscivorous fishes, can cause shifts in the composition and relative abundances of crustacean species. Nutrient loading and pollution by toxic

Table 16. Comparison of sampling areas, methods, and dates as well as the most abundant crustacean species in nine major take Erie studies.


Table 16 continued.

| Author | Areas and No. of Stations | Tow Type, Net Size, Mesh Size | Cruise Dates | Most Abundant Species, in Descending Order |
| :---: | :---: | :---: | :---: | :---: |
| Czaika, $1978$ | off <br> Cleveland <br> Harbor, <br> 5 (NS) | vertical just off bottom, 0.5 m diam., $64 \mu$ | June, Aug., Nov., 1973, Apr. 1974 | Bosminids with mucro, Eubosmina coregoni, D. retrocurva, C. b. thomasi, D. g. mendotae, C. vernalis, Ceriodaphnia lacustris, M. edax |
| Cap: 1980 | Eastern Basin, No. not stated. | vertical, 0.5 m diam. . $64 \mu$ | June, July, <br> Aug., Sep., 1974 | D. g. mendotae, D. retrocurva, <br> C. b. thomasi, D. oregonensis, <br> $\overline{\mathrm{M}}$. edax, mucronate bosminids, <br> $\bar{\star}_{\text {nonmuc }}$ onate bosminids, *D. <br> longiremis, ${ }^{\text {D D. }}$ leuchtenbergianum |
| this study | Central <br> Basin, <br> 30 (NS) | ```vertical from 2m above bottom, 0.5 m diam., 243 \mu``` | May, June, Aug. -Sep., Oct. 1978 | D. retrocurva, E. coregoni, <br> $\overline{\mathrm{C}}$. b. thomasi, $\overline{\mathrm{D}} . \overline{\mathrm{g}}$. mendotae, mucronate bosminids, <br> D. leuchtenbergiana, D. oregonensis, <br> D. Siciloides, Eubosmina with <br> pseudomucro, <br> C. vernalis |
| this study | Central <br> Basin, <br> 6 (NS) | vertical from 1 m above bottom, 0.5 m diam., $64 \mu$ and $243 \mu$ | Apr., June, Aug., Oct. 1979 | D. g. mendotae, D. retrocurva, E. Coregoni, C. Sphaericus, Eubosmina with pseudomucro, C. b. thomasi, Bosmina sp., T. prasinus mexicanus, M. edax, D. ashlandi, D. oregonensis |

* Present in approximately equal proportions.
** Study area included nearshore (NS) stations.
substances, which infiuence zooplankton species in various ways, often occur at the same locations, and it may thus be difficult to separate the influence of the types of pollutants (Gannon and Stemberger 1978). These complex interactions probably are especially operative in the harbors of the southern nearshore zone of the Central Basin, where the zooplankton abundance in 1978 differed noticeably from harbor to harbor.

Gannon and Stemberger (1978) have summarized the literature concerning indicator crustacean zooplankton species in the Laurentian Great Lakes. The calanoid copepods Limnocalanus macrurus and Senecella calanoides appear to be reliable indicators of oligotrophic conditions. Both are rarely encountered in waters warmer than 15 C and below $0.6 \mathrm{mg} / \mathrm{L}$ dissolved oxygen. Because of their stringent environmental requirements, changes in the populations of these two species may serve as an early indicator of changes in lake conditions. Limnocalanus, which was relatively abundant in Lake Erie during the $1920^{\prime}$ s, became rare by the late 1950 's (Gannon and Beeton 1971, cited by Gannon and Stemberger 1978) and early 1960's (Britt et al. 1973). Diaptomus sicilis, another cold stenotherm, appears to be a characteristic oligotrophic $\overline{\text { species }}$ in the Great Lakes. It has only been found in low numbers at sporadic locations in Lake Erie in recent years (Cap 1980, Britt et al. 1973, Davis

1968, 1969), including the present study, when it was found during both cool and warm water periods. However, it was an important species numerically in the 1928 study (Fish 1929, Wilson 1960).

The cladocerans Bosmina and Eubosmina have been considered to be trophic indicators (Watson 1974, Deevey and Deevey 1971, Gannon and Stemberger 1978), demonstrating a species shift during eutrophication from the oligotrophic Eubosmina coregoni to the eutrophic Bosmina longirostris. However, as reviewed by these same authors, the continuing uncertainty as to the systematics and ecological tolerances of the several morphotypes in the Great Lakes greatly reduces their role as indicator organisms. Nevertheless, this species shift seems to have occurred to some degree in Lake Erie within the past 30 years (Table 16). Although Bosmina longirostris ("mucronate bosminids") was relatively scarce in the summer of 1928, it was the most abundant species in the Cleveland area in 1956-1957 and ranged from most abundant to fifth most abundant in later studies. Eubosmina coregoni ("nonmucronate bosminids") first appeared as an important component of the zooplankton in the July 1967 study of the open lake, generally ranging from first to third in abundance through the present study.

Chydorus sphaericus has also been employed as an indicator of eutrophy. Based on the reports in Table 16, this species first appeared in relatively large numbers in 1956-1957, but its abundance has been inconsistent since that time, due possibly to the varying sampling dates.

Diaptomus siciloides and Cyclops vernalis may be good indicators of eutrophic conditions, although $\underline{C}$. vernalis may be less reliable because of morphological variability and cryptic speciation. Both species were found only at eutrophic locations in western Lake Erie in 1930 but were found throughout the lake by 1967. In the upper Great Lakes these species are mainly restricted to the most eutrophic areas (Gannon and Stemberger 1978). Table 16 reveals that D. siciloides was an abundant species only after the early 1950's, whereas D. sicilis was no longer one of the most abundant species after that time. Davis (1962) noted that D. siciloides had been absent or nearly so in Lake Erie in 1929 but by 1956 had become one of the two most abundant diaptomids in all three basins. He postulated that this change may indicate eutrophication or a gradual warming of the lake reported by other investigators. In the present study, D. siciloides was the second most abundant calanoid in 1978, but was relatively scarce in 1979.

Because the calanoid copepods appear to be the crustacean group best adapted for oligotrophic conditions, several investigators (Patalas 1972, Gannon and Stemberger 1978) have considered the ratio of calanoid copepods to cyclopoid copepods plus cladocerans as a measure of the extent of eutrophy. Gannon and Stemberger (1978) successfully demonstrated the application of this ratio in several areas in Lake Michigan and in the Straits of Mackinac region where water masses demonstrated only subtle differences in water quality. In the latter study they obtained ratios between 0.2 and 6.6 (with one value of 13.2). They did not, however, suggest ranges of values which would indicate the particular trophic status of a lake.

This ratio was applied to the semiquantitative data from the 1978 samples (Table 17) and to the quantitative data from the 1979 samples (Table 18). The 1978 data produced ratios for the different areas between 0.03 and 0.62 , with

Table 17. Ratios of Calanoida to Cyclopoida plus Cladocera in areas of the southern nearshore zone of the Central Basin in 1978.

| Area | May | June | Cruise <br> August | October |
| :--- | :---: | :---: | :---: | :---: |$\quad$ All

Table 18. Ratios of Calanoida to Cyclopoida plus Cladocera at six stations in the southern nearshore zone of the Central Basin in 1979.

|  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Cruise | 59 | 69 | 72 | 96 | 111 | 139 |
| April | .85 | .74 | .72 | .27 | .39 | .40 |
| July | .03 | .03 | .07 | .04 | .11 | .06 |
| August | .26 | .14 | .61 | .19 | .44 | .34 |
| October | .03 | .05 | .08 | .08 | .14 | .29 |

a station maximum of 1.06. Similarly, the 1979 data produced ratios at the individual stations of 0.03 to 0.85 . By grouping the 30 stations sampled in 1978 into several geographical areas, it was possible to compare different parts of the nearshore zone (Table 17). The ratio did not reveal any consistent differences from cruise to cruise between alongshore areas nor between harbor and open areas. When the data for all of the cruises were combined, however, the ratios for the Cleveland and harbor station groupings

Table 19. Ratio of calanoids to cyclopoids plus cladocerans in studies on Lakes Erie and Lanao.

| Author | Lake | Ratio | Comments |
| :---: | :---: | :---: | :---: |
| Lewis, 1979 | Lanao (Phillipines) | 0.14 | Based on total copepodids collected weekly and monthly Sep. 1970 to Nov. 1971. |
| $\begin{gathered} \text { Lewis, } \\ 1979 \end{gathered}$ | Lanao | 0.073 | As above, except ratio includes nauplii. |
| $\begin{gathered} \text { Davis, } \\ 1968, \\ 1969 \end{gathered}$ | Erie Eastern Basin | $\begin{aligned} & 0.067 \\ & 0.054 \end{aligned}$ | Based on copepodid stages. <br> Stations on midlake transect. <br> July 1967 <br> 0ctober 1967 and January 1968 |
|  | Central Basin | $\begin{aligned} & 0.098 \\ & 0.066 \end{aligned}$ | July 1967 <br> October 1967 and January 1968 |
|  | Western Basin | $\begin{aligned} & 0.024 \\ & 0.10 \end{aligned}$ | July 1967 <br> October 1967 and January 1968 |
| ```Britt et al., 1973``` | Erie |  | Based on copepodids, station 4, east of South Bass Island. |
|  |  | 0.13 | 13 June 1961 |
|  |  | 0.0097 | 11 July 1961 |
|  |  | 0.027 | 14 August 1961 |
|  |  | 0.13 | 12 September 1961 |
| ```Britt et al., 1973``` | Erie |  | As above, station 6, n.w. of Pelee Island. |
|  |  | 0.12 | 13 June 1961 |
|  |  | 0.091 | 11 July 1961 |
|  |  | 0.30 | 14 August 1961 |
|  |  | 0.27 | 21 September 1961 |

indicated that the abundance of calanoid copepods was relatively suppressed, which may reflect adverse environmental conditions in those areas.

The ratio was further applied (Table 19) to other studies on Lake Erie and, for general comparison, to a detailed study on the zooplankton of Lake Lanao, a highly productive but nitrogen limited tropical lake in the Phillipines (Lewis 1979). The Lake Lanao study reveals the effect that
inclusion or exclusion of the naupliar stages can exert on the ratio, although a two-fold difference may be irrelevant to its interpretation. The fact that both ratios are low compared to those reported by Gannon and Stemberger (1978) in the Straits of Mackinac confirms the association of low ratios with eutrophic and highly productive waters. The studies of Davis (1968, 1969) along a midlake transect of the three basins of Lake Erie also yielded low ratios for each basin. Differences in the ratio between the basins were not consistent, however, indicating, as in the present study, that small differences in the ratio are not meaningful. The same conclusions derive from the ratios computed from the data of Britt et al. (1973) for two stations in the Western Basin.

Compared to the high ratios found by Gannon and Stemberger (1978) in the Straits of Mackinac, all regions of Lake Erie appear to be relatively eutrophic. It is obvious that this ratio is heavily influenced by the seasonal dynamics of the cladoceran populations: The ratios in the present study were highest in April and August, when the Cladocera were present in relatively low numbers. A similar pattern is evident in the ratios for the data of Britt et al. (1973). A more accurate indication of the trophic status of a lake by use of this ratio might be obtained by deriving an average ratio from the individual ratios calculated from samples gathered at regular intervals (e.g., biweekly or monthly) during the ice-free months, or by some other compositing technique. Such a method would smooth out the effects of population pulses of particular species at the individual sampling times. Additional application of the ratio to studies in the Great Lakes and elsewhere is necessary before its utility in assessing the extent of freshwater eutrophication can be established.

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[^0]:    Paired $t=-0.315$, N.S. at alpha $=0.05$ with 12 degrees of freedom.

