## THE UNIVERSITY OF MANITOBA

The crustacean zooplankton communities of three prairie lakes subject to varying degrees of anoxia
by

## Alexander George Salki

A Thesis
Submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science

Department of Zoology
Winnipeg, Manitoba

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## ABSTRACT

The crustacean zooplankton communities in three small prairie lakes subject to varying degrees of anoxia were studied for 14 months from February 1976 to April 1977. Ten or twelve samples were collected with a tube in both the deep and shallow zones of each lake once weekly during summer, biweekly in spring and fall and monthly during winter.

Local terrain was important to lake trophy and stratification. Physical and chemical observations indicated that shallow hypertrophic Lake 885 periodically stratified, exhibited winter and summer anoxia and had extreme nutrient and algal biomass levels. Shallow, meso-eutrophic Lake 255 was holomictic, displayed winter anoxia, and had lowest nutrient and phytoplankton amounts. Deeper, eutrophic Lake 019, stratified through summer, was not completely exhausted of oxygen and contained intermediate nutrient and algal concentrations. Dense populations of planktivorous fish Pimephales promelas and Culaea inconstans occurred in Lake 019 while Salmo gairdneri were stocked in Lakes 255 and 885.

Zooplankton community abundance and biomass, ranging on a mean annual basis from 124.7 to 289.9 ind $L^{-1}$ and 1.9 to 10.3 mg wet weight $L^{-1}$ respectively were governed by lake productivity and morphometry. Biomass in Lake 019 was also influenced by intense planktivory. A total of 25 species were identified, of which 10 , Cyclops bicuspidatus thomasi, Cyclops vernalis, Eucyclops agilis, Macrocyclops albidus, Diaptomus siciloides, Diaptomus leptopus, Daphnia schoedleri, Daphnia rosea, Daphnia parvula and Bosmina longirostris were common to all three lakes. The number of species, highest in Lake 255 with 21 and lowest in Lake 885 with 15, was inversely related to trophy. More eulittoral species in Lake 255 were associated with extensive macrophyte development. Numerically, cyclopoids were most
important in Lakes 885 and 255 while calanoids and cladocerans were most abundant in Lake 019, these trends being related to the frequency and severity of anoxia. Observed differences in the horizontal distribution of community and species abundance were associated with macrophytes, fish predation and morphology.

Seasonal community development in Lake 019 was basically monacmic with a mid summer pulse. Although diacmic patterns were observed in both Lake 885 and 255, in the former lake, spring densities were triple those of fall, the two pulses separated by a strong depression in late August. Lake 255 exhibited more equitable spring and fall pulses and a mid summer minimum. Highest community abundance during winter occurred in Lake 019. These variations were related to lake trophy, temperature, dissolved oxygen, nutrients, phytoplankton and predation.

Significant differences were observed in the seasonal dynamics of C. b. thomasi, D. siciloides and D. schoedleri. Instar analysis revealed spring emergence of $\mathbb{C}$. $\underline{b}$. thomasi from winter diapause only in Lakes 885. and 255. In Lake 019, ㄷ. b. thomasi survived through the winter carrying on reproduction. No evidence for summer diapause of this species was found in all three lakes. Spring ㄷ. ․ . thomasi densities were related to the severity of oxygen depletion during the preceeding winter and the intensity of invertebrate predation. Summer anoxia did not affect C. b. thomasi copepodids but was apparently fatal to nauplii.
D. schoedleri's presence only in Lakes 885 and 255 reflected reduced planktivory in winterkilled lakes. Delayed seasonal development of $\underline{D}$. schoedleri in Lake 885 suggested possible predation by abundant C. ․ . thomasi. High variation in abundance and polycyclic ephippial production by $\underline{D}$. schoedleri in Lake 885 reflected the omnipresent threat of Cyanophyte bloom
collapse. Summer anoxia severely impacted all stages of D. schoedleri.
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Relatively small differences in lake trophy and morphology appeared to effect considerable differences in oxygen conditions and seasonal crustacean plankton community composition and dynamics.

DEDICATED TO MY CHILDREN

MATTHEW
AND
KERRI

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## INTRODUCTION

The understanding of crustacean zooplankton ecology in western Canada has grown appreciably over the past 50 years. To a large extent, the evolution of this knowledge was governed by the size, remoteness and the economic development of this region. Early studies by Baikov (1930, 1934), Rawson (1947, 1960) and Reed (1964) among others concentrated primarily on documenting fundamental limnological data from some of the more prominent lakes in the west.

As investigations continued, post glacial dispersion patterns of crustacean species were also considered. Studies by Carl (1940) and Anderson (1974) on montaine lakes in British Columbia, the saline lakes of Saskatchewan by Rawson and Moore (1944) and Moore (1952), on North American daphnids by Brooks (1957), large North American lakes by Patalas (1975), the Yukon lakes by Archibald (1977) have contributed towards our understanding of this process.

To complement this fundamental research, more effort is now being directed towards examining the temporal and spatial variability of zooplankton communities as well as the environmental and biotic factors governing plankton dynamics. Because of technical difficulties involved in remote sampling, the earlier works were usually restricted to a single sampling period in mid-summer or to one limnetic station. In the past, this approach was adequate for classifying lacustrine productivity and trophic status (Larkin and Northcote 1958, Rawson 1961). Today, when the environmental impacts of toxins, petroleums, acids, radioactive wastes and other contaminants associated with cultural eutrophication need to be accurately assessed, a clear idea of "natural" community and population
fluctuations is an important prerequisite. Likewise, the horizontal variation of plankton distributions within lakes needs quantitative refinement. Information is available for larger eastern Canadian lakes (Langford 1938; Davis 1966; Rigler and Langford 1967; Schindler and Noven 1971; Patalas 1969, 1971, 1972; Davis 1973; Watson and Carpenter 1974; Clark and Carter 1974; McNaught and Buzzard 1974) but few studies have been undertaken in the west (Bajkov 1929; Hammer and Sawchyn 1968; Anderson 1970; Donald 1971; Lei and Clifford 1974; Herzig et al. 1980). Although comparison with other data is instructive, the high degree of crustacean community variability recorded throughout the literature (Hutchinson 1967) impresses the need of further regional sampling. As Schindler (1978) points out, more complete data are still needed for many areas.

Prairie pothole lakes are characteristically shallow, nutrient rich and often covered with aesthetically unappealing algal scums, perhaps the reason for their lack of attention. As a result of their physicochemical properties, many are impacted by catastrophic "summer or winterkills", periods of low ( $<1.0 \mathrm{mg} \mathrm{O}_{2} \mathrm{~L}^{-1}$ ) oxygen concentration which are often fatal to resident fish but allow for development of extremely dense invertebrate populations. This invertebrate resource currently supports rainbow trout aquaculture in the Erickson-Elphinstone area of western Manitoba. Several lakes in the district, because of their relatively larger size, do not exhibit periods of complete anoxia and consequently support perrenial fish populations. This combination of "kill and non-kill" lakes provided a unique opportunity to examine the effects of anoxia on crustacean zooplankton development as well as to compare zooplankton community structure, seasonal dynamics and trophic interrelationships within three lakes 019, 255, and 885. Differences between the plankton of deeper, central and shallower, nearshore zones of each lake were also considered. Winter
sampling formed a significant part of the study since data on planktonic growth during the ice cover period are relatively scarce.

This research was conducted as one part of a joint program involving the efforts of V. Srisuwantach (1978) - nutrients and phytopiankton, P. Tavarutmaneegul (1978) - rainbow trout production and J. Boonsom, zooplankton-fish interactions. The study, supported by the Freshwater Institute, provided for a comprehensive analysis of the prairie pothole ecosystem. Perhaps it can be considered a forerunner of the cooperative thesis concept advocated by Vallentyne (1974).

## THE LAKES

Lakes 885, 255 and 019 are located in west central Manitoba near the town of Erickson, positioned at $50^{\circ} 30^{\prime} \mathrm{N}$ and $99^{\circ} 55^{\prime} \mathrm{W}$, approximately 330 km northwest of Winnipeg (Fig. 1). The study area lies on the Manitoba Escarpment which rises between 460 and 760 meters above the lowland plains of central Manitoba at 450 m a.s.1. Morrainal deposits characterizing the region were remnants of the final, Wisconsinan stage of Pleistocene glaciation. With the retreat of Lake Agassiz, hundreds of small, shallow ponds and lakes remained which ultimately became domestic and livestock watering sources for many farms developing in the area. Lake 019 currently receives drainage from a barnyard and farmhouse on its northern shore while lake 885 is situated on an abandoned farmstead (Figs. 2a, c). Both lakes are largely surrounded by trees and are adjoined by grainfields of predominantly grey wooded or fertile black soils. Lake 255 (Fig. 2b), situated between a railroad track and a provincial highway, is comparatively removed from direct agricultural influence although a cultivated field exists a short distance to the east.

Figure 1. The location of Lakes 019, 255 and 885 in the Erickson-Elphinstone, Manitoba study area.


Figure 2a. Bathymetric map of Lake 019 (contours in meters) showing the distribution of shallow(s) and deep (D) zone sampling stations each with a pair of subsampling sites ( 0 and or and ). Subsamples from similarly designated sites within each zone combined, resulting in two composite samples from each zone. Extent of emergent macrophytes...... and borderline of trees and cultivated fields-.... also indicated. Trees, farm buildings and roadways approximately to scale.


Figure 2b. Bathymetric map of Lake 255 (contours in meters). Description as for Lake 019.


Figure 2c. Bathymetric map of Lake 885 (contours in meters). Description as for Lake 019.


An expansive bush surrounds most of the lake except on its south, highway side. The small northern bay of Lake 255 is basically a marsh with nesting facilities for several ducks and some nutrient exchange with the main body may occur.

The three lakes, like most in the area, can be classified according to Hutchinson (1967) as the open seepage type whose water levels are primarily sustained by groundwater flow. Mean annual precipitation receipts of $400-500 \mathrm{~mm}$ plus $120-160 \mathrm{~cm}$ of snowfall are exceeded by potential evapotranspiration values of $600-700 \mathrm{~mm}$ (Fish. and Enviro. Can. 1978). Some additional surface influents from surrounding crop lands may reach the lakes during rainstorms, particularly in 019 where a small stream enters on its western edge. The region is characterized by mean daily July temperatures between $17.5-20^{\circ} \mathrm{C}$ and January temperatures near $-20^{\circ} \mathrm{C}$. Annual mean ice-free and ice-over dates are May 1 and November 1, respectively.

The basic morphometric parameters of the study lakes are given in Table 1. Lake 019, with a 3.4 m mean depth, was not subject to any lethal anoxia during the study and supported perennial Pimephalis promelas and Culaea inconstans populations. Lakes 255 and 885, however, because of their shallower mean depths, 1.6 and 1.7 m respectively, experienced oxygen depletion under winter ice. In addition, due to an algal bloom collapse, Lake 885 was deoxygenated in the latter part of August. This "summerkill" was a recurring phenomenon in 885 which had been monitored for several previous years, along with 255 , as part of a trout stocking program.
le 1. Morphometric parameters of Lakes 019, 255 and 885 (1976-1977).

| Lake Parameter | 019 | Lake <br> 255 | 885 |
| :---: | :---: | :---: | :---: |
| rface area (ha) | 28.72 | 4.09 | 2.36 |
| ximum length (km) | . 86 | . 28 | . 22 |
| ximum width (km) | . 49 | . 23 | . 15 |
| ximum depth (m) | 6.8 | 2.5 | 2.9 |
| san depth (m) | 3.4 | 1.6 | 1.7 |
| stal volume ( $\mathrm{m}^{3}$ ) | 974,618 | 63,454 | 41,299 |
| hallow zone volume ( $\mathrm{m}^{3}$ ) | 54,316 | 12,754 | 6,146 |
| eep zone volume ( $\mathrm{m}^{3}$ ) | 920,302 | 50,700 | 35,153 |
| 'eriod of anoxia | None | Winter | Winter \& summer |

## METHODS

## Field Work

Sampling of Lakes 019, 255 and 885 began in February 1976, with one or two trips in each of February, March and April followed by two or three trips in May and weekly collections during June-September. Lake 885 was sampled on two additional dates in late August for a more detailed examination of "summerkill". Through the period October 1976 to February 1977, collection frequency was once per month and finally twice per month in March and April 1977. In total, Lake 019 was sampled 29 times, Lake 255 31, and Lake 885 on 33 occasions.

In order to estimate seasonal zooplankton abundance, a systematic randomized sampling scheme (Elliot 1971) was applied, resulting in a permanent network of stations covering all areas of each lake (Figs $2 a, b, c$ ). Of the 12 stations in Lake 019, 6 were selected to represent the near shore or shallow zone (depth $\leq 1.5 \mathrm{~m}$ ) and 6 the open water or deep zone. In each of Lake 885 and 255,5 deep and 5 shallow zone stations were established. Within the vicinity of each station, 2 duplicate subsamples were taken, each combined randomly with the corresponding "replicates" from other stations of a zone resulting in a pair of composite samples from each zone on each sampling date. Although compositing sacrificed information on horizontal variation sample analysis became a manageable task (approximately 500 composite instead of 2700 separate samples) and zonal population means with ranges were still available.

To evaluate the precision of these population estimates, surveys determining horizontal variation were conducted on Lakes 019 and 255 on July 27, 1977 wherein all subsamples were treated separately. In addition,
the routine collections from Lake 885 on August 29, 1976 were analyzed separately. Species and total community counts were assessed with a packaged Shapiro-Wilks test provided by I. Davies, Freshwater Institute.

Because this study was not primarily concerned with the vertical distribution of zooplankton, a device which could secure an integrated sample from the total water column was designed. Initially, a 7.6 cm inner diameter (I.D.) aluminum pipe of 4 m length, extendable to 8 meters by coupling a second section, was used to collect zooplankton samples from the deep zone of the study lakes. The sampler worked efficiently but the extended tube proved unwieldly during a strong wind so it was replaced July 15,1976 by a simpler, more convenient version patterned after that used by Pennak (1962) which retained the same sampling principle. Construction of the sampler was from flexible plastic dryer venting of 7.6 cm I.D. fitted with a 30 cm long piece of transparent plexiglass tubing to minimize avoidance by plankton and a short section of heavy iron pipe around the upper end of the plexiglass to ensure rapid sinking (Fig. 3).

The water column captured by the descending sampler was emptied into a small conical net of $73 \mu \mathrm{~m}$ mesh following retrieval of the mouth by an attached sideline. Between stations, the sampler was stored in a large garbage pail. Composite zooplankton samples were transferred from the net collecting bucket into jars containing a few ml of narcotizing methanol (Gannon and Gannon 1975) to reduce egg losses and then preserved as a $10 \%$ formalin solution. Zooplankton sample volumes calculated from sampler dimensions were field verified. They did not deviate from true volumes by greater than $\pm 5 \%$. Sample depths were taken from the calibrated sideline to avoid any effect of seasonal temperature change on the plastic sampler material. Concern about retention of zooplankton on the inside

Figure 3. Flexible tube sampler used to collect zooplankton.

walls of the sampler was unfounded. Operation of the sampler and nets during the winter was accomplished with a sledge-drawn heated wooden shelter. A special survey on September 9, 1976, revealed the aluminum and flexible plastic sampler efficiencies to be comparable ( $t=.13$ ).

Shallow zone samples were collected with a 7.6 cm I.D., 2 m long clear plexiglass tube quickly lowered to the lake bottom, the upper opening then closed with a large rubber stopper. The lower end of the tube was then raised upwards diagonally and stoppered before the entire sampler was removed from the water and emptied into the collecting nets.

The possibility of predation on copepods and cladocerans by Gammarus and/or Chaoborus spp. occurring within the net collecting bucket during interstation travel on a lake was examined. No significant differences ( $F=.38 \mathrm{df} 3,12, \mathrm{P}>0.05$ ) in abundance were noted among samples fixed 0,10 , 20 and 40 minutes after collection.

On each occasion, water transparency and vertical temperature profiles were recorded at most if not all stations using a 20 cm white Secchi disc and a YSI model 43T tele-thermometer, respectively. Percentage cloud cover, wind speed and direction, wave height, air temperature, water level fluctuations, ice and snow thickness were other variables noted.

Detailed studies of dissolved oxygen, water chemistry, phytoplankton communities and primary production of Lakes 019,255 and 885 were conducted during February 1976 - February 1977 as a complementary program by V. Srisuwantach (1978). Oxygen conditions during the period FebruaryApril 1977 were measured by the author using the modified Winkler technique. Stocked trout, released from cages in Lakes 255 and 885 on May 12 were monitored by P. Tavarutmaneegul (1978). In non-stocked Lake 019, estimates of the natural fathead minnow and stickleback populations were gained from a series of near shore seining hauls taken by the author during July
1977. At the same time, a Miller high speed sampler (Miller 1961) was used in an attempt to measure open water fish populations.

Lake 019 bathymetry was determined with a Furuno FG-11/200 Mark-3 echo sounder while Lakes 255 and 885 had been previously sounded (Sunde and Barica 1975). Lake shorelines and emergent macrophyte bed outlines were traced from aerial photographs taken in June 1976 by an EPS-LACS team. Lake surface area and volume were obtained planimetrically from photo enlargements.

Laboratory Analysis of Zooplankton Samples
After settling overnight or longer, zooplankton samples were concentrated to 40 ml by siphoning off excess liquid through a tube covered with $50 \mu \mathrm{~m}$ mesh Nitex and transferred to convenient $45-\mathrm{m} 1$ storage vials. Following very thorough mixing of each vial to ensure randomness, a one ml subsample was quickly withdrawn using a calibrated 4 mm I.D. $x 15 \mathrm{~mm}$ long glass tube and placed in a Sedgewick-Rafter cell where it was counted in its entirety under a compound microscope. A minimum of 400 in dividuals (i.e. 200 in each duplicate subsample) were counted from each zone on each date to obtain total zooplankton abundance estimates thus qualified by counting errors of less than $5 \%$ (i.e. coefficient of variation $=\frac{1}{\sqrt{400}} \times 100$ Cassie 1971). Generally more than 100 individuals of each dominant species were counted resulting in a coefficient of variation no greater than $10 \%$. For the largest ( $>2.5 \mathrm{~mm}$ ) and/or rarest zooplankters, (Gammarus sp., Diaptomus leptopus) a 10 mm I.D. glass tube was used to dispense a larger subsample ( 6.8 ml or $17 \%$ of the total sample) into a $2 \times 2 \times 18 \mathrm{~cm}$ trough of 6 mm clear plexiglass. Individuals were enumerated under a Wild M5 stereo microscope. Often, entire samples were examined
in this manner. Subsample counts were expressed as individuals per litre since the relative shallowness of the study lakes was expected to favour well mixed conditions. In fact, as previously discussed, some stratification was noted in lakes 019 and 885 which may have slightly altered the vertical distribution of plankton but likely not permanently. In Lake 019, as more than $90 \%$ of the water volume was above 5 m , the usual depth of mixing, most of the habitat was accessible to the plankton at all times. Additionally, of the 12 samples collected at the six deep stations, four or six were always from above the 5 m isobath, while the remaining six or eight were generally from five to six $m$ (i.e. only 1 m below the mixed layer) so that water possibly devoid of plankton represented a minor proportion of the total volume sampled. From the duplicate subsample counts representing each particular zone on each date, arithmetic means were calculated and tabulated as the basic abundance data from which biomass estimates were also derived (Appendices $F$ to $Q$ ).

To compare the communities of each lake, data were weighted on the basis of the volumetric proportion of deep and shallow zones in each lake. In Lake 019, the deep zone represented .94 of the total lake volume, while the shallow accounted for .06. Similarly, in Lake 255 the deep represented .80 , the shallow .20 and in Lake 885 , the deep was .85 with the shallow. 15.

Because bottom detrital materials were frequently collected in zooplankton samples, lignin pink stain was added where necessary to assist in counting crustaceans.

Identification of mature cyclopoids and calanoids to species was based on the keys of Yeatman (1959) and Wilson (1959) respectively while Brooks (1957) was used as a reference for cladocerans. Adult copepods were classified into three categories, females, females with eggs, and
males whereas adult cladocerans were grouped as females, females with eggs, females with ephippia or males.

All copepodid instars were identified to species using size and morphological discriminants. Copepodids I through III (CI-III) were enumerated as one class with IV and V (CIV-V) as another. Nauplii were separated into either cyclopoid or calanoid categories (Harpacticoid nauplii were occasionally found and recorded separately). Cladoceran juvenile instars, combined as one category, were identified to the species level. Small or rare cladocerans were not all classified in such detail.

To estimate seasonal changes in community biomass, 10 ovigerous females of each species were randomly selected from each sample (i.e. 20 females from each zone), the eggs counted and body lengths measured, copepods from the anterior tip of the cephalothorax to the base of the caudal setae and cladocerans from the top of the head to the base of the shell spine. On the basis of the gravid female average weekly sizes, two overall seasonal mean lengths were calculated for each species, one representing the period when adults were noticeably larger (usually related to cooler water temperatures $<20^{\circ} \mathrm{C}$ ) and the other when animals were distinctly smaller (generally confined to warmer temperatures $>20^{\circ} \mathrm{C}$ ).
These seasonal mean values were then used to estimate the mean lengths of other developmental categories. For copepods,

$$
\begin{array}{ll}
\bar{L} \text { non-ovigerous females } & =\bar{L} \text { ovigerous female } \\
\bar{L} \text { males } & =.85 \bar{L} \text { ovigerous female } \\
\text { copepodid group CIV-V } & =.764 \mathrm{M} . \mathrm{A} . \mathrm{L} . \\
\text { copepodid group CI-III } & =.487 \mathrm{M} . \mathrm{A} . \mathrm{L} .
\end{array}
$$ where $\bar{L}=$ mean length in $m m$ M.A.L. $=$ mean adult length

To obtain these proportions, individual copepodid stages CI-VI of the most common species, Cyclops bicuspidatus thomasi and Diaptomus
siciloides, were measured on selected dates when all population elements were simultaneously present. A reasonably consistent ratio of 1.1 to 1.3 was found between the lengths of successive stages, in agreement with the 1.2 value generally recognized for crustacean moulting (Brooks 1886 cited from Teissier 1960, Gurney 1929) and which was adopted for defining the mature-immature relationship for all copepod species. For copepodid group CIV-V,

$$
\bar{L}_{\text {CIV }-V}=\frac{\frac{\text { M.A.L. }}{1.2}+\frac{\text { M.A.L. }}{1.2^{2}}}{2}=.764 \text { M.A.L. }
$$

and for group CI-III,

$$
\bar{L}_{C I-I I I}=\frac{M \cdot A \cdot L .}{1.2^{3}}+\frac{M \cdot A \cdot L .}{1.2^{4}}+\frac{M \cdot A \cdot L .}{1.2^{5}}=.487 \text { M.A.L. }
$$

3

The mean adult length (M.A.L.) was a weighted value based on the seasonal total numbers of gravid and non-gravid females plus mature males.

To the mean length of each copepodid category, the formula of Klekowski and Shushkina (1966 cited from Edmondson 1971), $W=0.055 L^{2.73}$ was applied giving an average wet weight ( $W$ in mg ) per individual and these values used to estimate zooplankton biomass on consecutive sampling dates. Nauplii wet weights were based on volumes approximated from mean length, width and depth measurements and on a specific weight of 1.0 .

For daphnid cladocerans,
$\bar{L}$ non-ovigerous females $=\bar{L}$ ovigerous females
$\bar{L}$ ephippial female $=$ determined from weekly measurements
$\overline{\mathrm{L}}$ male (mature $\&$ immature) $=.78 \overline{\mathrm{~L}}$ all females

## $\bar{L}$ immature female $=.51 \bar{L}$ mature female

These ratios were developed for measurements of 336 randomly selected immature and mature Daphnia schoedleri from Lake 885 on July 20 and September 16, 1976, and 83 specimens of Daphnia parvula from Lake 019 on June 2, 1976. A similar analysis was conducted for Bosmina longirostris in Lake 019 and results were applied to other similarly shaped smaller cladoceran species. The formula of Pechen ( 1965 cited from Edmondson 1971), $W=0.052 L^{3.012}$ for Daphnia spp., $W=0.124 L^{2.181}$ for Bosmina spp. and similarly shaped small cladocerans, and $W=0.092 L^{2.449}$ for Diaphanosoma leuchtenbergianum were used for cladoceran biomass estimates.

To verify the preceding group averaging approach for daphnid biomass determination, the average weight of $\underline{D}$. schoedleri females was also calculated from individual length-determined weights. The group approach was found to only slightly ( $5-9 \%$ ) underestimate zooplankton biomass, an error well within sampling and counting variance. Also, the application of a static size ratio to continually developing populations is acceptable on grounds that (1) on three separate occasions, calculated immature/ mature ratios were almost identical (. 51 June 2 Lake 019; . 50 July 20 Lake 885; . 52 September 16 Lake 885) and (2) with the abundance of gravid females regularly between 1 to $5 \%$ of the total D. schoedleri population, particularly in Lake 255, and average number of eggs per female between 1-2 during most of the reproductive period, recruitment was generally constant, usually favoring a relatively uniform size structure.

Copepod biomass estimates were also burdened with errors related to the assignment of fixed size ratios to groups CI-III and CIV-V. The magnitude of error was checked in Lake 885 on May 13 and 26, June 1 and 23 , 1976 by à length frequency analysis which yielded biomass values for
individual C.b. thomasi stages. Comparison with the "group averaging" method revealed differences in the range $\pm 5-30 \%$, tolerable when considering the application of an empirical formula rather than direct weighing to obtain biomass estimates.

## Physical and Chemical Measurements

A. Water temperature, Sechi disc visibility, ice and snow depth.

Lakes 019,255 and 885 occur within a 15 km radius of each other, lie at approximately the same elevation (550-600 m) and generally are subjected to the same climatic conditions. However, differences in seasonal water temperature, transparency and ice and snow depth were observed.

The upper 2 metre water layers of Lakes 019,255 and 885 had respective mean temperatures of $17.6,18.3$ and $17.7^{\circ} \mathrm{C}$ during the 1976 open water season (Figs. 4a,b,c). Noteworthy seasonal differences were found beginning in late March 1976 when Lake 255 appeared slightly warmer than Lakes 885 and 019. On the first ice-free sampling date in late April, the trend continued with an average temperature of $10.9^{\circ} \mathrm{C}$ in Lake 255 as compared to $7.7^{\circ} \mathrm{C}$ in Lake 019 and $8.2^{\circ} \mathrm{C}$ in Lake 885. During May, Lake 255 was still warmer than larger Lake 019 by about $2^{\circ} \mathrm{C}$ and smaller Lake 885 by approximately $1^{\circ} \mathrm{C}$. All three reached $20^{\circ} \mathrm{C}$ by early June and subsequently, until late August, showed basically similar trends with a cooling in mid-June, maximum temperatures near $24^{\circ} \mathrm{C}$ in early July, and a gradual decline throughout August. Mean upper water temperatures during this period were 20.5, 21.3 and $20.5^{\circ} \mathrm{C}$ in Lakes 019,255 and 885 respectively. Temperatures declined in late August falling to near $4^{\circ} \mathrm{C}$ by mid-October.

Following ice cover formation, on approximately November 15 for Lakes 255 and 885 and November 19 for Lake 019 , Lake 019 maintained an average $0-2 \mathrm{~m}$ temperature above $2.4^{\circ} \mathrm{C}$ as late as January 18, 1977. On the other hand, Lakes 255 and 885 , cooled below $2^{\circ} \mathrm{C}$ earlier in December and November respectively. Between mid-November 1976 and late March 1977, average upper

Figure 4a. Water temperature $\left({ }^{\circ} \mathrm{C}\right)$ of Lake 019, February 1976 to April 1977. Upper panels: Depth-time distribution of deep zone isotherms ( $2^{\circ} \mathrm{C}$ intervals except $1^{\circ} \mathrm{C}$ under ice). Mean stratum temperatures on sampling dates ( $\mathbf{\Delta}$ ) usually derived from profiles at 5 or 6 stations. Ice thickness ( $m$ ) indicated. Lower panels: $0-2 \mathrm{~m}$ shallow (....) and deep ( $-\ldots-$ ) zone mean water temperatures. Before noon samplings indicated as $B$, afternoons as A. 5 or 6 day period mean maximum and minimum air temperatures obtained from DOE weather in proximity of each lake.


Figure 4b. Water temperature $\left({ }^{\circ} \mathrm{C}\right)$ of Lake 255, February 1976 to April 1977. Descriptions as for Lake 019.


Figure 4c. Water temperature ( ${ }^{\circ} \mathrm{C}$ ) of Lake 885, February 1976 to April 1977. Descriptions as for Lake 019.


2 metre temperatures were $1.8,1.7$ and $1.3^{\circ} \mathrm{C}$ in Lakes 019,255 and 885 respectively. Mean bottom temperatures for the same period were $3.9^{\circ} \mathrm{C}$ in Lake $019,3.0^{\circ} \mathrm{C}$ in Lake 255 and $2.7^{\circ} \mathrm{C}$ in Lake 885 . Again, as in the preceding spring, Lake 255 was $2.6^{\circ} \mathrm{C}$ warmer than larger Lake 019 on the first ice free date in late April 1977. Lake 885 more closely resembled Lake 255 , being only $.6^{\circ} \mathrm{C}$ cooler.

Deep and shallow zone temperatures were significantly different only in Lake 019 during spring 1976 when shallow waters averaged $.5^{\circ} \mathrm{C}$ warmer from April 29 to June 2 and during winter when deep waters averaged about $.5^{\circ} \mathrm{C}$ warmer between December 1976 and March 1977.

Substantial vertical temperature differences were evident among the three lakes. Following ice out and vernal circulation, Lake 019 exhibited a temporary stratification on April 29, with temperature decreasing from 7.8 to $4.7^{\circ} \mathrm{C}$ between 4 and 5 meters. By mid May, waters were homothermal at $11.2^{\circ} \mathrm{C}$ but by late May stratification was re-established and persisted until the end of August. During this period, surface to bottom temperature differences ranged between $2.2^{\circ} \mathrm{C}$ to $9.8^{\circ} \mathrm{C}$ with an average of $6.1^{\circ} \mathrm{C}$. Division between upper, warmer mixed and deeper, cooler stagnant waters waivered between 4 and 6 meters throughout this period. After overturn in early September, vertical homothermy persisted until freeze up.

In contrast, Lake 255 was holomictic during most of the open water season. Brief periods of thermal layering were restricted to intense diurnal heating during July.

Although Lakes 885 and 255 were of comparable depth, Lake 885 was not as well mixed. Lake 885 stratified briefly in late April and then remained stratified with a top to bottom difference of up to $8.0^{\circ} \mathrm{C}$ from late May to mid-June. In contrast with deeper Lake 019, Lake 885 was affected by cool mid-June weather, resulting in vertical homothermy on June 17.

Whereas surface to bottom temperature differences during early July to mid-August never exceeded $2.5^{\circ} \mathrm{C}$ in Lake 255 , they were always greater than $3.2^{\circ} \mathrm{C}$ in 885 and often approached $5.0^{\circ} \mathrm{C}$. This difference occurred despite the early morning sampling of Lake 885 when cooler surface temperatures could be expected. In the second half of August, vertical temperatures equalized gradually through slow mixing. Strong mixing and cooling occurred between August 26-29 resulting in upward transport of anoxic bottom waters. In mid-September, during a short warm spell, some stratification occurred in Lake 885 wi.th a $3.7^{\circ} \mathrm{C}$ surface to sediment difference as compared to only $0.8^{\circ} \mathrm{C}$ in Lake 255.

After freeze-up, all three lakes stratified inversely as they continued cooling from the surface. By February 1977, with an insulating cover of snow and ice, Lakes 885 and 255 began to warm from the sediments. Deeper, less protected Lake 019 did not show signs of warming until late March.

A unique thermal inversion was measured beneath the melting ice cover of Lake 885 on April 13, 1977. Temperatures of $2.9,8.0,4.7,3.9$ were recorded at just under the ice layer, $1.0,2.0$ and 2.9 m respectively. This same phenomenon was also detected by other observers but its duration was not more than a few days.

Lake 255 was most transparent with $80 \%$ of mean Secchi values greater than 2.5 m (to the lake bottom) during the open water season (Fig. 5). Transparencies below 1.0 m were only found briefly in both spring periods. On the other hand, in Lake $88596 \%$ of Secchi readings were less than 2.5 m with $55 \%$ of these less than 1.0 m . Spring Secchi values of .5 m increased dramatically to over 3.0 m in the last quarter of June. Within a week, following a period of mixing, transparency again dropped below 1 metre, remaining low until early August when relatively high Secchi values, over 2.4 m were observed by September 1, 1976. Intermediate Secchi values were

Figure 5. Secchi disc visibility (m) in the deep zones of Lakes 019, 255 and 885, April to October 1976. Means and ranges usually derived from 5 or 6 stations. Arrows $(\downarrow)$ indicate lake bottom visibility.

characteristic of Lake 019 with $65 \%$ of readings between 1.0 and 2.0 meters. A pulsed pattern was noted on consecutive April to mid-June dates with transparencies gradually decreasing through the summer. The amplitude of seasonal changes in Lake 019 Secchi values was considerably smaller than in Lake 885, the range being . $65-1.65 \mathrm{~m}$.

Although some horizontal variation in Secchi visibility was noted among stations and between zones within each lake, in most cases, it was inconsistent and insignificant (Appendices A to C). In Lake 019, centred in a shallow bay adjoined by cultivated fields, station VD (Fig. 2a) generally had lower Secchi values during the period June 28 to August 24 $(\bar{x}=.99 \mathrm{~m})$. Also, the mean Secchi readings in four of six shallow stations for the same period were lower than the corresponding deep zone values.

During March 1977, Lake 019 was covered by the thinnest snow but thickest ice with average depths of 27 and 104 cm respectively (Figs. 4a, $\mathrm{b}, \mathrm{c}$ ). Deepest snow, 38 cms , found on Lake 255 , was associated with thinnest ice, averaging 60 cm . On Lake 885, snow and ice depths were intermediate with 29 cm and 85 cm respectively. The same trend in ice depth, 70 , 62 and 40 cm on Lakes 019,885 and 255 respectively was observed in February 1976 when snow mantles were generally deeper.
B. Dissolved Oxygen, Water Chemistry and Phytoplankton

Seasonal changes in dissolved oxygen are presented in Fig. 6, modified from Srisuwantach (1978). During the ice-free season, oxygen concentrations in Lake 255 were consistently near $10 \mathrm{mg} \mathrm{L}^{-1}$, surface to bottom, with saturation values always well above $80 \%$. In contrast, Lake 885 oxygen levels fluctuated widely, surface values ranging from $5.5 \mathrm{mg} \mathrm{L}^{-1}$ ( $61 \%$ saturation) on June 27 to $16.9 \mathrm{mg} \mathrm{L}^{-1}$ ( $190 \%$ saturation) on July 20. Near
bottom concentrations frequently departed from surface readings and were often below $50 \%$ saturation. Between August 15 and 24 a hot dry spell occurred with maximum air temperatures consistently above $26.7^{\circ} \mathrm{C}$ (August 23 was summer's warmest day at $35.0^{\circ} \mathrm{C}$ ). Trees surrounding most of Lake 885 allowed only slow mixing, insufficient to replenish oxygen combusted in decay of a collapsing Aphanizomenon bloom and the lake went "anoxic" on August 22. A sudden weather change with considerably cooler air temperatures $\left(15^{\circ} \mathrm{C}\right)$ rain and strong northwest winds occurred between August 27 and 29, thus improving oxygen levels. By August 29 , central lake bottom and surface oxygen concentration were 2.2 and $3.9 \mathrm{mg} \mathrm{L}^{-1}$ respectively with further amelioration to $5.7 \mathrm{mg} \mathrm{L}^{-1}$ at the surface by August 31. More rain during the first week of September helped to restore oxygen to normal levels.

In deeper Lake 019, which remained stratified for extended periods during open water bottom strata were usually anoxic. However, in surface waters, oxygen was always plentiful usually well above $70 \%$ saturation.

Beneath winter ice, oxygen levels declined most rapidly in Lake 885 to less than $2.5 \mathrm{mg} \mathrm{L}^{-1}$ (17\% saturation) by mid December. On February 15, 1977, no oxygen was detected below 1 m with only $0.6 \mathrm{mg} \mathrm{L}^{-1}(4.2 \%$ saturation) immediately under ice. On April 13, central lake bottom oxygen concentrations had risen to $1.2 \mathrm{mg} \mathrm{L}^{-1}$ and supersaturation ( $26.1 \mathrm{mg} \mathrm{L}^{-1}$ ) was observed at 1.0 m beneath the ice. Oxygen depletion proceeded more slowly in Lake 255 with levels still elevated ( $9.9 \mathrm{mg} \mathrm{L}^{-1}$ or $75 \%$ saturation) in mid December. During late March, in both years, twice as much oxygen was measured in Lake 255 than in Lake 885 with 1.5 and $0.8 \mathrm{mg} \mathrm{L}^{-1}$ just beneath the ice, respectively. Deeper Lake 019 usually carried more than $5.0 \mathrm{mg} \mathrm{o}{ }^{2} \mathrm{~L}^{-1}$ in its upper strata through both winters. Some annual variation, however, was "

Figure 6. Dissolved oxygen concentrations ( $\mathrm{mg} \mathrm{O}_{2} \mathrm{~L}^{-1}$ ) in the deep zone ( $0-2 \mathrm{~m}$ or $0-3 \mathrm{~m}$ layer and the bottom) of Lakes 019, 255 and 885, February 1976 to April 1977 (modified after Srisuwantach 1978).

noted in bottom layers with more oxygen during February - March 1977 than
in the corresponding 1976 period.
Seasonal chemical profiles clearly reflected the degree of water circulation within each lake (Srisuwantach 1978). By comparing four chemical parameters on approximately the same date during August, it was apparent that Lake 255 was vertically uniform while Lakes 885 and 019 exhibited significant differences between surface and bottom values (Table 2). All four parameters displayed similar trends during most of the summer. Mean concentrations of total dissolved phosphorus (TDP), total dissolved nitrogen (TDN) and dissolved organic carbon (DOC) in Lake 885 during July-August were approximately double those in Lakes 255 and 019 (Table 3). Mean mid-summer values of gross primary production were very high in Lakes 885 ( $3863 \mathrm{mg} \mathrm{C} \mathrm{m}^{-2} \mathrm{day}^{-1}$ ) and 019 ( $2810 \mathrm{mg} \mathrm{C} \mathrm{m}^{-2}$ day ${ }^{-1}$ ) but somewhat lower ( $631 \mathrm{mg} \mathrm{C} \mathrm{m}{ }^{-2}$ day $^{-1}$ ) in Lake 255. Contributing to the extreme productivity in Lake 885 was the overwhelming predominance $96.7 \%$, of Aphanizomenan flos-aquae. Seasonal chlorophyll-a concentrations (Fig. 7 from Srisuwantach 1978) were usually highest in Lake 885 and lowest in Lake 255 with moderate amounts in Lake 019. Minimum values in Lake 885 occurred during late June and October through February while lowest values in Lake 255 were found December through February 1977. Extremely high $\left(260 \mu \mathrm{~g}^{-1}\right)$ chlorophyll-a levels were observed in Lake 885 during July whereas maximums in Lake 019 and 255 were much lower at 42 and 18.9 $\mu \mathrm{g} \mathrm{L}^{-1}$ respectively. Annual average values were 39,22 and $7 \mu \mathrm{~g}$ chloro-phyll-a $L^{-1}$ in Lakes 885,019 and 255 respectively.

Algal biomass displayed a general seasonal bimodality in all three lakes (Fig. 8 modified from Kling unpublished) with an initial May pulse declining in response to cool, wet weather during June followed by a second increase peaking during July - August. In Lake 255, biomass was

Table 2. Vertical profiles of total dissolved phosphorus (TDP) and total dissolved nitrogen (TDN) ( $\mu \mathrm{g} \mathrm{L}^{-1}$ ), dissolved organic carbon (DOC) and dissolved oxygen (DO) (mg L-1) in Lakes 019, 255 and 885 in early August 1976 (after Srisuwantach 1978).


Table 3. Average water column nutrient concentrations, gross and net primary production and respiration (mg $\mathrm{Cm} \mathrm{m}^{-2}$ day ${ }^{-1}$ ), and phytoplankton species percent composition in Lakes 019, 255 and 885 during July-August 1976 (modified from Srisuwantach 1978).

|  | 255 | 019 | 885 |
| :---: | :---: | :---: | :---: |
| TDP $\mu \mathrm{g} \mathrm{L}^{-1}$ | 25.50 | 26.73 | 57.64 |
| TDN $\mu \mathrm{g} \mathrm{L}^{-1}$ | 1460.63 | 1297.25 | 2401.5 |
| DOC mg $\mathrm{L}^{-1}$ | 17.91 | 15.17 | 23.20 |
| Gross Primary Production (G.P.) | 631 | 2810 | 3863 |
| Net Primary Production (\% of G.P.) | $\begin{array}{r} 281 \\ 45 \end{array}$ | 667 24 | 1478 38 |
| $\begin{aligned} & \text { Respiration } \\ & \text { (\% of G.P.) } \end{aligned}$ | $\begin{array}{r} 350 \\ 55 \end{array}$ | 2143 76 | $\begin{array}{r} 2385 \\ 62 \end{array}$ |
| Phytoplankton <br> Cyanophyta | 58.1\% | 22\% | 96.7\% |
| Chlorophyta | 6.6\% | 7\% | 0.8\% |
| Euglenophyta | - | 3\% |  |
| Chrysophyceae | - | 16\% | - |
| Diatomeae | 9.0\% | 29\% | 2.5 |
| Crytophyceae | 6.8\% | 5\% | 2.5\% |
| Peridineae | 19.5\% | 18\% | - |



Figure 7. Chlorophyll-a concentrations ( $\mu \mathrm{g} \mathrm{L}^{-1}$ ) from integrated samples over 0-2 m Lakes 019, 255 and 885, February 1976 to February 1977 (after Srisuwantach 1978).


Figure 8. Seasonal changes in algal and protozoan biomass ( $\mu \mathrm{g}$ wet weight $L^{-1}$ ) in the deep zones of Lakes 019,255 and 885, February 1976 (modified after Kling, unpublished).

consistently an order of magnitude lower except briefly in May. During July, biomass increased rapidly in Lake 885, reaching levels two orders of magnitude higher than in Lake 255 but by late August had fallen sharply.

Seasonal protozoan biomass basically displayed a similar bimodal pattern in all lakes except that levels were lowest in Lake 885 and highest in Lake 019.

## Lake 019 Fish Population Estimates

The five seining net hauls taken from various shore sites around Lake 019 yielded two species, Pimephales promelas and Culaea inconstans in the proportion 9.3:1 with an estimated combined density of 86,400 fish per hectare (55,600-117,200 95\% C.I.), certainly an underestimate as smaller juveniles were not all retained by the $\frac{17}{4 \prime \prime}$ mesh net (Table 4). Since an attempt to gain abundance estimates from the open water region using a Miller sampler was unsuccessful, the only recourse was extrapolation from near shore values. Assuming possible inshore/offshore density ratios varying between $1 / 0,1 / 1$ and $3 / 1$, minimum population estimates ranged from 4300 to 86000 fish ha ${ }^{-1}$. This approach could only provide a rough comparison with the 1500 trout ha-1 stocked in Lakes 885 and 255 but clearly differences were significant.

## Zooplankton

A. Precision of community and population estimates

Results of the Shapiro-Wilks test indicated a normal horizontal variance in all three lakes $\left(W_{.99}=.91\right.$ and .95 in the deep zones at Lakes 019 and 255 respectively and $W=.98$ in both shallow and deep zones of Lake 885). Mean total community abundance could be estimated within

Table 4. Estimates of the relative abundance of Pimephales promelas and Culaea inconstans in Lake 019 during 1976-1977.


[^0]| Species | $\begin{gathered} 019 \text { (July 27/77) } \\ \mathrm{D} \\ \mathrm{n}=12 \end{gathered}$ | $\begin{gathered} 255(\text { July 26/77) } \\ \text { D } \\ n=11 \end{gathered}$ | $\begin{aligned} & \text { Shallow } 885 \text { (Aug } \\ & \mathrm{n}=10 \end{aligned}$ | $\begin{gathered} \text { Deep } \\ n=10 \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: |
|  |  | $9.91 \pm 3.95$ (40\%) | $30.10 \pm 11.52$ (38\%) | $16.84 \pm 5.33(32 \%)$ |
| Cyclops bicuspidatus th. | $16.87 \pm 5.49$ (33\%) | $9.91 \pm 3.95$ (40\%) |  | - |
| Tropocyclops prasinus m. | $11.33 \pm 3.48$ ( $31 \%$ ) | $\pm$ |  | - |
| Mesocyclops edax | - | $20.48 \pm 8.90$ ( $40 \%$ ) | $15.59+9.09$ (58\%) | $32.05 \pm 4.71$ (15\%) |
| Cyctopoid nauplii | $44.77 \pm 7.04$ (16\%) | $56.14 \pm 19.10$ (34\%) | $15.59 \pm 9.09$ (58\%) |  |
| Diaptomus siciloides | $52.96 \pm 17.59$ ( $33 \%$ ) | $43.97 \pm 19.46$ (44\%) | - |  |
| Diaptomidae nouplii | $28.07 \pm 5.94$ ( $21 \%$ ) | $11.20 \pm 2.62$ (23\%) |  | - |
| Daphnia parvula | $3.15 \pm 1.69$ (54\%) | - - 3.98 (24\%) |  | - |
| Daphnia rosea | - | $16.36 \pm 3.98(24 \%)$ | $7.31 \pm 6.36$ (87\%) | $12.13 \pm 6.66$ ( $55 \%$ ) |
| Daphnia schoedleri | - | $15.88 \pm 3.38$ (21 |  | - |
| Bosmina longirostris | $122.35 \pm 26.69$ (22\%) | - |  |  |
| Ceriodaphnia lacustris | $1.80 \pm 1.13$ (63\%) | - - |  |  |
| Chydorus sphaericus | - | $1.45 \pm 0.58$ ( $40 \%$ ) | $54.46 \pm 13.12$ (24\%) | $62.2 \pm 9.41$ (15\%) |
| Total Community | $283.59 \pm 48.53$ (17\%) | $178.10 \pm 45.09$ (25\%) | $54.46 \pm 13.12$ (24\%) |  |

$\stackrel{\rightharpoonup}{0}$

17-25\% (95\% C.I.) (Table 5) and mean population densities of common species within $16-44 \%$. Comparison of these confidence intervals with the means and ranges obtained from each pair of seasonal composite samples confirmed the adequacy of the systematic approach since ranges were generally well within those of the "pilot" surveys.
B. Annual Mean Abundance and Biomass of Zooplankton in Lakes 019, 255 and 885

Total Lake Plankton

1. Total community

A total of 25 crustacean species, 12 copepods and 13 cladocerans were identified in the annual zooplankton communities of the study lakes. In Lake 255, 21 species ( 11 copepods and 10 cladocerans) were recorded, 18 ( 7 copepods and 11 cladocerans) in Lake 019 and 15 ( 9 copepods and 6 cladocerans) in Lake 885 (Table 6).

Of the 25 species found (excluding harpacticoid nauplii), 10 were common to all three lakes, four additional ones common to both Lakes 885 and 255 and four others found in Lakes 019 and 255. Seven species were found exclusively in either Lake 255 or 019. According to Raabe's (1952) percent similarity index, the communities of Lakes 885 and 255 were most similar ( $54.6 \%$ ) those of Lakes 885 and 019 the least similar ( $10.1 \%$ ) with a $30.8 \%$ similarity between Lakes 255 and 019.

Although Lake 885 had the fewest number of species, its mean annual zooplankton density of 289.74 and $L^{-1}$ was approximately double that of both Lake 255 at 149.55 and Lake 019 at 124.35 ind $L^{-1}$. With abundance expressed per $\mathrm{cm}^{2}$, the 59.5 ind $\mathrm{cm}^{-2}$ in Lake 885 remained twice the 26.3 ind $\mathrm{cm}^{-2}$ in Lake 255. However, because of Lake 019's greater mean depth its 56.3 ind $\mathrm{cm}^{-2}$ were closer to abundances in Lake 885. Lake 885's annual mean total biomass of 10.33 mg wet weight $L^{-1}$ was about double that of Lake 255 at
 255 AND $\$ 5$, APRIL 1976-APRIL 197, GROUPINGS REFECT SPECIES COMTON TO ALL OR PAIRS OF LNEES. LAKE TOTAL EXCLDES HAPPACTOID NULPLI.

|  | Density (ind $\mathrm{L}^{-1}$ ) |  |  | Biomass (mgww ${ }^{-1}$ ) |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 019 | 255 | 885 | 015 | 255 | 885 |
|  | $9.69(14.28)$ | 44.98 (53.68) | 157.10 (90.85) | . 310 (16.51) | . 844 (18.33) | 1.905 (18.64) |
| Lops bicuspidars thorasi | 9.69 (14.28) | 4.88 (5.6) | . 06 | . 016 (.89) | . 038 (.82) | . 004 (.04) |
| LPPS VERNLLIS | . 99 (1.46) | 36 (1.15) | . 30 (.06) | . 006 (.31) | . 084 (1.83) | . 003 (.03) |
| YeLops Aglis | . 18 (.26) | . 46 (2.94) | . 10 (.06) | . 006 (.3) | . 017 ( .37$)$ | . 015 (.15) |
| Rocrclops anidus | 0.01 (.01) | .21 (.25) | . 12 (.07) | . 001 (2.01) |  | . 020 |
| LOPOID MUPLII | 14.38 | . 69 | 106.34 | . 009 | . 008 | . 002 (.02) |
| PTaws sicilides | 29.63 (34.21) | 18.90 (18.24) | . 03 (.02) | 1.079 (56.87) | . 991 (21.54) | . 084 (.82) |
| PTons Leptopus | 0.01 (-.01) | . 27 (.26) | . 28 (.23) | . 001 (<.01) | .081 (1.7) |  |
| ANOID Malplil | 13.04 | 9.21 | . 42 | . 013 | . 009 | . 020180 |
| XNIA SCHoedileri | . 01 (c.01) | 9.02 (5.97) | 25.15 (8.68) | . 001 (<.01) | 1.873 (40.38) | 8.292 (80.26) |
| HNIA Scherumi | 40.16 (32.20) | . 08 (.05) | .08(.03) | . 211 (10.99) | . 001 (.02) | . 001 (.01) |
| sMINA LONGIROSTRIS | 0.01 (<.01) | 3.07 (2.04) | 0.01 (<.01) | . 001 (<.01) | . 255 (5.51) | . 001 (<.01) |
| PANIA ROSEA | 0.01 (..0) | . 03 (.02) | 0.01 (<.01) | .181 (9.43) | . 001 ( $(.01$ ) | . 001 (<.01) |
| praia parvea | 8.32 (6.67) |  | . 12 (.04) | . 001 (<.01) | . 001 (c.01) | . 001 (<.01) |
| RPACTICOID NUPLII | . 38 (.30) |  | .12 (.04) | . 001 (.01) |  |  |
|  |  | 1.43 (1.71) | . 03 (.02) |  | .008 (.17) | . 001 (.01) |
| COPPS VARICANS RUBELLUS |  | . 02 (.02) | . 01 (<.01) | - | . 001 (<.01) | . 001 (c.01) |
| IAPTOMS MCOUS |  | . 02 (.02) | . 01 (<.01) | - | . 001 (c.01) | . 001 (<.01) |
| intans oreconevis | - | O1 (.01) | . 03 (.01) | - | . 033 (.71) | . 003 (.03) |
| ERIODAPNIA OLANRAGGLA | - | . 75 (.50) |  |  |  |  |
|  | . 01 (2.01) | 7.39 (4.90) | - | . 001 (<0.1) | . 044 (.95) |  |
| InPorus Sphaericus | $.11(.09)$ | 5.79 (3.84) | - | . 001 (.05) | . 059 (1.27) |  |
| Lena rectanzla | 1.18 (.95) | . 01 (.01) | - | . 015 (.78) | . 001 (<.01) | - |
| ERIOOAPPNIA LaCUSTRIS | . 29 (.23) | . 30 (.20) | - | . 017 (.89) | . 026 (.56) | - |
| Dapania mask | . 01 (<.01) | - | . 01 (<0.1) | . 001 ( $\times .01$ ) | - - | . 001 (<.01) |
| Tropecraops Ppasinus Mexicanus | 6.31 (9.29) | - | - | . 061 (3.23) | - |  |
| Pacrotrix laticornis | . 07 (.06) | - |  | . 001 (.05) |  |  |
| Sida cristalina | . 01 ( 6.01 ) |  |  | .001 (<.01) | 168 (3.64) |  |
| Hesocrcliops max | - | 2.00 (2.39) |  |  | . 099 (2.13) | - |
| ACANTHDIAPTOUS DENICOPNIS | - | . 97 (.93) |  |  |  |  |
| Sitccepraus vetuus | - | . 01 (<0.1) | - |  | . 001 (<.01) |  |
|  |  | 150.90 (100.00) | 289.86 (100.00) | 1.920 (100.00) | 4.638 (100.00) | 10.330 (100.00) |
| $\text { ino } \mathrm{cm}^{2}$ | 56.27 | 26.28 | 59.53 | . 934 | . 838 | 1.857 |

4.64 and five times that of Lake 019 at $1.92 \mathrm{mg} \mathrm{L}^{-1}$.

## 2. Individual species

The 10 species common to all three lakes, Cyclops bicuspidatus thomasi, Cyclops vernalis, Eucyclops agilis, Macrocyclops albidus, Diaptomus siciloides, Diaptomus leptopus, Daphnia schoedleri, Daphnia rosea, Daphnia parvula and Bosmina longirostris accounted for the bulk of mean annual crustacean abundance in Lakes 885, 255 and 019 at 99.9, 89.4 and $85.5 \%$ respectively.

In Lake 885, only two, C. $\mathbf{B}$. thomasi and D. Schoedleri, were prominent at 90.9 and $8.7 \%$ of total abundance respectively. Their contributions to community biomass were strikingly reversed with $\underline{D}$. schoedleri representing $80.3 \%$ and C.b. thomasi $18.6 \%$. C. b. thomasi was also a dominant plankter in Lake 255 at $53.7 \%$ and Lake 019 at $14.3 \%$ of total crustacean abundance. D. schoedleri was relatively common in Lake 255 at $6.0 \%$ but was rarely found in Lake 019 (. $01 \%$ annual mean abundance).

In Lake 019, D. siciloides ( $34.2 \%$ ) and B. longirostris ( $32.2 \%$ ) were the most abundant species, although as biomass, the contribution of $\underline{D}$. siciloides at $56.9 \%$ was most significant with B. longirostris at $11.0 \%$. Two final species, Tropocyclops prasinus mexicanus, exclusive to Lake 019, and D. parvula accounted for $9.3 \%$ and $6.7 \%$ of zooplankton numbers and $3.2 \%$ and $9.4 \%$ of biomass respectively.

In Lake 255 , D. siciloides was the second most abundant crustacean after C.b. thomasi, at $18.2 \%$ of the total abundance and $21.5 \%$ of annual . biomass. D. schoedleri held the largest share, $40.4 \%$ of biomass in Lake 255. D. rosea, a second cladoceran which was fairly common, shared $2.0 \%$ of the community density and $5.5 \%$ of the biomass.

Lake 885 possessed two dominant species (those contributing more than $5 \%$ on an annual basis), C.b thomasi and D. schoedleri. Three dominants, C. ․ . thomasi, D. siciloides and D. schoedleri occurred in Lake 255 while Lake 019 contained five, D. siciloides. B. longirostris, C.b. thomasi, I.p. mexicanus and D. parvula. Further, a simple indication of relative community diversity was given by the number of species sharing at least $1 \%$ of annual community totals. In terms of abundance, Lake 255 was most diverse with 10 species, Lake 019 had six and Lake 885 only two. Similarly at least $1 \%$ of annual biomass was held by 9 species in Lake 255, five in Lake 019 and two in Lake 885.

## 3. Taxonomic groups

The share of community abundance and biomass held by cyclopoids, calanoids and cladocerans varied among the lakes. Cyclopoids accounted for $91.0 \%$ (263.75 ind $L^{-1}$ ) of total mean annual abundance of zooplankton in Lakes $885,62.7 \%$ ( 93.7 ind $L^{-1}$ ) in Lake 255 and $25.4 \%$ ( 31.5 ind $L^{-1}$ ) in Lake 019 (Fig. 9). Calanoids were most prevalent in Lake 019 at $42.67 \mathrm{ind}^{-1}$ or $34.3 \%$ of the annual value, less abundant in Lake 255 at 29.38 ind $L^{-1}$ ( $19.6 \%$ ) and scarce in Lake 885 at .73 ind $L^{-1}(0.3 \%)$. Cladocerans decreased in importance from 50.13 ind $L^{-1}(40.3 \%)$ in Lake 019 to 26.44 ind $L^{-1}$ ( $17.7 \%$ ) in Lake 255 and 25.26 ind $L^{-1}(8.7 \%)$ in Lake 885. Thus, while the communities of Lakes 885 and 255 were numerically dominated by cyclopoids, that in Lake 019 was more equally divided among the three crustacean groups.

These trends in abundance were not all repeated by biomass values. Cladocerans, rather than cyclopoids were the major group in both Lakes 885 and 255 , with $80.3 \%$ and $49.4 \%$ of total community biomass respectively while calanoids constituted over half ( $56.9 \%$ ) of the biomass in Lake 019.

Figure 9. Annual mean relative abundance and biomass of cyclopoids, calanoids and cladocerans in Lakes 019, 255 and 885, April 1976 to April 1977.


Cyclopoids forms a rather consistent part, between 19 and $25 \%$ of the biomass in all three lakes.

## Deep and Shallow Zone Plankton

## 1. Total community

Because differences between deep and shallow zone plankton could depend on the composition and abundance of vegetation, surveys of macrophyte development in each lake were conducted during August 1976. Vegetation was most abundant and diverse in Lake 255 with emergent Typha and Scirpus spp. growing in 10-15 m wide bands near shore. Submergent Ceratophyllum sp., Myriophyllum sp., Potamogeton sp. and Chara sp. covered most of the lake bottom except in regions below the 2.5 m isobath. Stands of Scirpus sp., occasionally extending 22 m offshore, were the dominant element in Lake 019 but quantities were proportionally smaller than in Lake 255 and submerged vegetation was restricted close to shore. In Lake 885, narrow, usually less than 6 m wide, discontinuous strips of Typha sp. and Carex sp . surrounded most of the shore with thin scattered patches of submerged Chara sp. also present. Proportional to lake surface area, vegetative development in Lake 885 ranked third below that in Lake 255.

Interzonal differences in mean annual crustacean density were largest in Lake 255 with roughly double the concentration, 217.1 ind $L^{-1}$, in the shallow than in the deep zone, 133.8 ind $L^{-1}$ (Fig. 10). In Lake 019, the pattern was reversed with 1.5 times higher densities in the deep zone (126.8 ind $L^{-1}$ )than near shore ( 85.8 ind $L^{-1}$ ) No horizontal differences were seen in Lake 885 with 286.3 and 290.6 ind $L^{-1}$ in the shallow and deep zones respectively. Distribution of biomass corresponded with abundance in Lakes 255 and 019 but not in Lake 885. Mean annual biomass was greater in the shallow zone ( $5.70 \mathrm{mg} \mathrm{L}^{-1}$ ) of Lake 255 than in its deep zone ( $4.37 \mathrm{mg} \mathrm{L}^{-1}$ )

Figure 10. Annual mean crustacean zooplankton community abundance (ind $L^{-1}$ ) and biomass (mg w w L-1) in the shallow and deep zones of Lakes 019, 255 and 885, April 1976 to Apri1 1977.

and in Lake 019 's deep ( $1.98 \mathrm{mg} \mathrm{L}^{-1}$ ) than in its shallow zone ( $1.04 \mathrm{mg} \mathrm{L}^{-1}$ ). In Lake 885 , near shore biomass ( $21.70 \mathrm{mg} \mathrm{L}^{-1}$ ) was almost three times higher than offshore ( $8.32 \mathrm{mg} \mathrm{L}^{-1}$ ).

## 2. Taxonomic groups

Cyclopoids appeared evenly distributed between the deep and shallow zones of Lakes 019 and 885 with slightly higher densities in the shallow region of Lake 255 (Fig. 11). Calanoids were more numerous in the deeper regions of Lakes 019 and 255 but were centered closer to shore in Lake 885. Cladocerans were almost twice as abundant offshore in Lake 019 while in Lakes 255 and 885 inshore concentrations were higher, by 4.8 and 2.3 times respectively. The horizontal distribution of group biomass was generally similar to abundance. An exception was the greater spatial uniformity of cladoceran biomass than abundance in Lake 255.

## 3. Individual species

In all three lakes, no species were found exclusively in either zone throughout the year. Certain species, however, tended to concentrate more in one zone than the other (Table 7). In Lake 255, a relatively high proportion of primarily littoral species i.e. C. quadrangula, C. varicans, E. agilis, M. albidus, C. vernalis, C. sphaericus and A. rectangula occurred. The latter two species were respectively 9.3 and 30.1 times more dense near shore and were responsible for most of the zonal difference. D. siciloides, averaging 20.9 ind $L^{-1}$ offshore and 10.8 ind $L^{-1}$ inshore was the only dominant form concentrated more in the deep zone of Lake 255.

In Lake 019, significantly fewer eulittoral species, i.e. E. agilis, M. laticornis and A. rectangula, were collected and only in low amounts. Dominants B. longirostris, D. siciloides, ․ ․ . thomasi and D. parvula were

Figure 11. Annual mean abundance (ind $L^{-1}$ ) and biomass ( $m g w w L^{-1}$ ) of cyclopoids, calanoids and cladocerans in the shallow and deep zones of Lakes 019, 255 and 885, April 1976 to April 1977.


Table 7. Shuliow to deep zone ratios of mean anlal species density and biomass in Lakes 019, 25 and 885, April i976-April. 1977.

| Species | 019 |  | 255 |  | 885 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Abundance | Biomass | Abundance | Biomass | Abundance | Biomass |
| Cyclops bieuspidatue thomasi | $\frac{5.69}{9.95}=.6$ | $\frac{.108}{.325}$ - 3 | $\frac{42.68}{45.53}=.9$ | $\frac{.834}{.846}=1.0$ | $\frac{110.16}{105.46}=.7$ | $\frac{1.282}{2.015}=.6$ |
|  |  |  | $\frac{3.70}{}=13.7$ | $\frac{.132}{132}=11.0$ | $\frac{.24}{-03}=8.0$ | $\frac{.012}{002}=6.0$ |
| Cychope vermatis | $\frac{1.25}{.97}=1.3$ | $\frac{.020}{.016}=1.3$ | ${ }^{3} .27=13.7$ | . 012 - 11.0 |  |  |
| Eucyclops agilis | $\frac{.58}{16}=3.6$ | $\frac{.017}{.005}=3.4$ | $\frac{9.41}{.72}=13.1$ | $\frac{.315}{.027}=11.7$ | $\frac{.48}{.03}=16.0$ | $\frac{.017}{.001}=17.0$ |
| Nacrocyolops albidus | - 01. | <. 001 | $\frac{.79}{.06}=13.2$ | $\frac{.060}{.005}=12.0$ | $\frac{.27}{.10}=2.7$ | $\frac{.041}{.011}=3.7$ |
| cyalopoid nauplii | $\frac{12.05}{14.49}=.8$ | $\frac{.007}{.009}=.8$ | $\frac{56.16}{38.14}=1.5$ | $\frac{.011}{.007}=1.6$ | $\frac{125.41}{102.96}=1.2$ | $\frac{.024}{.019}=1.3$ |
| Dicptarus aioiloides | $\frac{17.92}{29.96}=.6$ | $\frac{.622}{1.108}=.6$ | $\frac{10.80}{20.93}=.5$ | $\frac{.568}{1.096}=.5$ | < $\frac{.01}{.08}=.1$ | < $\frac{.001}{.003}=.1$ |
| Diaptamus Leptopus | 29.96 -0.01 - | -. 001 | $\frac{.49}{.21}=2.3$ | $\frac{.169}{.059}=2.9$ | $\frac{.29}{.27}=1.1$ | $\frac{.083}{.083}=1.0$ |
| Dieptomidae nauplii | $\frac{12.12}{13.10}=.9$ | $\frac{.012}{.013}=.9$ | $\frac{8.32}{9.43}=.9$ | $\frac{.008}{.009}=1.1$ | $\frac{.78}{.36}=2.2$ | $\begin{aligned} \frac{.001}{.001} & =1.0 \\ 20.231 & =3.3\end{aligned}$ |
| Daphnia schoedleri | $\frac{8.01}{<-01}=1.0$ | $e_{<.001}^{<.001}=1.0$ | $\frac{10.32}{7.97}=1.3$ | $\frac{2.066}{1.810}=1.1$ | $\frac{47.57}{21.19}=2.2$ | $\begin{aligned} \frac{20.231}{6.182} & =3.3 \\ 007 & =35.0\end{aligned}$ |
| Bosmina Longirostris | $\frac{22.14}{41.3!}=.5$ | $\frac{.114}{.217}=.5$ | $\frac{.07}{.08}=.9$ | $\frac{.001}{.001}=.3$ | $\frac{.52}{.01}=52.0$ | $\frac{.007}{2.001}=35.0$ |
| Daphnia rasea | - | <.001 | $\frac{7.60}{2.66}=2.9$ | $\frac{.667}{.166}=4.0$ | c.01 | ¢.001 |
| daphnia parsula | $\frac{1.85}{8.73}=.2$ | $\frac{.020}{.192}=.1$ | $\frac{.05}{.02}=2.5$ | <.001 001 - 3 | . 01 | . 001 |
| Cyclope varicans mubellus | - | - | $\frac{5.14}{.50}=10.3$ | $\frac{.025}{.003}=8.3$ | $\frac{.05}{.03}=1.7$ | $\frac{.001}{. .001}=.3$ |
|  | - | - | . $07=23.3$ | $\frac{.008}{001}=26.7$ | $\times .01$ | $\times$ |
| Diaptomus nucus |  |  |  |  |  |  |
| Diçtarnus oregonensis | - | - | . 07 |  | <. 01 | <. 001 |
| ceriodaphnia quadrangula | - | - | $\frac{2.57}{.29}=8.9$ | $\frac{.107}{.016}=6.7$ | $\frac{.07}{.03}=2.3$ |  |
| Chydorus ephaericus | $\frac{2.01}{201}=1.0$ | - 2.001 - 001.0 | $\frac{25.22}{2.11}=9.3$ | $\frac{.157}{.016}=9.8$ | - | - |
| Alona rectangula | $\frac{1.04}{.05}=20.8$ | $\frac{.007}{\times .001}=23.3$ | $\frac{25.54}{.85}=30.1$ | $\frac{.257}{.009}=28.6$ | - | - |
| Ceriodaphnia lacustris | $\frac{.79}{1.20}=.7$ | $\frac{.010}{.015}=.7$ | -01 - | <.001 | - |  |
| Diaphanosoma Veuchtenbergianum | $\frac{.11}{.30}=.4$ | $\frac{.006}{.017}=.4$ | $\frac{.17}{.33}=.5$ | $\frac{.015}{.029}=.5$ | - | - |
| Daphnia magna | $\stackrel{.01}{-}$ - | $\stackrel{0}{001}-$ | - | - | - 0.01 | $\stackrel{\square}{8.001}$ |
| Tropocyclops prasimus maxiocmus | $\frac{8.30}{6.18}=1.3$ | $\frac{.085}{.059}=1.5$ | - | - | - | - |
| Macrothrix Latioomie | $\frac{.63}{.04}=15.8$ | $\frac{.011}{.001}=11.0$ | - | - | - |  |
| sida erystallina | $\stackrel{.01}{-}$ | <. 001 | - | - | - | - |
| Hesocyclope edar | - | - | $\frac{2.04}{1.98}=1.0$ | $\frac{.159}{.169}=.9$ | - | - |
| Aconthodiaptomus denticornis | - | - | $\frac{1.12}{.86}=1.3$ | $\frac{.135}{.090}=1.5$ | - | - |
| Simocephalue vetulus | - | - | <.01 - | $\stackrel{001}{-}$ | - | - |
| Earpactiooid nouplit | $\frac{1.34}{.32}=4.2$ | $\frac{.001}{<.001}=3.3$ | $\frac{4.74}{.29}=16.3$ | $\frac{.003}{<.001}=20.0$ | $\frac{.43}{.06}=7.2$ | $\frac{.001}{<.001}=10.0$ |
| Total annual mean ind $L^{-1}$ | $\frac{85.81}{126.76}=.68$ | $\frac{1.041}{1.977}=.53$ | $\frac{217.08}{133.84}=1.62$ | $\frac{5.703}{4.37 I}=1.30$ | $\frac{286.28}{290.56}=.99$ | $\frac{21.703}{8.320}=2.61$ |

respectively $1.9,1.7,1.8$ and 4.7 times more numerous offshore while only I.p. mexicanus was 1.3 times more abundant nearshore.

In Lake 885 , populations of E. agilis and C. vernalis, though low in numbers, were found primarily near shore with abundances of diaptomidae nauplii, D. schoedleri, and M. albidus also generally higher, about 2.5 times, in the shallow than in the deep zone. C.b. thomasi, D. leptopus, and cyclopidae nauplii were distributed relatively evenly throughout the lake.

Zonal variation of individual species biomass was generally consistent with abundance. Comparison of abundance and biomass, shallow to deep ratios, however, revealed a few noteworthy exceptions. In Lake 019, although $\underline{C}$. thomasi was about 1.8 times more numerous offshore, its deep zone biomass was 3.0 times greater than its shallow values. Similarly, D. parvula, with densities 4.7 times higher offshore had 9.6 times more biomass in the deep than shallow zone. In Lake 885, D. schoedleri, 2.2 times more abundant near shore, exhibited 3.3 times as much biomass near than offshore.
C. Seasonal Crustacean Community in Lakes 019, 255 and 885

Total Lake Zooplankton Community
Seasonal community dynamics in Lakes 885,255 and 019 were distinctly different (Fig. 12). In Lake 885, extremely high late May densities, 1515 ind $L^{-1}$, were over three times those found in Lakes 019 and 255. Plankton abundance declined through most of the summer in Lake 885 , except for a small pulse in early August, until a minimum ( 60.9 ind $L^{-1}$ ) occurred in late August coincidentally with a period of oxygen depletion. The community recovered rapidly to 469.5 ind $L^{-1}$ by mid September. Densities then fell gradually to less than 1.0 ind $L^{-1}$ in January and remained

Figure 12. Seasonal changes in crustacean zooplankton community abundance (ind $\mathrm{L}^{-1}$ ) and biomass (mg w w $\mathrm{L}^{-1}$ ) in Lakes 019, 255 and 885, February 1976 to April 1977.

very low until late April.
Biomass in Lake 885 increased through June and July in contrast to declining abundance, and peaked at $41.6 \mathrm{mg} \mathrm{L}^{-1}$ in early August. Within three weeks, levels were down to $5.2 \mathrm{mg} \mathrm{L}^{-1}$ when the lake suffered its "summerkill". By mid September, biomass attained $22.1 \mathrm{mg} \mathrm{L}^{-1}$, remaining relatively high, between $8.0-15.8 \mathrm{mg} L^{-1}$ until January when it declined to near zero ( $<.01 \mathrm{mg}^{-1}$ ).

In Lake 255, crustacean densities during May and June were considerably lower than in Lake 885 , although the spring peak of 421.5 ind $\mathrm{L}^{-1}$ occurred two weeks earlier. Following a three month period with abundance between $100-200$ ind $L^{-1}$, numbers rose steadily to a late September maximum of 257.7 ind $L^{-1}$. Relatively high densities, 115.2 ind $L^{-1}$, persisted into January in contrast with Lake 885. Significant numbers (.7-3.4 ind $L^{-1}$ ) were also found in February and March, mainly in the littoral zone. Densities began to rise by early April 1977 and by late April were higher than in Lake 885.

Variations in Lake 255 biomass, unlike Lake 885, were generally synchronized with abundance. The initial peak ( $20.2 \mathrm{mg} \mathrm{L}{ }^{-1}$ ) in late May, gave way to a mid summer depression of $3-5 \mathrm{mg} \mathrm{L} \mathrm{L}^{-1}$ followed by generally elevated values near $8.5 \mathrm{mg} \mathrm{L}^{-1}$ during mid August to mid September. Considerably higher levels of biomass were found in Lake 255 than in Lake 885 during January 1977.

In Lake 019, a distinct lag in the attainment of maximum community abundance was noted. A peak of 705.7 ind $L^{-1}$ occurred in late June, about $1 \frac{1}{2}$ months behind that in Lakes 255 and 885. By mid August, abundance declined to 28.4 ind $L^{-1}$, even lower than densities in "summerkill" Lake 885 , and then recovered to 55.3 ind $L^{-1}$ in early September. Midwinter
minimum numbers in Lake 019 were substantially higher, 16.1-45.2
ind $\mathrm{L}^{-1}$, than densities in either Lake 885 or 255.
The pattern of Lake 019 biomass was basically similar to its abundance with a late June peak of $9.3 \mathrm{mg} \mathrm{L}^{-1}$, well below maximal levels in Lake 885 but comparable to summer minimum values in Lake 255. During the January-March period, biomass was well above that in Lakes 885 and 255.

Thus in Lake 885, seasonal development was heavily weighted towards the spring-early summer period when total numbers averaged 826.93 ind $L^{-1}$ or 2.9 times the seasonal average, followed by a general decline (Appendix U). In Lake 255, seasonal community development was more uniform with extended periods close to the annual average of 149.6 ind $\mathrm{L}^{-1}$. Lake 019, on the other hand, had a mid-summer bell-shaped community abundance curve ( 518.8 ind $L^{-1}$ June-July mean) with remaining periods of the year well below the seasonal average ( 124.4 ind $\mathrm{L}^{-1}$ ).

Deep and Shallow Zone Zooplankton Communities
Seasonal variation in crustacean abundance and biomass within both zones of each lake were basically synchronized although certain differences in timing and amplitude were significant (Fig. 13). In Lake 019, offshore levels of plankton density and biomass were consistently higher except for periods in the spring and late fall.

The converse was evident in Lake 255 which usually had higher shallow than deep zone concentrations. In January, prior to "winterkill", abundance was higher in the deep zone. Biomass was also generally higher near shore, particularly in early August and mid September. During June and late winter, total biomass was uniformly distributed throughout the lake.

Figure 13. Seasonal changes in crustacean zooplankton community abundance (ind $L^{-1}$ ) and biomass ( $\mathrm{mg} w \mathrm{w}^{-1}$ ) in the shallow and deep zones of Lakes 019, 255 and 885, February 1976 to April 1977.


In contrast to Lakes 019 and 255, the horizontal distribution of plankton in Lake 885 was less consistent. Higher shallow zone concentrations in early May, were followed by greater offshore densities from late May to early July. Subsequently on most occasions, abundances were greater near shore. Plankton biomass, extremely rich in Lake 885, was usually much higher near shore. Only during the spring peak and immediately following "summerkill" in late August were deep zone biomasses higher. Maximum near shore biomass, $145.3 \mathrm{mg} \mathrm{L}^{-1}$, in Lake 885 was 5 times that found offshore and much higher than values in Lakes 019 and 255 ( 9.3 and $20.9 \mathrm{mg} \mathrm{L} \mathrm{L}^{-1}$ respectively). The extreme variability in Lake 885's shallow zone was a dramatic contrast to the relative stability of its own deep zone and particularly those of the other two lakes.

## Individual Species

## 1. Seasonal occurrence

More species were present continuousily throughout the year in Lake 019 than in either of Lake 255 or 885 (Fig. 14). Three species, C. b. thomasi, D. siciloides and B. longirostris were always found either in the deeper (black bars) or the shallower (white bars) regions of Lake 019. Cyclopoid nauplii, undifferentiated among cyclopoid species, were also always present. I. p. mexicanus occurred consistently except for a short absence in spring and D. parvula was always present, mainly in the deep areas, exclusive of a short period in August and during March-April 1977.

On the other hand, in both Lakes 255 and 885 , only C. b. thomasi was found all year, though E. agilis and C. vernalis in Lake 255 persisted almost as long. D. siciloides in Lake 255 was first encountered in mid-May and survived until mid February 1977. Its presence was further restricted in Lake 885 where it was sporadically seen between June and October.

Figure 14. Seasonal occurrence of crustacean zooplankton species in the shallow (white strips) and deep (black strips) zones of Lakes 019, 255 and 885, February 1976 to April 1977. Numbers of species per month per community total indicated at base of each figure. Sampling during ice cover period indicated by sub line markings.

B. longirostris was found only occasionally through the summer in Lakes 255 and 885. The number of overwintering species in each lake was distinct with 7 species B. longirostris, D. siciloides, C. b. thomasi, D. parvula I. p. mexicanus, A. rectangula, and M. laticornis, observed in Lake 019 during March when $5.0 \mathrm{mg}_{2} \mathrm{~L}^{-1}$ was detected in the upper 3 meters of water. With traces of oxygen in Lake 255 during March, 5 species, all cyclopoids, C. b. thomasi, E. agilis, M. edax, ․ vernalis, and C. varicans were present in the plankton. Only two species, both cyclopoids, C. ㅂ. thomasi and M. albidus, were seen in anoxic Lake 885 during the late winter. In early August, prior to summerkill, Lake 885 was surprisingly diverse with 10 species. During the final stages of lake collapse in late August, three species, C. ․ . thomasi, D. leptopus and ‥ schoedleri remained in the deep zone while the above three species in addition to E. agilis, M. albidus and C. quadrangula persisted near shore indicating that localized refugias were available for survival (Appendices $N$ and $P$ ).

Differences in the number of sporadic species (those present in less than one quarter of all samples) in each lake were apparent. In Lake 885, a high proportion of species, $60 \%$ ( 4 copepods - C. varicans, D. siciloides, D. oregonensis, D. nudus and 5 cladocerans - C. quadrangula, B. longirostris, D. parvula, D. rosea, D. magna), occurred infrequently while 39\% (2 copepods M. albidus, D. leptopus and 5 cladocerans - C. sphaericus, D. schoedleri, D. rosea, D. magna, S. crystallina) in Lake 019 and $28 \%$ (2 copepods D. nudus, D. oregonensis and 4 cladocerans - B. longirostris, C. lacustris, S. vetulus, D. parvula) in Lake 255 were only occasionally found. Thus in fact a "core" of 15,11 and 6 species formed the basic established communities in Lakes 255 ( 9 copepods, 6 cladocerans), 019 ( 5 copepods, 6 cladocerans) and 885 ( 5 copepods, 1 cladoceran), respectively.

## 2. Seasonal Dynamics of the Core Species

Lake 885
Of the six core species in hypertrophic Lake 885, only two $\underline{\text { C. }}$. thomasi and $\underline{D}$. schoedleri were numerically important and prominent in community succession, the other four accounting for less than $1 \%$ of the mean total (Fig. 15).
C. b. thomasi became the numerical dominant beneath March ice and did not relinquish this position at any time. During April and May, the community was essentially monospecific with extremely high C. b. thomasi nauplii and copepodid densities. Minor cyclopoids began appearing in May but remained marginal throughout the entire study. D. schoedleri also emerged in May but achieved a maximum only in the latter part of June as C. b. thomasi was declining. Nauplii, almost exclusively C. b. thomasi, began increasing again during July, reached a second peak in early August and then quickly declined. D. schoedleri flourished from July until mid August when densities declined dramatically prior to deoxygenation of the lake. During the late August summerkill, all species were numerically low. Postkill, ㄷ. b. thomasi population growth was rapid, with peak September nauplii and copepodid densities exceeding those of August. D. schoedleri recovered almost to prekill values. Throughout the fall, both populations declined until concentrations were minimal by mid-January. The emergence of C. b. thomasi from diapause in April 1977 marked a new cycle of community growth.

Community biomass, like abundance, was initially dominated by C. ㅂ. thomasi (Fig. 16). However, by mid-June and thereafter, D. schoedleri accounted for the bulk of wet weight. Overlapping of these two species was further minimized by some spatial separation. ㄷ. ㅂ. thomasi copepodids demonstrated higher densities and biomass offshore consistently from mid-

Figure 15. Seasonal changes in the abundance (ind $L^{-1}$ ) of core zooplankton species in the shallow and deep zones of Lake 885, February 1976 to April 1977. Lake abundance weighted on volumetric share of each zone (shallow $=.15$ lake volume; deep $=.85$ lake volume).


Figure 16. Seasonal changes in the biomass (mg w w $\cdot 10^{-1} \mathrm{~L}^{-1}$ ) of core zooplankton species in the shallow and deep zones of Lake 885, February 1976 to April 1977. Lake biomass weighted on volumetric share of each zone (shallow $=.15$ lake volume; deep $=.85$ lake volume).


May to mid August (Fig. 15). In contrast, D. schoedleri abundance and biomass occurred in the shallow zone throughout the season (Fig. 16). The first zooplankton to appear in Lake 885 were $\underline{C}$. b. thomasi CIV-V, emerging from the mud in February, their densities reaching 83 ind $L^{-1}$ by March 21 (Fig. 17). By. April 27, mature gravid females bearing up to 70 eggs clutch $^{-1}(\bar{x}=44$ and 51 deep and shallow zones respectively) had produced large quantities of eggs (Appendix $R$ ).

Nauplius abundance peaked at 1369 ind $L^{-1}$ in the shallow zone on May 13 (deep $=1023$ ind $L^{-1}$ ) with maximal copepodid numbers, 1428 ind $L^{-1}$, occurring two weeks later in the deep zone (shallow $=603$ ind $L^{-1}$ ) indicating either higher mortality near shore or migration to the deep zone.

The second cohort of mature males and females began to appear during early June, maximum densities occurring on July 6 with 78.9 and 47.7 ind $L^{-1}$ in the deep and shallow zones respectively. Eggs were produced continuously throughout this period but in smaller amounts because of reduced fecundity ( $\bar{x}$ between 7 and 17 eggs female $e^{-1}$ ) and lower percentages of egg bearing females. As the population continued to mature and the proportion of gravid females increased, total egg production rose to a maximum on July 27 in the deep zone. During the first three weeks of August, clutch sizes increased ( $\bar{x}=17-25$ eggs female ${ }^{-1}$ ) but with gravid female densities falling, egg production fell to a minumum by August 17. Although more eggs were produced offshore during the July-early August period, nauplius numbers were once again higher near shore. The nauplius peaks on August 4 were substantial ( 382 and 286 ind $L^{-1}$ shallow and deep respectively), but only meager quantities ( $<4$ ind $L^{-1}$ ) of CI-III were found in early August, solely in near shore regions (no CI-III were found in the deep region on eight consecutive sampling dates between July 6 and August 22) indicating high nauplius or CI-III mortality. On August 22,

Figure 17. Seasonal changes in the abundance of life history stages of Cyclops bicuspidatus thomasi in the shallow and deep zones of Lake 885, February 1976 to April 1977.

one day after all stocked trout were asphyxiated, near shore densities of CIV-V peaked at levels, 85.5 ind $L^{-1}$, significantly higher than those in the deep region, 16.3 ind $L^{-1}$. Through the next several days of anoxia CIV-V numbers slowly declined until minima of 6 ind $L^{-1}$ were reached in both zones on September 1 by which time oxygen levels had returned to normal.

In spite of anoxia, an upswing in egg production was observed on August 22, with the appearance of a third cohort of reproducing adults marked by substantial numbers of males near shore. Fecundities during kill and post kill periods were very high, second only to those during the spring. Higher natality and lower mortality of nauplii in early September, when temperatures were falling, led to a substantial autumnal peak of CI-III. By September 16, fourth generation adults appeared and continued to produce eggs until the last gravid females were observed on October 14. Most copepodids, however, did not advance beyond CIV-V but entered diapause or died by December 15. A few CI-III and CIV-V instars were found, mostly in the deep zone, surviving during February and March 1977 when only traces of oxygen ( $0.6 \mathrm{mg} \mathrm{L}^{-1}$ ) were detected immediately beneath the ice layer. First indications of renewed activity occurred on March 24 when substantial numbers of CIV-V (12 and 6 ind $L^{-1}$ in shallow and deep zones respectively) were seen just as oxygen concentrations beneath the ice improved slightly. By April 13, sexual reproduction was underway and all stages were present by the last sampling date on April 26.

Mature males were present continuously from April 27, 1976 to October 14 in the shallow zone and to December 15 in the deep zone (Appendices $N$ and $P$ ). Four male abundance peaks were observed in the shallow zone with the first, 37.6 ind $L^{-1}$, in late April, the second, 37.7 ind $L^{-1}$, on July 6 following a gradual increase from 2.7 ind $L^{-1}$ in late May, the third, 23.5
ind $L^{-1}$, on August 22 with densities declining slowly to 2.3 by September 1 and the final occurring in mid September with counts lower at 13.4 ind $L^{-1}$.

In the deep zone, a slightly different pattern was observed. The first and second male peaks corresponded closely to those near shore, with 29.3 ind $L^{-1}$ on April 27 and 57.7 ind $L^{-1}$ on July 6. The third near shore peak was, however, complemented by a deep zone minimum of 2.0 ind $L^{-1}$ on August 22. A damped third peak, 10.0 ind $L^{-1}$, occurred offshore on August 26. Little, if any, increase was noted in mid September in contrast to the clear shore-zone pulse at the time. Thus, in both zones, peak, male and mature female densities generally preceded population maxima. Annually, male average densities were identical in both zones with 9.2 and 9.6 ind $L^{-1}$ in the shallow and deep zones respectively. While males were as common offshore as females (Table 8), they outnumbered females in the shallow zone.
D. schoedleri development began slowly in the shallow zone with a few immature specimens, likely hatched from resting eggs, on the first ice free date in late April (Fig. 18). The first mature females appeared on May 26, bearing up to 22 eggs each (Appendix R). With more gravid females offshore a larger egg pulse was produced in the deep zone on June 17. Six days later, daphnid numbers peaked in both regions but now approximately three times more matures occurred near than offshore, indicating either better survival or shoreward migration. Gamogenetic production of ephippia commenced early, on June 17, jointly with the appearance of males. Egg production declined in late June as fecundities, which had remained high ( $\bar{x}=9-19$ egg female $e^{-1}$ ) until mid June, fell to 1-2 eggs female $e^{-1}$. Immatures subsequently decreased to 20 ind $L^{-1}$ in both zones by July 12.
e 8. Mature female to male sex ratios of crustacean, zooplankton species in Lakes 019, 155 and 885, February 1976 - April 1977.

|  | 885 |  | 255 |  | 019 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | S | - D | S | D | S | D |
| ops bicuspidatus th. | . 63 | 1.03 | 1.09 | 1.37 | . 52 | . 84 |
| ops vernalis | 1.38 | 18.40 | 2.69 | 1.67 | . 30 | . 65 |
| clops agilis | 4.13 | 1.36 | 2.25 | 3.17 | . 52 | . 31 |
| rocyclops albidus | 1.39 | 1.25 | . 47 | . 27 |  |  |
| nthodiaptomus <br> ticomis <br> otomus siciloides |  |  | .68 1.35 | 1.44 1.19 | . 68 | . 86 |
| ptomus leptopus | . 98 | 1.36 | . 98 | . 99 |  |  |
| hnia schoedleri | 13.43 | 7.60 | 18.41 | 13.62 |  |  |
| hnia rosea |  |  | 3.09 | 1.30 |  |  |
| Inia parruza |  |  |  |  | . 94 | 2.69 |
| mina longirostris |  |  |  |  | 760.57 | 489.65 |

Figure 18. Seasonal changes in the abundance of life history stages of Diaptomus leptopus and Daphnia schoedleri in the shallow and deep zones of Lake 885, February 1976 to April 1977.


Daphnia populations did not develop synchronously in both zones during July and early August. With water temperatures reaching their maximum of $23.5^{\circ} \mathrm{C}$ during the first week of July, and remaining above $20^{\circ} \mathrm{C}$ until late August, a period of intense parthogenesis began near shore where mature female densities had risen rapidly. Along with the abundance of males, many ephippia were also produced forming surface scums near shore for several weeks. Warm temperatures likewise hastened developmental rates as evidenced by closeness of embryonic and postembryonic peaks on July 28, the date of maximum daphnid density, 303.6 ind $L^{-1}$.

In contrast, deep-zone mid-July densities of $\underline{D}$. schoedleri were depressed. Minimum prekill densities were recorded on July 20, about the time highest bluegreen biomass (Fig. 8) and lowest Sechi visibilities (Fig. 5) were detected offshore. A remarkable differentiation of inshore and offshore habitats was observed on the same date with large quantities of decaying algal material found only in deep zone plankton samples (Fig. 19). As mature female abundance did not increase dramatically offshore during July and August, reduced quantities of eggs were produced. Juvenile growth was also much slower in the deep zone with immature peaks on July 27 and August 17 lagging behind respective egg pulses on July 13 and August 10.

Effects of summerkill on D. schoedleri were first observed in the deep zone where algal catabolism originated. From the second population peak ( 101.2 ind $L^{-1}$ ) on August 17, densities fell sharply to 18.9 ind $L^{-1}$ by August 22 when oxygen was undetectable in mid lake. On the other hand, numbers continued to rise in the shallow region during this period and peaked at 213.0 ind $\mathrm{L}^{-1}$ on August 22. As these increased inshore concentrations could not be related to recruitment from an egg pulse,

Figure 19. Comparison of composite replicate total net plankton samples from the shallow and deep zones of Lake 885 on July 20 retained by a $73 \mu \mathrm{~m}$ mesh net.

immigration of deep zone inhabitants was the likely source of daphnids. Ultimately, lethal conditions diffused slowly shorewards and by August 26 , with the lake still warm and gently stirred, a large segment of the shallow zone population was decimated, densities dropping to only 7.0 ind $L^{-1}$. Males were scarce during anoxia. Some horizontal variation in daphnid survival was noted throughout the summerkill period in the shallow samples taken with the transparent plexiglass tube. On August 22, no living cladocerans were visible in shallow stations I and II, whereas red-colored $\underline{D}$. schoedleri were swimming near station IIIS. Red daphnids were also observed active at the surface near station ID on August 26 while yellowish Daphnia were seen at station IIIS.

The first significant "postkill" response by $\underline{D}$. schoedleri was a sizeable egg pulse on August 26 in the deep zone where oxygen levels showed a slight improvement ( $0.1,0.2,06$ and $0.0 \mathrm{mg} \mathrm{L}^{-1}$ at $0,1,2$ and 2.7 m respectively). Shallow zone totals were smaller because of fewer gravid females. Both zones exhibited doubled fecundity levels and higher gravid to non gravid ratios over prekill values. With brood sizes averaging 5.0 eggs female ${ }^{-1}$ (max. 10), second only to those of early June, egg production peaked in the deep zone on September 1 and ten days later near shore.

Juvenile development peaked simultaneously in both zones by September 10 with 1.4 times higher densities near shore. Adolescent numbers declined throughout late September and October until the last few disappeared by mid November in both zones.

Mature daphnids were more abundant near shore after summerkill, peaking at 112 ind $L^{-1}$ on September 16 . Only 17 ind $L^{-1}$ were found offshore on that date. As dapnid abundance began to decline in late September, male densities reached their seasonal maximum near shore. By mid October with
highest ( $40 \%$ ) seasonal proportion of ephippial females present, substantial numbers of resting eggs were produced. Although offshore adult numbers remained relatively constant, $10-15$ ind $L^{-1}$, between mid September and mid December, densities near shore appeared to increase in December before their final collapse in January.

No D. schoedleri were present during the period of reduced (0.7$0.8 \mathrm{mg} \mathrm{O}_{2} \mathrm{~L}^{-1}$ ) oxygen levels in January and the anoxia of late winter. On April 13, several immatures ( 0.05 ind $^{-1}$ ) appeared, likely hatching from numerous ephippia floating in the open water near shore. By April 26, the lake was ice free and more juveniles (2.6 ind $L^{-1}$ ) and a few recently matured females ( 0.3 ind $L^{-1}$ ) were found in the deep zone.
D. leptopus, commonly found in shallow or temporary prairie ponds (Sawchyn and Hammer 1968), was the only calanoid of significance in Lake 885 (Fig. 18). D. leptopus existed from late April to mid December 1976, a rather extended period in comparison to the shorter cycles usually found in congeneric species associations (Hammer and Sawchyn 1968). Seasonal development was basically similar in both zones. Nauplii, from overwintering eggs, appeared on April 17 with the first cohort of sperma-tophore-laiden females producing subitaneous eggs by June 10. Large clutch sizes, averaging 41-62 eggs, between June 10 and July 13, resulted in maximum copepodid densities by mid July, coincident with relative minimums of $\underline{D}$. schoedleri in either zone. An abundant supply of males was present throughout the entire season with sex ratios usually 1 to 1 (Table 8). A brief egg laying near August 4, when fecundities had fallen to 24-30 eggs female, gave a second copepodid pulse, more obvious near shore, in mid August. With high temperatures $\left(>20^{\circ} \mathrm{C}\right)$, prevailing transition from CI-III to CIV-V was brief, likely even less than the three
days reported by $0^{\prime}$ Brien et al. (1973) for D. leptopus at $15^{\circ} \mathrm{C}$ and consequently the younger CI-III instars were missed in sampling. As oxygen levels declined, D. leptopus copepods began to evacuate the deep zone on August 10 and move towards shore where densities increased. By August 26, only a few individuals, exclusively adults, remained, the nauplii peaks on August 17 apparently failing to develop further. Egg production resumed at that time, however, with slightly larger clutch sizes, 36-55 female ${ }^{-1}$. By late September, a final cohort of CIV-V and adults appeared. From October to December, with chlorophytes and cryptophytes dominating the phytoplankton (Sriswantach 1978), fecundity levels rose (56-88 eggs female ${ }^{-1}$ ) and substantial numbers of overwintering eggs were produced.

The limnoplanktonic insect larvae Chaoborus sp. and the amphipod Gammarus lacustris, two invertebrate predators known to feed on zooplankton (Anderson and Raasveldt 1974), were found in Lake 885 during the study (Fig. 20). Although occasionally there was some spatial overlap of these species, Chaoborus was generally more abundant in the deep zone particularly during periods of winter and summer anoxis. Absent from late June through July, Chaoborus densities began to increase with the onset of deoxygenation in the deep zone in early August and then persisted through the remaining fish-free period of the study.

Gammarus, on the other hand, was more abundant near shore, particularly from late May to mid June and then from late August until mid October. Offshore, it was relatively common only during the vernal heating phase of 1976. Although not observed in plankton samples from February to late March 1977, gammarids were present just beneath the ice in shallow zone stations, many being brought up through the sampling holes in uprushing water.

Figure 20. Seasonal changes in the abundance (ind $L^{-1}$ ) of Gammarus lacustris and Chaoborus sp. in the shallow and deep zones of Lakes 019, 255 and 885 February 1976 to April 1977.


## Lake 255

In Lake 255, the annual cycle of $\underline{\text { C. }}$. . thomasi, the numerical dominant, involved two main periods of development, a strong spring pulse and uniform, moderate densities from October to January (Fig. 21). Minima coincided with warmest water temperatures during July and lowest oxygen concentrations through February and March. Abundance was consistently higher in the shallow than deep zone during the spring but lower nearshore, except in December throughout the remainder of the cycle. More CIV-V were present near shore by late March 1977 than March 1976 indicating annual variation in overwinter survival and onset of spring emergence.

The seasonal pattern of biomass (Fig. 22) basically agreed with that of density.

Following emergence as CIV-V in March, C. b. thomasi copepodids matured and were producing large numbers of eggs by April 26 (Figs. 23a and b). Maximum annual mean fecundities, from 65 to 80 eggs per female, were recorded from April 26 to May 12. The last few ovigerous females of the spring cohort were seen on May 25 with clutches of 40 eggs.

During late April, nauplii concentrated near shore ( 420 ind $L^{-1}$ ) and after roughly 12 days, with mean temperatures between 10.8 and $13.8^{\circ} \mathrm{C}$, developed into a large pulse ( 290 ind $\mathrm{L}^{-1}$ ) of CI-III on May 12. Through mid May with lake temperatures surpassing $15^{\circ} \mathrm{C}$, transformation from CI-III to CIV-V occurred in approximately two weeks. Final development to CIV-V during early June took place within nine days at $20^{\circ} \mathrm{C}$.

The second cohort of adults appearing in late May was small with ovigerous females bearing only 13 to 16 eggs per clutch (see also Appendices $J$ and L). Reproduction was brief, ending by June 17 near shore and five days later offshore. Subsequent copepodid pulses occurring

Figure 21. Seasonal changes in the abundance (ind $L^{-1}$ ) of core cyclopoid species in the shallow and deep zones of Lake 255, February 1976 to April 1977. Lake abundance weighted on volumetric share of each zone (shallow $=.20$ lake volume; deep $=.80$ lake volume).

Figure 22. Seasonal changes in the biomass ( mg w w $\cdot 10^{-1} \mathrm{~L}^{-1}$ ) of core cyclopoid and calanoid species in the shallow and deep zones of Lake 255, February 1976 to April 1977. Lake biomass weighted on volumetric share of each zone (shallow = . 20 lake volume; deep $=.80$ lake volume).


Figure 23a. Seasonal changes in the abundance (ind $L^{-1}$ ) of life history stages of core cyclopoid species in the shallow and deep zones of Lake 255, February 1976 to April 1977.


Figure 23b. Seasonal changes in the abundance (ind $L^{-1}$ ) of life history stages of core cyclopoid species in the shallow and deep zones of Lake 255, February 1976 to April 1977.

in late June were less than $4 \%$ of respective spring peaks. Minimal summer copepodid densities of approximately 2 ind $L^{-1}$, were observed in late July when the lake, at $21-22^{\circ} \mathrm{C}$, was fully saturated with oxygen at all depths (Fig. 6).

In late July, a third small cohort of adults resumed reproduction in the deep zone gravid females were seldom seen in the shallow zone following the initial spring pulse). Copepodids I-III reappeared offshore on August 17 and matured through late August and mid September to form a fourth adult generation with females carrying 22 to 27 eggs. In spite of lowered egg production, proportionally higher nauplial and copepodid densities indicated improving survival during fall as compared to spring. By mid October, with water at $4^{\circ} \mathrm{C}$, immature densities stabilized at approximately 85 ind $L^{-1}$ offshore with a consistent $60 / 40$ CI-III to CIV-V ratio maintained until mid December when nauplii disappeared. By February 16, when little oxygen remained, all CI-III had advanced to CIV-V which then left the water column to diapause in the sediments (Fig. 23a).

In the shallow zone, fall egg production was minimal with only a few mature females present during September. Consequently, CI-III densities through fall and early winter averaged less than one-half those in the deep zone. Increases of CIV-V in November and December may have been related to interzonal migrations. These increases were observed for most species in Lake 255; for e.g. M. edax, C. vernalis, C. varicans, A. denticornis and D. siciloides. In late December, CIV-V densities declined as they moved from the shallow zone water column into either diapause or the deep zone. Low numbers of CIV-V and mature females persisted through late February and early March, but approximately five times more copepodids were present near than offshore indicating some environmental advantage in the shallow zone. Emergence from diapause was earlier near shore with
11.6 CIV-V L-1appearing on March 24 but only 0.7 CIV-V L ${ }^{-1}$ in the deep zone where oxygen levels were still depressed. By mid April 1977, CIV-V peaks in both zones were higher than the corresponding ones in 1976. On April 26, $95 \%$ of copepodids were mature with females bearing many eggs (64-68 eggs female ${ }^{-1}$ ). Very high nauplii densities, 663 and 317 $L^{-1}$ in the shallow and deep zones respectively, were recorded.
C. b. thomasi adult males were common in Lake 255 , occurring in $71 \%$ and $53 \%$ of all deep and shallow zone samples, respectively. Mature females were found in 65 and $66 \%$, respectively, of all deep and shallow samples. On an annual basis, female/male abundance ratios were 1.37 in the deep and 1.09 in the shallow zones of Lake 255 (Table 8).

The seasonal occurrences of the five other core cyclopoids were principally confined to summer when $\underline{C}$. b. thomasi densities were minimal although $\underline{C}$. vernalis was relatively abundant during the fall increase of C. b. thomasi (Figs. 21 and 22). M. edax existed throughout the entire C. b. thomasi minimum in relatively consistent, low numbers. E. agilis, M. albidus and C. varicans occurred mainly in late August and September, preceeding the fall rise of $\underline{C}$. $\underline{b}$. thomasi.
M. edax emerged as CIV-V and adults from winter diapause, several weeks after C. ․ . thomasi climbing to a peak by late April (Fig 23a and b). Not until mid May, however, were ovigerous M. edax females first seen offshore, some three weeks after commencement of ㄷ. b. thomasi egg production. Consequently, M. edax copepodid recruitment was delayed, the spring cohort peaking offshore finally in late June. Near shore, only a few females were present during late April - early May.
M. edax produced eggs continuously from mid May to mid August (Fig. 23b). May females were most fecund, each with 52-54 eggs, while fecundities
averaged between 26 and 36 eggs female $e^{-1}$ during the remainder of reproduction. Abundant ovigerous females in late July, led to copepodid peaks in late August. M. edax densities declined in October as waters cooled and C. ․ . thomasi regained dominance.

In contrast to $\underline{C}$. ㅌ. thomasi, M. edax adults usually represented a prominent fraction of the population, particularly during the fall decline indicating their overwintering, additionally with CIV-V stages, in diapause (Elgmork 1967). Only a few CIV-V stages were observed through winter anoxia compared to the relative abundance of $\underline{C}$. b. thomasi. Adults and CIV-V reappeared simultaneously on April 24, 1977 to initiate a new cycle.
M. edax seasonal biomass (Fig. 22) deviated from its abundance. The offshore biomass peak in April was disproportionately large whereas no late August maximum was obvious. These differences were related to seasonal variation in animal size (between mid June and early September M. edax mature females decreased in size $15-20 \%$ ) and population structure.

Eucyclops agilis occurred mainly in the shallow zone of Lake 255 where it dominated July - early August cyclopoid densities (Fig. 21). It first appeared near shore on May 12 as CI-III and females carrying 35 eggs clutch ${ }^{-1}$, the seasonal maximum (Figs. 23a and b). Following the main egg hatch in mid June, reproduction was continuous, but diminished with clutches between 15-25 eggs, until termination in late September. Copepodid pulses in June and September consisted primarily of immatures but adults predominated as densities fell in late autumn. By mid December, the population was exclusively mature. Males were generally abundant until January 1977, their mean annual concentrations approximately one half those of females (Table 8).

Although variation of E. agilis biomass (Fig. 22) corresponded with density during the summer, fall and winter biomass was relatively higher since adults were more prominent later in the cycle. Shallow zone biomass averaged 11.7 times higher than that of the deep zone (Table 7).

Cyclops vernalis was the second cyclopoid preferring the near shore habitat, being found only sporadically in the deep zone (Fig. 21). Although present on 28 out of 31 sampling dates, numbers were usually low and concentrated in three main pulses, late July, late August and mid October. It first appeared on April 24 as females bearing high numbers of eggs, 80-138 per clutch, almost twice as many as co-occurring C. b. thomasi (Fig. 23a). However, with $\underline{C}$. vernalis female densities considerably lower (1/30) than those of C. b. thomasi total egg production (Fig. 24b) was smaller resulting in 35 times fewer spring CI-III. With temperatures rising and C. b. thomasi declining through June, ́. vernalis began increasing towards its first peak on July 26 along with E. agilis. Densities of both species fell during early August but their cycles then lost synchrony, the early September $\underline{C}$. vernalis minimum contrasting with the $E$. agilis peak. The autumn maximum and early winter decline of $\underline{C}$. vernalis consisted mainly of immature copepodids which persisted into January, unlike the pattern for E. agilis. Whereas E. agilis adults continued through the ice period, C. vernalis adults disappeared by late February prior to the reappearance of CIV-V stages in late March 1977.
C. vernalis seasonal biomass (Fig. 22) was basically a reflection of numerical change.

The two final cyclopoids, Macrocyclops albidus and Cyclops varicans, both found primarily near shore, were aestival species peaking in September shortly after highest summer temperatures (Figs. 21 and 22). While

## M. albidus achieved only 6.9 ind $L^{-1}$ in its fall maximum, C. varicans

 with 48.2 ind $L^{-1}$ was the dominant cyclopoid during September.The cycle of M. albidus was similar to that of E. agilis, both populations originating in the spring from adults (Fig. 23b). However, while E. agilis mature females were active in the plankton throughout winter, M. albidus adults appeared to diapause from March to late April (Elgmork 1967). In addition, seasonal pulses of M. albidus and E. agilis were synchronized. M. albidus egg production was confined to three periods, an initial mid May pulse, a second from June 28 to July 13 and finally in mid August. Although females were present more frequently, males outnumbered females by two to one in the shallow zone.
C. Varicans was initially seen on March 21 in the deep zone as CIV-V with first cohort females maturing by April 30 and producing eggs by May 12 (Fig. 23b). Gravid females, never found offshore, and other matures were then absent near shore from May until late July, only a few juvenile copepodids occurring during this period. With the appearance of a second cohort of males in late July-early August, reproduction resumed and a prominent copepodid peak developed in September. Egg production ceased by late September and the last copepodids, stage CIV-V, which entered diapause to overwinter, were seen on December 16.

Seasonal changes in M. albidus and C. varicans biomass (Fig. 22) were basically similar to those of abundance.

The seasonal development of the main calanoids in Lake 255, Acanthodiaptomus denticornis, Diaptomus leptopus and Diaptomus siciloides generally spanned shorter periods than that of cyclopoids, particularly D. leptopus which was recorded only from late May to mid November (Figs. 24 and 22). Significant size differences likely allowed for the co-existence of these

Figure 24. Seasonal changes in the abundance (ind $L^{-1}$ ) of core calanoid and cladoceran species in the shallow and deep zones of Lake 255, February 1976 to April 1977. Lake abundance weighted on volumetric share of each zone (shallow $=.20$ lake volume; deep $=.80$ lake volume).

species in Lake 255. Mature D. siciloides females ranged from .98 to 1.39 mm , A. denticornis from 1.41 to 1.83 mm , and D. leptopus between 2.01 and 2.32 mm in length. Additionally, since each species belonged to a separate subgeneric group, A. (Acanthodiaptomus) denticornis, D. (Leptodiaptomus) siciloides, and D. (Aglaodiaptomus) leptopus, different morphological traits permitted them to utilize different food particle sizes(Cole 1961). Of the three, ㅁ. leptopus showed the greatest preference for the shallow zone with 2.3 and 2.9 times greater density and biomass, respectively, near than offshore. D. siciloides, in contrast, was twice as abundant in the deep as in the shallow zone. A. denticornis was distributed relatively uniformly throughout the lake with perhaps a slight shoreward tendency.
D. siciloides nauplii, hatching from overwintering eggs appeared in late April and by May 12, CI-III were present in both zones (Fig. 25). Within two weeks, egg production began, persisting until mid December offshore and mid January near shore. Like all species under study, D. siciloides spring clutches were the year's largest, averaging between 24 to 27 eggs per female. Over the summer, a gradual decline in brood size was noted with smallest clutches, 2 to 3 eggs, during the period from mid July to late August. The final gravid females seen in winter each carried 14 to 16 eggs. Total egg production in both zones was comparable and moderate from late May to late June with similar high proportions of gravid females ( $40 \%$ of matures) present. During mid July, production declined lakewide with less than $15 \%$ of females carrying eggs. During the remainder of the year, egg production offshore, with 45-50\% of females gravid, surpassed that near shore where only $12 \%$ carried eggs. Eggs produced after September 17 in the shallow and October 14 in the deep zones were likely of the overwintering variety.

Figure 25. Seasonal changes in the abundance (ind $L^{-1}$ ) of life history stages of core calanoid species in the shallow and deep zones of Lake 255, February 1976 to April 1977.


Subitaneous egg production by D. siciloides led to three main offshore pulses of nauplii, on June 13, on July 26 and in early September. Whereas nauplius instar duration was roughly two weeks in early May, transformation to CI-III took place within five days in mid June and slightly longer, 8 days, in both July-August and September. These instar durations agreed very closely with values presented by Comita (1972) for D. siciloides nauplii in Severson Lake. Better nauplii survival in the fall than in summer was indicated by higher CI-III/nauplii ratios (. 7 versus .3 respectively).

Shallow zone nauplius production in June was comparable to that offshore and resulted in similar densities of CI-III. During August and September, however, reduced egg production led to lower concentrations of CI-III.
D. siciloides copepodids exhibited three offshore pulses during open water which were correlated with the main nauplius peaks. The adult peak in December could not be explained through recruitment. Copepodid densities were fairly consistent ranging between 23.0 and 41.1 ind $L^{-1}$ during summer and fall. While maturation proceeded rapidly during mid summer, longer instar duration was observed during the fall, in agreement with Comita (1972).

Near shore, CI-III, benefitting from water temperatures, peaked on June 17, a week earlier than the population offshore. Proportionally fewer CIV-V and adults were seen near shore in June. Densities of immatures remained relatively stable, $1-5$ ind $L^{-1}$, from mid July until mid October. The high peaks of 31.7 and 35.3 total ind $L^{-1}$ in August likely involved shoreward migration by deep zone adults. Subsequent adult densities were consistently $7-12$ ind $L^{-1}$ until December when offshore adults migrated shorewards.
D. siciloides males were the last mature stages seen swimming offshore in February 1977. Annual female to male density ratios were 1.35 and 1.19 in the shallow and deep zones respectively (Table 8).
A. denticornis, a species in Western Canada usually associated with small, densely populated lakes and ponds having diverse communities (Anderson 1974), was much less abundant(x.05)than D. siciloides, accounting for only $0.9 \%$ of mean annual crustacean abundance. Pennak (1957) reported the same relationship between dominant and subdominant calanoids. A. denticornis biomass was, however, only $x .1$ smaller than that of D. siciloides (Figs. 22 and 24).

Immature copepodids of A. denticornis were present on May 25, two weeks later than D. siciloides (Fig. 25). By May 31, females were carrying 25 to 36 eggs, with clutch sizes increasing to 50 eggs during the next three weeks. By late June, fecundities declined in both zones, reaching 10 eggs per female from mid July to the second week of August. The final summer gravids seen August 22 in the deep and September 9 in the shallow zone each carried 20 eggs on average. Following a three month lapse, egg production resumed briefly in mid December in both zones with females carrying 22 eggs.

Maximal egg production during the first half of June led to copepodid peaks of $6-8$ ind $L^{-1}$ in late June. These densities were approximately double those found in a temporary pond by Donald (1971) for A. denticornis though common temporal dynamics were generally shared by both populations. Densities stabilized offshore at 3-5 ind $L^{-1}$ during July and near 2 ind $L^{-1}$ in the shallow zone after declining in early July. Males usually formed more than $50 \%$ of the adult population throughout this period. Despite some reproduction, immature copepodids were scarce after July, the majority
of eggs being produced probably for overwintering. The last copepodids seen were shallow zone females in February 1977. Over the year, male to female ratios were $3: 2$ near shore but $2: 3$ offshore (Table 8).
D. leptopus, appeared initially as CIV-V on May 26 (Fig. 25) Mature females, first seen on May 31 were producing eggs offshore by June 8 and near shore by June 17, one week behind A. denticornis and two weeks behind D. siciloides. June brood counts were high averaging between 54-72 eggs per clutch. Minimal fecundities, 20-30 eggs per female, occurred from mid July to mid August. Gravid females then disappeared from the shallow zone until late September but remained offshore with clutches averaging 45 eggs, until mid October when maximum broods, 88 eggs per clutch, were noted. Three peaks of total egg production were visible near shore, June 22, August 3 and October 14 while two were observed offshore, July 6 and August 22.

Copepodid abundance offshore peaked between June 28 and July 6. D. leptopus existed primarily as adults for the remainder of the cycle which terminated in November.

In the shallow region, maximum total copepodid density, 5.2 ind $L^{-1}$, was reached on July 10, about two weeks later but significantly higher than offshore. Following a gradual decrease of adults to . 14 ind $L^{-1}$ on August 22, a small third generation of immatures developed in September producing a fall adult peak. After the final clutches of overwintering eggs were produced in October adults died during November. Mature males were always present at densities rivalling those of females (Table 8).

The durations of cladoceran occurrence in Lake 255 varied from six months for $\underline{C}$. quadrangula to eight months for $\underline{D}$. rosea (Figs. 24 and 26). In general, they were shorter than cyclopoid but similar to calanoid occurrences. Although cladoceran succession was evident, some temporal

Figure 26. Seasonal changes in the biomass (mg w w $\cdot 10^{-1} \mathrm{~L}^{-1}$ ) of core cladoceran species in the shallow and deep zones of Lake 255, February 1976 to April 1977. Lake biomass weighted on volumetric share of each zone (shallow $=.20$ lake volume; deep $=.80$ lake volume).

overlapping of species occurred. D. schoedleri was first to appear in late April, and dominated the May-June cladoceran community. A. rectangula and D. leuchtenbergianum followed on May 25 but remained marginal until September when they proliferated, particularly the former in the shallow zone. Next to appear was D. rosea, remaining low through mid summer and peaking in September. C. sphaericus also began to emerge at the end of May and together with D. schoedleri were the main cladocerans in July. C. spahericus, however, did not reach prominence until October November in the shallow region. C. quadrangula was the final cladoceran emerging in mid June. Following the D. schoedleri peak of early August, rising densities of the other cladocerans resulted in a period of maximal overlap from late August to early September. By late September, all species except C. sphaericus were waning, D. leuchtenbergianum the first to disappear in October followed by D. schoedleri and C. quadrangula in November. D. rosea was last seen in mid December while C. sphaericus and A. rectangula persisted into January.

The pattern of seasonal biomass of smaller cladocerans $\mathbb{C}$. sphaericus A. rectangula and C. quadrangula, generally followed their abundance (Fig. 26). Daphnid seasonal biomass on the other hand, deviated somewhat from abundance. While offshore densities of $\underline{D}$. schoedleri had a ninefold range (54.3-5.7 ind $L^{-1}$ ) during June, biomass showed a corresponding thirteenfold variation ( $17.58-1.36 \mathrm{mg} \mathrm{L}^{-1}$ ) mainly because of substantial numbers of very large ( $\bar{L}=2.67 \mathrm{~mm}$ ) mature females present on May 31 . Similarly, in July and September when adults formed a sizeable fraction of the population offshore, ㅁ. schoedleri biomass peaks were relatively larger than the corresponding density maxima. D. rosea offshore biomass increased six fold through August and September as the population matured in contrast to its doubled abundance during this period.

Immature D. schoedleri, recently hatched from ephippia, appeared in Lake 255 in late April (Fig. 27). On May 25, females carried 11-12 eggs each. Brood sizes dropped quickly, by June 8 averaging 1.0-1.5 eggs. These fecundities were maintained until reproduction ceased in mid October except for a brief increase to 3.0 eggs per female in early July.

Four egg pulses were observed in the deep zone, late May, early July, in mid August and in late September. Ephippial eggs formed a large fraction of the first and last pulse with fewer produced during the summer. In the shallow zone, egg production was basically similar with the exception of much fewer ephippial eggs being produced during the first three pulses.

Offshore, maximum daphnid abundance, 66.6 ind $L^{-1}$ occurred by late May with numbers declining through June. Adult densities steadied near 5 ind $\mathrm{L}^{-1}$ through most of June and into July. Total densities averaged approximately 20 ind $L^{-1}$ from July to September with adults abundant during August. Juvenile and mature daphnids finally disappeared by late October and late November respectively.

Near shore, D. schoedleri seasonal densities were generally similar to those offshore except for the maximum, 103.3 ind $L^{-1}$, which occurred in early August.
D. schoedleri males were encountered more commonly offshore, in association with ephippial production. Densities were highest, 4-5 ind $\mathrm{L}^{-1}$, during the spring population peaks. Males were possibly overlooked in deep zone July samples and shallow zone fall samples when ephippia were present. Annual male abundance was between $5.4 \%$ (shallow) and $7.6 \%$ (deep) of female abundance (Table 8).

Figure 27. Seasonal changes in the abundance (ind $L^{-1}$ ) of life history stages of core cladoceran species in the shallow and deep zones of Lake 255, February 1976 to April 1977.

D. rosea, although present in all three lakes, was abundant only in Lake 255. It was essentially a late summer-fall species that complimented the spring-early summer pattern of D. schoedleri (Fig. 24). Young immatures from ephippia were present offshore in mid June with a few gravids occurring on June 22 (Fig.27). A single particularly large ( 1.76 mm ) female, carrying 9 eggs, was observed on July 6. From this low level of reproduction, a small pulse of immatures developed in early July.

Near shore, immatures were first observed in late June. The first shallow zone eggs were not seen until July 13.

Most eggs were produced in the shallow zone during August and September when high densities of mature females occurred. Average brood sizes were between 1.3-2.6 eggs on July 26, comparable to those of D. Schoedleri at the time, and remained close to 1.5 eggs per female until September 24 when parthogenesis ceased.
D. rosea juveniles increased rapidly in early August, particularly near shore, concurrently with diminishing numbers of cyclopoids. Immature densities were basically similar in both zones in fall, although adults were always significantly more abundant near than offshore, indicating higher survival rates in the heavily vegetated shallow areas. Maximum adult densities, 46.0 ind $L^{-1}$,were recorded on September 17 near shore. By October 15, the entire shorezone population consisted of adults. Sexual reproduction peaked on that date in both zones with greatest amounts of ephippia produced near shore. The last ephippial females were seen in mid December.
D. rosea males appeared near shore in August but not until the fall daphnid peak did they become abundant, reaching 12.9 ind $L^{-1}$ on September 17. They were not present in the plankton after mid November. Annually,
male-female ratios were approximately .32 near shore and .77 offshore, substantially higher than respective $\underline{D}$. Schoedleri values (Table 8).

Of the four remaining core cladocerans, $\underline{C}$. quadrangula, $\mathbb{C}$. sphaericus and A. rectangula (Figs. 24 and 26 ) were closely associated with the near shore habitat. D. leuchtenbergianum, the least abundant core cladoceran, showed a slight preference for the deep zone.
A. rectangula and $\underline{D}$. leuchtenbergianum, although appearing initially in late May, occurred in very low numbers through much of the summer. Development of these species was typically aestival with maximum September population densities following warm water temperatures in August. The 231.6 A. rectangula $L^{-1}$ shallow zone peak on September 24 was the second highest crustacean species density recorded in Lake 255 . In fact, A. rectangula had the highest annual average density, 25.5 ind $L^{-1}$ of all cladocerans in Lake 255. On most occasions, gravid $A$. rectangula females, including those carrying darkened overwintering eggs, formed a substantial fraction of the mature shorezone population. Males appeared on September 9 as population densities were rising and peaked at $18.5 \mathrm{~L}^{-1}$ in mid October. Over the season, male densities were roughly $7 \%$ those of females. A. rectangula females were the last cladocerans seen carrying eggs, on January 16, 1977.
C. sphaericus, the smallest cladoceran in Lake 255, occurred from late May to mid-January with two pulses, a brief one in latter July and the main one extending from late August to mid November (Fig. 24). Gravid females were initially seen on June 17 with reproduction continuing until December 16. Males appeared on September 9 when population counts were high to mark the beginning of overwintering egg production. Thus, reproduction during spring-summer was exclusively asexual and was supplemented by sexual activity during the major fall pulse.

Figure 28. Seasonal changes in the abundance (ind $L^{-1}$ ) of core cyclopoid and calanoid species in the shallow and deep zones of Lake 019, February 1976 to April 1977. Lake abundance weighted on volumetric share of each zone (shallow = . 06 lake volume; deep $=.94$ lake volume).


Figure 29. Seasonal changes in the abundance (ind $L^{-1}$ ) of core cladoceran species in the shallow and deep zones of Lake 019, February 1976 to April 1977. Lake abundance weighted on volumetric share of each zone (shallow = .06 lake volume; deep $=.94$ lake volume).


Ceriodaphnia quadrangula, the smallest Daphnidae in Lake 255, occurred principally during August although low numbers were found earlier in July (Fig. 24). Ephippial females were first observed in mid August and remained until latter November. Males were prevalent in early September, as in other minor cladoceran species, following the main population pulse in August.

Chaoborus appeared in the deep zone of Lake 255 only during late winter anoxia and briefly in June in both zones at low densities (Fig. 20). Gammarus, on the other hand, was much more prevalent particularly in the shallow zone among the vegetation. It was noted on the first sampling of the deep zone in February and became relatively abundant in mid May, attaining . 7 ind $L^{-1}$. Thereafter, offshore densities remained below 4 ind $L^{-1}$. Closer to shore, Gammarus was present continuously throughout the period May 12 to December 16 and displayed three abundance peaks, the first in mid June at 1.1 ind $L^{-1}$, the second a seasonal maximum of 3.2 ind $L^{-1}$ on July 26 and finally in September when densities ranged between .6 and .9 ind $L^{-1}$. It also occurred throughout the winter at densities between 0.4 and .3 ind $L^{-1}$.

## Lake 019

In contrast to Lakes 885 and 255, Lake 019 did not exhibit complete winter oxygen depletion mainly because of its larger size, 31.7 ha , and greater depth, $Z_{\max }=6.8 \mathrm{~m}$. This basic environmental difference was reflected in the development of two dominant species, ㄷ. b. thomasi and D. siciloides whose life cycles extended through winter without major disruption.

Some degree of species succession was evident in the unimodal seasonal pattern of Lake 019 crustacean abundance (Fig 12, 28 and 29). Cyclopoids were among the initial plankters to emerge in Lake 019. C. b. thomasi again
dominated the spring community, peaking at 36.1 ind $L^{-1}$ on May 27 in the shallow zone, much below levels in Lakes 255 and 885 . The appearance of C. vernalis and E. agilis was considerably advanced in Lake 019, in comparison to Lake 255. By late May, calanoids and most cladocerans were beginning a phase of rapid growth. D. parvula was the first herbivore to gain prominence on June 2 at 122.5 ind $L^{-1}$ in the deep zone where it was always more abundant. It quickly declined, however, and was succeeded by sharply increasing densities of $\underline{D}$. siciloides nauplii during the second week of June. The subsequent rise in D. siciloides copepodids through mid June was accompanied by a second D. parvula pulse with both reaching maximums on June 23. At the same time, with C. b. thomasi densities depressed. I. P. mexicanus developed a small initial pulse in the shallow zone. B. longirostris, displaying extremely rapid growth, was next to peak offshore on June 28. Concurrently, cyclopoid nauplii exhibited the second wave of a diacmic pattern characteristic of several other species in Lake 019. The early July C. b. thomasi maximum coincided with relative minima of ㅁ. siciloides, B. longirostris and declining D. parvula values. July 5 also saw $\underline{C}$. lacustris achieve its highest seasonal densities offshore. Maximum water temperatures in early July were coincident with declining C. ․ . thomasi concentrations.
B. longirostris, however, recovered for a brief period between July 12 and 19 and was followed by a second D. siciloides maximum on July 26. Two species, D. parvula and D. siciloides appeared to develop a small third generation, the former in late July and the latter beginning in late August as nauplii. With most species development decreasing through August, I. p. mexicanus gradually replaced all other cyclopoids and achieved its highest abundance by late September. During October and November, C. b. thomasi densities began to increase as I. p. mexicanus decreased.

By mid January C. ․ . thomasi copepodids had accumulated in substantial numbers beneath the ice with reproduction by adults leading to a cyclopoid nauplial peak in late March. As these nauplii declined in April, D. siciloides nauplii began another calanoid cycle.

Macrothrix laticornis, Alona rectangula and Diaphanosoma leuchtenbergianum occurred only in very low numbers. D. leuchtenbergianum developed mainly in July while $A$. rectangula exhibited a slight maximum in September-October.

In general, seasonal changes in species biomass were similar to those of abundance (Figs. 30 and 31). However, the fall-winter biomass of D. siciloides and C. $\underline{\text { b. }}$ thomasi was proportionally greater than their corresponding density because of larger fractions of matures. In addition to their temporal separation, the dominant cyclopoids in Lake 019 were of varying size. $\underline{C} . \underline{b}$. thomasi mature females ranged from . $85-1.3 \mathrm{~mm}$ while I.p. mexicanus was much smaller at $.58-.66 \mathrm{~mm}$. The sole calanoid, D. siciloides, measured from .93 to 1.30 mm over the season. Cladoceran sizes were also well separated with $B$. longirostris from $.23-.47 \mathrm{~mm}$, C. lacustris from . $43-.83 \mathrm{~mm}$ and D. parvula from .68 to 1.28 mm .

Development of C.B. thomasi was relatively comparable in both zones of Lake 019 through spring and summer but differed during winter (Fig. 32). In addition to immature instars, mature males and females were present in the deep zone on the first sampling date. Reproduction, however, did not begin until mid May when large clutches, 65-73 eggs per female, resulted in substantial egg and nauplial pulses in both zones. Brood sizes declined through June to 22-28 eggs per female and by mid July reproduction ceased. Egg production was noticeably stronger offshore during June, contributing to a larger cyclopoid nauplii pulse towards the end of the month. Reproduction occurred briefly in mid October and then resumed in January,

Figure 30. Seasonal changes in the biomass ( mg w w $10^{-1} \mathrm{~L}^{-1}$ ) of core cyclopoid and calanoid species in the shallow and deep zones of Lake 019, February 1976 to April 1977. Lake biomass weighted on volumetric share of each zone (shallow $=.06$ lake volume; deep $=.94$ lake volume).


Figure 31. Seasonal changes in the biomass (mg w w $10^{-1} \mathrm{~L}^{-1}$ ) of core cladoceran species in the shallow and deep zones of Lake 019, February 1976 to April 1977. Lake biomass weighted on volumetric share of each zone (shallow = .06 lake volume; deep $=.94$ lake volume).


Figure 32. Seasonal changes in the abundance (ind $L^{-1}$ ) of life history stages of core cyclopoid species in the shallow and deep zones of Lake 019, February 1976 to April 1977. For Cyclops vernal is and Eucyclops agilis only total copepodids presented.

exclusively offshore, with fecundities consistently high, between $60-80$ eggs per female, until its conclusion in mid April 1977. By mid March, 38.0 nauplii $L^{-1}$ had accumulated in the deep zone. Some shoreward migration was evident as shallow zone nauplius densities rose, in the absence of significant egg production, to 45.0 ind $L^{-1}$ by mid April.

In both zones, the initial $\underline{\text { C. }} \underline{\text { b }}$. thomasi copepodid pulses in late May - early June consisted primarily of immatures. With maturation, copepodid numbers declined to less than 10 ind $^{-1}$ by June 23 when $50 \%$ of the deep zone population consisted of adults. From the nauplii cohorts of late June, second copepodid pulses developed in early July, but adults never formed more than $10 \%$ of the populations at any time. By early August, most immature instars had disappeared from both zones. Low numbers of CIV-V and adults, mainly males, persisted for the next six weeks until September 24 when rising densities of CI-III and CIV-V signalled a resumption of reproduction. A few females matured and were producing eggs offshore by mid October. Through winter, all copepodid stages were substantially more abundant offshore than near shore with high proportions of adults present. By April 26, the first ice-free sampling date, copepodid densities were comparable in both zones with 19.2 ind $L^{-1}$ near shore. Lower offshore copepodid densities during late winter 1976 as compared to 1977 reflected the reduced oxygen tensions in the former year (Fig. 6).
I. p. mexicanus was basically a late summer-fall replacement for ㄷ. ㅎ. thomasi. It initially occurred, however, from February to April 1976 as mature females which were completing the previous year's cycle. The species was absent during May but reappeared on June 2 as immatures, mainly CI-III, initially accumulating in the slightly warmer inshore waters. A week later, mature males and gravid females occurred offshore. With significantly higher ( $5-10 \mathrm{x}$ ) densities of gravids near shore, a substantial egg pulse
first developed in the shallow zone. Average clutch sizes during this period were the year's highest, varying between $23-42$ eggs female ${ }^{-1}$, but stabilized between 12-18 eggs for the remainder of the reproductive cycle ending in early September. Although total egg production was higher offshore by mid June, developing copepodids tended to congregate near shore ( 13.2 ind $L^{-1}$ ) where fewer C.b. thomasi CIV-V and adult stages were present. With I.P. mexicanus fecundities declining in late June, CI-III recruitment fell and total copepodid densities were minimal by July 19. With lakewide depletion of C.b. thomasi towards the end of July, I.p. mexicanus began to increase. Significantly higher gravid female densities offshore from latter July to mid August resulted in a larger deep zone egg pulse during that period. Nonetheless, copepodid numbers were comparable in both zones in early September, about 25 ind $L^{-1}$, with adults forming an important fraction. By mid October, more than $90 \%$ of copepodids were adults in contrast to the much lower fraction of $C$. $b$. thomasi adults and by mid November, as densities declined, the population was completely mature. From December to late March, significantly higher I.p. mexicanus concentrations were consistently found near shore. A few mature females were seen near shore on the last sampling date at the end of April.

The two less commmon cyclopoids in Lake 019, C. vernalis and E. agilis were found predominantly during May and June (Fig. 32). Both species were producing eggs under deep zone ice in March and April 1976. E. agilis continued to reproduce near shore until early June with a few final brief efforts in July. The main reproductive period of $\mathbb{C}$. vernalis occurred in the second half of June in both zones.

The dominant species in Lake 019, D. siciloides, attained the highest abundance of any calanoid under study with an offshore peak on July 26

Figure 33. Seasonal changes in the abundance (ind $L^{-1}$ ) of life history stages of Diaptomus siciloides and Daphnia parvula in the shallow and deep zones of Lake 019, February 1976 to April 1977.

of 202.8 copepodids $L^{-1}$ (Fig. 33). The annual average density of D. siciloides was 29.6 ind $L^{-1}$.

Reproduction of D. siciloides was continuous throughout the year, except during mid February 1976 and early March 1977 (Fig. 33 and Appendix T).

Largest clutches, averaging 20.5 eggs (range 15.4 to 26.0 ), were observed between May 12 and June 23. During the fall and early winter average broods were relatively high at 12.5 eggs (range 8.8-14.8). Total egg production was greater offshore than near shore, particularly during July, as a result of twice higher gravid female densities in the deep zone.
D. siciloides nauplii exhibited three pulses. The small quantities of nauplii in mid May originated either from reproducing adults or overwintering eggs. Highest nauplius density, 170 ind $L^{-1}$, occurred near shore on June 19 with 126.2 ind $L^{-1}$ in the deep zone a week later. After declining to a minimum of 5.0 ind $L^{-1}$ on July 5 , inshore nauplii rose to 54.9 ind $L^{-1}$ by July 12. The corresponding offshore maximum, 71.6 ind $L^{-1}$, took place in late July. The final nauplius pulse occurred offshore in late August and near shore in mid September before disappearing in mid October.
D. siciloides was relatively comparable in both zones with three CI-III pulses, corresponding to respective nauplius peaks, visible. The final pulse was considerably reduced. Gradual maturation and accumulation of later instars resulted in maximum copepodid densities, offshore on July 26. Near shore, slightly lower peak densities, 177.5 ind $L^{-1}$, and a reduced proportion of adults were observed in mid July. Abundances declined rapidly through early August and by months end, only a few adults remained in the lake. The small third pulse of CI-III appearing in early September,
eventually led to very consistent adult numbers throughout winter.
In common with all other Copepoda in Lake 019, males of D. siciloides were more numerous than females, particularly in the deep zone (Table 8).

Of all species in Lake 019, ㅁ. parvula displayed the greatest intrazonal differences, averaging 4.7 times higher densities and 9.6 times higher biomass levels offshore than inshore (Table 7). In both zones, however, growth was basically similar with two main periods, the first in late May - early June and the second in latter June. Several overwintering mature females, a few carrying single eggs were found offshore in February and March 1976. Soon after ice-out in late April, immatures, perhaps hatched from ephippia, were present in both zones. By mid May, gravid females were present in the deep zone carrying up to 11 eggs (mean 6.8), the seasonal maximum. Fecundities were high offshore during the remainder of May gradually falling to between 1 and 2 eggs per female in late July when reproduction became sporadic. Brood sizes were significantly(95\% C.I.) lower near shore during the only shallow zone reproductive period, May 12 to July 12, averaging about 2.0 eggs per female. Parthenogenesis resumed offshore briefly in early August and then finally for approximately one month from mid September to mid October when broods averaged from 3.5 to 5.9 eggs. Ephippial females were abundant ( 3.8 ind $L^{-1}$ ) offshore June 2, disappeared by July 5 and reoccurred in low numbers from October 15 to December 17. Near shore, occurrences of ephippial females were similar but abundances much lower. With adults and gravid female fractions increasing in late May, total egg production reached a peak offshore on June 2. On the same date, total female and male abundance maximized at 122.5 and 46.3 ind $L^{-1}$, respectively. In the shallow zone, corresponding peak values were 14.2 and 6.6 ind $\mathrm{L}^{-1}$. Offshore densities fell sharply within a week but recovered to $80.7 \mathrm{ind}^{-1}$
by June 23. Adults formed an average of $62 \%$ ( $47-75 \%$ range) of the deep zone population from the latter part of June to mid July while in the shallow zone, by contrast, immatures constituted the major portion, $81 \%$ (range $49-100 \%$ ), of the population, during this period. Males disappeared from the deep zone on July 12 (June 28 near shore) and were not seen until late September when they became involved in ephippial production during October and November (Appendices F and H). Total densities offshore were very low throughout August with a complete absence on August 26. Daphnids were generally not found in the shallow zone from mid July until late September. Some specimens occurred in the fall, mainly offshore, but numbers were always less than 2.5 ind $L^{-1}$. Immatures were last seen offshore on November 19, ephippial females on December 17, gravids on January 18 and females without eggs on March 10. Mature females left the shorezone on January 18.

Seasonal development of $B$. longirostris, the other major cladoceran in Lake 019, was centered within June and July during which time it occurred in higher concentrations offshore (Fig. 29). Gravid females were first detected offshore in February carrying 1.2 eggs and by mid May broods were averaging 4.6 eggs, the seasonal maximum (Appendix T). Fecundities gradually decreased to 1.1 eggs by July 26 when summer reproduction ceased. Egg densities peaked initially in mid June at 74 eggs $L^{-1}$ and even higher at 107.5 eggs $L^{-1}$ in mid July. Shallow zone fecundities were insignificantly lower during the comparable period April 29 to July 26 but total densities were $47 \%$ of that offshore because of reduced gravid female abundance. Corresponding near shore peaks were 30.3 egg L-1 on June 16 and $84.0 \mathrm{~L}^{-1}$ on July 12. Reproduction recommenced in November, exclusively in the deep zone, but with broods of usually only one egg and gravid
densities low, total production was minimal. It did, however, persist through winter until ice-out in late April 1977.

Males were not very abundant and occurred primarily offshore during June and early July. Highest quantities, 2.2 and 1.5 ind $L^{-1}$, were associated with population maxima in the deep zone on June 28 and in the shallow zone in early July respectively. Additionally, a few males were found offshore in mid December.

The occurrence of $\underline{C}$. lacustris was also mainly concentrated in June and July (Fig. 29). It was more uniformly spread throughout the lake than D. parvula, its average shallow densities almost $70 \%$ those offshore. During its reproductive period from June 9 to August 3, fecundities were similar in both zones with highest egg counts occurring in the earlier stages of its cycle (Appendix $T$ ). Males were found associated with ephippial females in late June - early July and finally in mid October, the last occasion on which the species was present.

The core species with the shortest appearance in Lake 019, D. leuchtenbergianum, was found primarily in the deep zone during July (Fig. 29). Mature females, ranging in size from .80 to 1.25 mm , carried 1 to 8 eggs only for a short duration in latter July although a few gravids were seen closer to shore in late June (Appendix $T$ ). No males were detected even in a re-examination of samples.
A. rectangula and M. laticornis were principally situated in the shallow regions of Lake 019 (Fig. 29), their mean densities approximately 21 and 16 times higher respectively, near shore than offshore. Alona was first found offshore in February and Macrothrix in late April but both were absent in the deeper zone on most remaining occasions. Highest Alona densities, 4.6 ind $\mathrm{L}^{-1}$, were observed inshore on September 24, making it the most abundant fall cladoceran. Under ice cover, densities
remained near . 5 ind $L^{-1}$ until the end of March when Alona disappeared. By late April 1977, development once again resumed.

Highest Macrothrix densities, 5.0 ind $\mathrm{L}^{-1}$, occurred in late May near shore. Through June and July it rose and fell in unison with Alona (Fig. 29). As with Alona, Macrothrix disappeared in late March but reappeared in late April.

Gammarus was almost completely absent from Lake 019 being found only on two occasions near shore, June 2 at .01 ind $L^{-1}$ and February 18, 1977 at .02 ind $\mathrm{L}^{-1}$ and once offshore on March 10,1977 at .004 ind $\mathrm{L}^{-1}$ (Fig. 20).

On the other hand, Chaoborus was relatively conmon in Lake 019. It was confined to the deep zone, except for three brief occurrences near shore, July 5 and 26 and August 19. Found in low numbers after ice-out in late April, it eventually left the plankton in late May to reappear in late June. Its presence was continuous until late August with peak development of .7 ind $L^{-1}$ on July 19. Fall and winter densities were very low, usually less than 0.1 ind $L^{-1}$.

## Variation of animal size and fecundity

Seasonal changes in body length of gravid females and their fecundity were consistent for most species. In general, all ovigerous females were larger and carried more eggs during cool water periods in spring and fall than mid summer (Figs. 34, 35 and 36). Some among lake variation in size and fecundity was noted. C.b. thomasi females were somewhat larger in Lake 019 from late May to early July and mid January to mid April (annual mean 1.18 mm , range $.91-1.34 \mathrm{~mm}$ ) than in Lake 255 (mean 1.04 mm , range $.81-1.23 \mathrm{~mm}$ ) or 885 (mean . 96 mm , range $.80-1.08 \mathrm{~mm}$ ) (Fig. 34). C.b. thomasi was largest in Lake 255 in mid May as well as during July and August. Highest

Figure 34. Seasonal changes in the length (tip of cephalothorax to base of caudal setae, mm) and fecundity (eggs female-1) of Cyclops bicuspidatus thomasi females in Lakes 019 255 and 885, April 1976 to April 1977. Data points represent means of measurements of 20 randomly selected deep zone gravid females.


Figure 35. Seasonal changes in the length (tip of cephalothorax to case of caudal setae, mm) and fecundity (eggs female ${ }^{-1}$ ) of Diaptomus siciloides females in Lakes 019 (March 1976 to Apri] 1977) and 255 (May 1976 to December 1976). Data points represent means of measurements of 20 randomly selected deep zone gravid females.


Figure 36. Seasonal changes in the length (tip of helmet to base of shell spine, mm) of ovigerous (-_) and ephippial (-------) Daphnia schoedleri and fecundity (eggs female ${ }^{-1}$ ) of ovigerous Daphnia Schoedleri (....) in the shallow and deep zones of Lakes 885 (0) and 255 (o), May 1976 to December 1976. Data points represent means of measurements of 20 randomly selected mature females.

fecundities were also usually found in Lake 019 except for early May in Lake 255 while lowest brood counts were found in Lake 885.
D. siciloides sizes in lakes 019 and 255, while not significantly different during summer, were larger in Lake 019 from September to November (Fig. 35) as well as in June.
D. schoedleri females were larger in Lake 885 than Lake 255 throughout the season except for late May individuals (Fig. 36). Whereas female sizes in Lake 255 declined through June from a May maximum, those in Lake 885 increased during June and fell later in July and August. While sizes stabilized near 2.00 mm through summer and fall in Lake 255, they increased steadily after mid August in Lake 885.

Ephippial females were also generally larger in Lake 885 than Lake 255. While ephippial and ovigerous female sizes in Lake 255 were comparable, in Lake 885 ephippial females were usually smaller than egg bearing specimens. No spatial variation in daphnid size was visible in Lake 255 but in Lake 885 larger individuals tended to accumulate nearshore during mid summer.

Average brood counts were highest in spring in both lakes and lowest during mid summer. Following summerkill in Lake 885, fecundities increased. While counts were usually similar in both zones of Lake 255, fecundities were higher in the deep zone of Lake 885 during the summer.
D. parvula in Lake 019's deep zone exhibited a mid summer depression of size and fecundity (Fig. 37). Ephippial female sizes in the fall were comparable with earlier parthogenetic females. Representative shallow zone data was not available because of low D. parvula densities.

Figure 37. Seasonal changes in the length (tip of helmet to base of shell spine, mm) of ovigerous ( _ _ ) and ephippial ( ----- ) Daphnia parvula and fecundity (eggs female $e^{-1}$ ) of ovigerous Daphnia parvula females in the deep zone of Lake 019, February 1976 to December 1976. Data points represent means of measurements of 20 randomly selected mature females.


## DISCUSSION

This study provided a detailed description of three zooplankton communities revealing significant qualitative and quantitative differences. To evaluate these differences, the chemical and primary production data of Srisuwantach (1978), the fish population data of Tavarutmaneegul (1978) and the results of Kling (unpublished) were used together with data collected by the author. This additional information simplified assessing the relative productivities of these lakes which represented a rather narrow range of eutrophy.

Morphological and Limnological Variations
Although Lakes 019,255 and 885 were situated within a 15 km radius, their thermal and chemical characteristics differed as a result of morphology and surrounding terrain. The degree to which vegetation enclosed the shorelines of Lakes 885 and 255 affected their mixing regimes as well as the amount of nutrients reaching them (Fig. $2 b, c$ ). For small, shallow Lake 255, exposure to prevailing southerly winds (Fisheries and Environment Canada) insured continuous complete circulation, indicated by the vertical homogeneity of seasonal temperature, oxygen and nutrient profiles (Fig. 4, 6; Table 2).

Small Lake 885, in contrast almost completely encircled by trees periodically stratified during summer leading to relatively steep thermal and chemical gradients (Figs. 4c; Table 2). Stagnation during a hot dry spell in late August ultimately resulted in complete oxygen depletion (Fig. 6). The importance of this shelter belt was shown in 1978 when, following removal of trees from a large extent of Lake 885 shoreline, summerkill did not occur and trout were harvested from the lake (G. Curry
pers. comm). In Lake 019, the longer fetch was responsible for mixing the upper 4-5 meter layer but was not enough to circulate bottom layers which remained cooler and anoxic through much of summer (Figs. 2a,4,6). Amount of exposure also influenced the accumulations of snow and ice. Prevailing northwesterly winds left highly exposed Lake 019 with thinnest snow but thickest ice during both winters. The narrow belt of trees on the western flank of Lake 885 offered only light wind protection giving a thicker snow mantle. Densely wooded north and west shore areas on Lake 255 allowed greater deposition of snow and a thinner ice cover. As a result Lake 255 opened and warmed most rapidly in spring. Heating of Lake 255 was also promoted by deeper penetration of light, as indicated by Secchi (Fig. 5) and light transmittance readings (Srisuwantach 1978) and greater absorption on submerged surfaces. Low water transparencies in Lake 885, particularly during heavy surface blooms, reduced light penetration and limited heating to upper strata. Density stabilization and minimal mixing resulted in bottom temperatures cooler than in Lake 255 (Fig. 4c). Thus in fact summer stratification in small Lake 885 more closely resembled that in deeper Lake 019 than in shallow Lake 255.

Although Srisuwantach (1978) termed all three lakes eutrophic, Lake 885 was clearly most productive, or hypertrophic, with lower Secchi visibility (Fig. 5), much higher chlorophyll-a and nutrient concentrations (Fig. 1, Tables 2,3), higher primary production and predominance of blue greens (Table 3). Despite the location of the lakes within a grey-black soil zone, Lakes 885 and 019 were underlain by medium textured soils developed on moderately calcareous boulder-till material (Erickson association) while Lake 255 was located on fine textured clay and sandy loams developed on lacustrine sediments (Onanole association, Sunde and Barica 1975).
As the lakes were landlocked, allochthomous nutrients entered via surface
runoff, groundwater flow and/or soil erosion. Thus Lake 885 , surrounded by cultivated, fertilized fields and adjoined by a farmstead, likely received considerable quantities of nutrients by seepage through a moderately coarse under burden. Nutrient inputs into Lake 255, on the other hand, were likely reduced by filtration through densely wooded shore areas and finely textured clays. Direct agricultural sources to Lake 255 were also lacking. Runoff and seepage from croplants, a barnyard and a domestic septic field contributed to the nutrient load of Lake 019.

Differences in seasonal oxygen concentrations, while influenced by mixing, were also related to lake trophy and morphology. In hypertrophic Lake 885, summer anoxia was related to the collapse of an Aphanizomenon bloom, followed by circulation of depleted bottom waters during a period of cooler, windy weather. Papst et al. (1980) found instantaneous oxygen demands of near bottom anoxic layers in Lake 885 to be as high as $24.8 \mathrm{mg} . \mathrm{L}^{-1}$. During winter, the severity of oxygen depletion and the accumulation of degradation by products were also related to lake trophy and morphology. Mathias and Barica (1980) found an inverse relationship between winter oxygen depletion rate and mean depth in prairie, southeastern Ontario, Arctic and ELA lakes. Lake trophic status also influenced winter oxygen depletion with sediments of eutrophic lakes consuming oxygen about 3 times faster ( $0.23 \mathrm{~g} \cdot \mathrm{~m}^{-2} . \mathrm{d}^{-1}$ ) than those of oligotrophic lakes ( $0.08 \mathrm{~g} \cdot \mathrm{~m}^{-2} \cdot \mathrm{~d}^{-1}$ ) although water column respiration was similar in both groups. Srisuwantach (1978) observed that Erickson lakes with maximum depths greater than 4.2 m rarely winter killed. Therefore, Lake $019\left(Z_{\max }=6.8 \mathrm{~m}\right)$ still contained approximately $5.0 \mathrm{mg} 0_{2} \mathrm{~L}^{-1}$ in its upper 3 meters in mid March 1977, while smaller shallower Lakes 255 and 885 had lower levels of oxygen in late winter (Fig. 6). Of these two, Lake 885 exhibited lower winter oxygen concentrations. By mid December,
for example, Lake 885 , at 1.0 m , was only $17 \%$ saturated with oxygen while Lake 255 was much higher at $75 \%$. In addition, the presence of hydrogen sulfide was initially noticed in mid December in Lake 885 but not until mid March 1977 in Lake 255. The extremely high concentrations of ammonia detected in Lake $885,2274-2430 \mu \mathrm{~g}^{-1}$, in mid February 1977 and corresponding lower values in Lake 019, $418-422 \mu \mathrm{~g}^{-1}$, and Lake 255, 330-346 $\mu \mathrm{g} \mathrm{L}^{-1}$, were positvely correlated with algal standing crops and production during the preceeding summer (Srisuwantach, 1978). As the pH remained above 8.0 throughout winter in 885 , much of the $\mathrm{H}_{2} \mathrm{~S}$ would have been in the highly toxic undissociated form (Schindler and Comita 1972). Similarly, some of the $\mathrm{NH}_{3}$, at these elevated pH levels, would occur as toxic $\mathrm{NH}_{4} \mathrm{OH}$. These compounds can be as important to crustacean survival as the level of oxygen depletion (Wierzbicka 1962, Elgmork 1973).

Periodic summer anoxic in Lake 885 may have possibly contributed to hypertrophy through regeneration of inorganic nutrients (Mortimer 1941, 1942; Hutchinson 1967; Richardson 1975). Schindler and Comita (1972) described the same mechanism maintaining a large phytoplankton population in Severson Lake.

Differences in phytoplankton, macrophytes, fish and invertebrate predators - other elements which appeared to influence zooplankton dynamics were also related to lake trophy and morphology. Srisuwantach (1978) concluded that blue greens were dominant, on an annual basis, in Lakes 885 and 019 with cryptomonads important in Lake 255 (Appendix E). However, in fact, during the main algal biomass peaks, Lake 019 was dominated by diatoms in late May and diatoms plus dinoflagellates in August-September. Similarly, blue greens were prevalent during the August-September biomass pulse in Lake 255. The mid summer Aphanizomenon bloom in Lake 885 was a response
to excessive nutrients and a low N:P ratio (4:1). Dominance of bluegreens is considered an indication of eutrophy (Teiling 1955; Rawson 1956). Higher N:P ratios of $12: 1$ and $41: 1$ in Lakes 255 and 019 respectively (Srisuwantach 1978), promoted diverse algal cultures (Schindler 1977) although biomass levels were reduced in these lakes. For example, algal biomass in Lake 255 was generally one order of magnitude lower than in Lake 885 (Fig. 8).

Extensive growth of submerged macrophytes in Lake 255, harbouring the highest number of littoral crustacean species, was associated with lake morphometry and trophy. Abundant daphnids may have also contributed to macrophyte development. With only minimal predation pressure by stocked trout, large D. schoedleri survived (Brooks and Dodson 1965), reaching sufficient densities by late May (Fig. 27) to reduce algal biomass (Fig. 8) resulting in higher Sechi visibility (Fig. 5). The same explanation for the clarification of several lakes and ponds was given by Shapiro. (1980). A proliferation of macrophytes followed, decreasing nutrient availability to phytoplankton and algal biomass declined further during June. During the second part of summer macrophyte growth slowed and algal biomass increased. Schindler and Comita (1972) described a similar chain of events in Lake Severson following winterkill. Elimination of fish with a corresponding increase in daphnids ultimately led to an "oligotrophication" of the lake marked by increased macrophyte production. The relative lack of macrophytes in Lake 885 was primarily related to reduced light penetration caused by dense algal blooms. Lake 885's bathymetry, similar to that of Lake 255, was not directly responsible for meagre plant development. In Lake 019, water transparency and bathymetry likely influenced the quantity and quality of macrophytes. Transparency and vegetative development were both moderate, relative to Lake 885 and 255 . The predominance of emergent

Scirpus and a general reduction in submergents, reflecting lower transparencies, contributed to reduced shorezone habitat diversity in Lake 019. Consequently, lower numbers of littoral crustacean species were found in Lake 019 than in Lake 255.

Only in Lake 019 were fish able to survive over winter. Crude estimates of Pimephales promelas and Culaea inconstants minimum total abundance, 43,000 to 86,000 fish $\mathrm{ha}^{-1}$, were well above levels known to initiate changes in nursery pond zooplankton (Grygierek 1965). Tavarutmaneegul (1978) estimated native Culaea inconstans densities in non winterkill Erickson Lake 200 at 80,000 fish ha ${ }^{-1}$ with a biomass of approximately $8.0 \mathrm{~g} \mathrm{~m}^{-2}$. He also described consumption of cladocerans by sticklebacks severe enough to depress the growth rate of competing stocked trout fingerlings.

In Lakes 255 and 885, annual winter oxygen depletion acting synergistically with $\mathrm{H}_{2} \mathrm{~S}$ and $\mathrm{NH}_{4} \mathrm{OH}$ likely prevented winter survival of fish. Intensive fishing during 1976 did not uncover either sticklebacks or minnows (Tavarutmaneegul 1978). Stocking programs since 1968 have not revealed overwintering fish in either lake (G. Curry pers. comm). The densities of rainbow trout stocked in these lakes, approximately 1500 fingerlings $h^{-1}$, had little effect on fish growth or survival (Lawler et al. 1974).

The abundance of invertebrate predators was clearly related to lake trophy and morphology. In Lake 019, Gammarus was cropped almost to extinction by dense schools of overwintering minnows and sticklebacks (Fig. 20). Chaoborus, however, attained maximum densities in the anoxic refuge of the deep zone during July. In winter killed Lakes 885 and 255 without native fish, Gammarus was much more abundant. Higher gammarid densities in Lake 255 were favoured by the dense vegetation for concealment from trout

Figure 38. Five parameters of the three study lakes compared with other North American lakes. Ranges ( $1-1$ ) and/or means ( $-\cdot \cdot$ ) of midsummer values presented; epilimnion values used for chemical parameters. ELA stands for Experimental Lakes Area, northwestern Ontario. Dotted vertical lines represent approximate trophic boundaries from Dobson et al. (1974) (modified from Archibald, 1977).

IPHYLL-A


PHOSPHORUS

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$\ldots$ ELA LAKES S.SASK. SALINE L. $\longmapsto$

DISSOLVED
$\left.n g l^{-1}\right)$


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019
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255 -885-1073


## ZOOPLANKTON

SS -ITY m) $\mathrm{g} / \mathrm{cm}^{-2}$ )

Table 9. Comparison of crustacean abundance in the Erickson study lakes during summer 1976 with several Canadian and Polish lakes.

\begin{tabular}{|c|c|c|c|c|c|c|c|c|c|c|c|}
\hline Lake \& Country \& Source \& \begin{tabular}{l}
Area \\
(ha)
\end{tabular} \& Max Depth (m) \& Mean Depth (m) \& Lake Type \& \[
\begin{aligned}
\& \text { Method } \\
\& \text { of } \\
\& \text { Collection }
\end{aligned}
\] \& \[
\begin{gathered}
\text { May- } \\
\text { ind/L }
\end{gathered}
\] \& Crust ober mg/L \& July-
ind/L \& ugus \(t\) mg/ \\
\hline Upinek \& Poland \& Patalas and Patalas (1968) \& 10.0 \& 5.0 \& 2.0 \& pond/eutrophic \& 5 liter trap \& 305 \& 4.470

2.455 \& 344
101 \& 5.542
1.587 <br>
\hline Piecek \& Poland \& Patalas and Patalas (1968) \& 23.3 \& 8.4 \& 3.4 \& dyst/eutrophic \& 5 liter trap \& 187
68 \& 2.455
0.857 \& 101
120 \& 1.294 <br>
\hline Smolak \& Poland \& Patalas and Patalas (1968) \& 5.3 \& 5.1 \& 2.4 \& dystrophic \& 5 liter trap \& 68

- \& 1.20 ${ }^{\text {a }}$ \& $52^{\text {b }}$ \& 1.29 <br>
\hline ELA 122 \& Canada \& Schindler and Novén (1971) \& 12.2 \& 12.8 \& 7.2 \& oligotrophic \& 29 liter trap \& - \& $2.60{ }^{\text {a }}$ \& $47^{\text {b }}$ \& - <br>
\hline ELA 132 \& Canada \& Schindler and Novén
(1971) \& 7.2 \& 8.4 \& 3.3 \& Oligotrophic \& 26 liter Schindler- \& \& \& 78.0 \& $3.61{ }^{\text {c }}$ <br>
\hline West Hal fway \& Canada (Yukon) \& Archibald (1977) \& 90 \& 4.7 \& \& oligotrophic \& 26 liter SchindlerPatalas trap \& \& \& 78.0
39.0 \& $1.66{ }^{\text {C }}$ <br>

\hline Pygmy \& Canada (Yukon) \& Archibald (1977) \& 50 \& 18.0 \& 5.0 \& oligotrophic \& | 26 Iiter Schindler- |
| :--- |
| Patalas trap |
| 10 liter Juday trap | \& \& \& $25^{\text {d }}$ \& <br>

\hline Hogans Pond \& Canada (Nfld.) \& Davis (1972) \& 60.1 \& 12.4 \& 5.0 \& mesotrophic \& 10 1iter Juday trap \& \& \& \& $66^{\text {e }}$ <br>
\hline Bauline Long Pond \& Canada (Nfid.) \& Davis (1973) \& 19.7 \& 9.0 \& 3.7 \& chthoniooligotrophic \& 10 Jiter Juday trap \& 214 \& 2.902 \& 319 \& 4.575 <br>
\hline 019 \& Canada \& present study \& 28.7 \& 6.8 \& 3.4 \& eutrophic \& modified Pennak tube \& 214 \& \& \& <br>
\hline 255 \& Canada \& present study \& 4.1 \& 2.7 \& 1.6 \& eutrophic \& modified Pennak tube \& 198 \& 7.161 \& 135 \& 6.869 <br>
\hline 885 \& Canada \& present study \& 2.4 \& 2.9 \& 1.7 \& hypertrophic \& modified Pennak tube \& 531 \& 17.418 \& 214 \& 24.169 <br>
\hline
\end{tabular}

a Converted to wet weight assuming dry weight $=0.06$ wet weight.

- Estimated from Schindler and Novén (1971).
c Includes rotifers.
d Estimated from Davis (1972).
e Estimated from Davis (1973).
(Holmstrom 1973). Chaoborus was least abundant in Lake 255 where oxygen was always plentiful near bottom throughout summer. It never formed more than $1 \%$ of trout diets. In Lake 885, Chaoborus survived winter anoxia but without the protection of submergent vegetation, they were preyed upon heavily during May comprising $90 \%$ by weight of trout food items. They subsequently remained marginal in the lake until the release of predation pressure by August summerkil1. Anderson and Raasveldt (1974) found Gammarus and Chaoborus to greatly influence the abundance and species composition of crustacean communities. In the study lakes, Chaoborus was collected during day time, indicating that it was permanently, rather than nightly, planktonic (Carter and Kwik 1977).

When viewed perspectively, prairie pothole lakes are thus extremely rich and productive (Fig. 38 modified from Archibald 1977). Mid summer mean values of chlorophyll-a, total phosphorus and Secchi visibility define Lake 885 as extremely eutrophic or hypertrophic, Lake 019 as eutrophic and Lake 255 as meso-eutrophic. This classification relates to open water regions rather and the lower trophy of Lake 255 is compensated by its rich macrophyte development. Lakes 019 and 255 are moderately saline while 885 is saline according to the criteria of Rawson and Moore (1944). However, because of the relative shallowness of the study lakes, their mean summer zooplankton biomass values, per unit area, fall within the same range as oligotrophic Yukon lakes. By considering instead, crustacean abundance per litre (Table 9), zooplankton densities within the Erickson lakes are among the highest recorded in the literature, being similar to eutrophic ponds in Poland (Patalas and Patalas 1968). Thus morphology and trophy directly influencing oxygen concentrations among other limnological parameters, played key roles in affecting biological productivity within

Lakes 019, 255 and 885
Annual Community Abundance, Biomass and Species Composition
Zooplankton abundance biomass and species composition were affected by a variety of factors of which morphology and trophy were most important. Greatest mean annual amounts of plankton per litre and per square centimeter occurred in shallow hypertrophic Lake 885 while lowest crustacean abundance and biomass per $\mathrm{cm}^{2}$ were found in meso-eutrophic Lake 255 (Table 6). Lake 019's abundance per $\mathrm{cm}^{2}$ was comparable to Lake because although Lake 019 was less eutrophic, the zone available to plankton was roughly twice as deep. Recalculating Lake 019 densities on the basis of the oxygenated strata only would raise abundances per litre above those in Lake 255. Substantially lower biomass in Lake 019 was the product of lower trophy, relative to Lake 885, and intense fish predation. Extremely abundant overwintering planktivores influenced crustacean biomass by selectively eliminating large daphnids. Although only a few immature D. schoedleri and D. magna were present in the plankton, numerous ephippia of both species were identified in samples containing sediment. Significantly smaller D. parvula ( .8 mm ) succeeded these larger species ( $>2.4 \mathrm{~mm}$ ) thus effecting a lower total biomass. Similar relative decreases in daphnid abundance under intense fish predation were observed by Grygierek (1962) Brooks and Dodson (1965), Galbraith (1967), Brooks (1968), Shapiro et al. (1975), Anderssonet al. (1975) and Shapiro (1980). On the other hand, Kajak and Zawisza (1973) saw no short-term changes in biomass with replacement of larger by smaller, more numerous filtrators in ponds stocked with two-year-old carp. Archibald (1977) reported changes in plankton composition but not biomass by planktivores in oligotrophic Yukon lakes. Lower annual biomass in Lake 019 was also associated with the
predominance of other small species such as $\underline{B}$. longirostris, and
I.P. mexicanus. The high abundance of these smaller crustaceans was likely related to the virtual elimination of their predators, Gammarus, (Anderson and Raasveldt 1974) by fish and their reduced vulnerability to fish predation. In Lakes 255 and 885, where Gammarus was abundant (Fig. 20), B. longirostris was scarce and I.p. mexicanus was absent. M. edax and $\underline{C}$. vernalis, found in Lake 255 , also also considered to have a profound effect on Bosmina populations (Kerfoot 1977). Gliwicz et al. (1978) found Mesocyclops leuckarti eliminating large portions of zooplankton biomass in the spring and considered Leptodora kindtii and Chaoborus flavicans more important predators than fish.

Zooplankton biomass per $\mathrm{cm}^{2}$ in mesotrophic Lake 255 was, despite its lower abundance, only slightly lower than in Lake 019 mainly because of large D. schoedleri and other medium sized species like D. rosea, M. albidus, D. leptopus, M. edax and A. denticornis which prevailed as a result of low fish predation (Hrbacek 1962; Brooks 1968). D. Schoedleri was also the main contributor to annual biomass in Lake 885. Coveney et al. (1977) reported a similar mean annual fresh weight biomass of $9.0 \mathrm{mg} \mathrm{L}^{-1}$ (range 3$29 \mathrm{mg} \mathrm{L}^{-1}$ ) from eutrophic Lake Bysjon where three species of Daphnia pulex, magna and longispina as well as Eudiaptomus graciloides dominated.

Rawson (1942) observed a positive correlation between zooplankton abundance and total dissolved solids as did Archibald (1977). Patalas (1972) found crustacean abundance related to chlorophyll-a as well as total phosphorus. Loadman (1980) suggested abundance was governed by primary productivity in four small lakes near Winnipeg, Manitoba. Annual crustacean abundance in her most eutrophic Lake 1, 151 ind $L^{-1}$ was similar to Lake 019; however, annual chlorophyll-a, $5.2 \mu \mathrm{~g}^{-1}$, was much below that of Lake 019 with $22.0 \mu \mathrm{~g} \mathrm{~L}^{-1}$ (Srisuwantach 1978). The large accumulations of algal
biomass in Lake 019 (Fig. 8) may be explained by the dominance ( $82 \%$ ) of B. longirostrus which could not utilize the larger algal cells. In Lake 1 , where summer cladoceran densities were $25 \%$ of levels in Lake 019, larger D. galeata mendotae, D. parvula and C. lacustris predominated over B. longirostris.

Litynski (1925), Bowkiewicz (1938) and Margalef (1968) cited in Gliwicz (1977)proposed that zooplankton species numbers as well as diversity decreased with increasing trophy. Although the Erickson lakes represented only the most productive end of the trophic spectrum, they conformed to this relationship, Lake 255 annually containing the highest number of species and Lake 885 the lowest (Table 6). Comparison of deep zone communities only, to minimize the bias of macrophytes, revealed the same trend though differences between Lakes 255 and 019 were not as wide (Table 7). The number of species sharing at least $1 \%$ of community annual mean abundance and biomass followed the same pattern with 7,5 and 2 species in Lakes 255, 019 and 885 respectively. Patalas and Patalas (1966) found crustacean species numbers decreasing with increasing trophy in Polish lakes. Decreased plankton diversity resulting from nutrient enrichment was found in Marion Lake by Dickman (1968). Roff and Kwiatkowski (1977) suggested that reduced zooplankton diversity in acidic Ontario lakes may have been related to the presence of blue-green algae. Of the two abundant species in Lake 885, ㄷ. ㅁ. thomasi is known to be eurytopic and ubiquitous, its distribution apparently limited by competition or predation, not by chemical factors (Reed 1958, Anderson 1974; Carter et al. 1980). It persisted as the sole crustacean species in aneutrophic arm of Schist Lake, Man. receiving mine tailings (Salki unpub.). D. schoedleri, is common to temporary ponds and winterkill lakes in western North America (Lei and Clifford 1974). Perhaps the ability of larger daphnids to synthesize haemoglobin for
adequate respiration of developing embryos during periods of reduced oxygen tensions (Fox et al. 1951, Pennak 1978), imparts a competitive advantage. Similar communities were described by George (1976) in Eglwys Nynydd, a shallow eutrophic Welsh reservoir where Cyclops vicinus and Daphnia hyalina co-existed and by Adalsteinsson (1979) in eutrophic Lake Myvatin inhabited by Cyclops abyssorum and Daphnia longispina.

Low diversity, as in Lake 885, was considered by Margalef (1968) and other characteristic of unstable environments. The absence of Chydoridae (C. sphaericus and A. rectangula) in Lake 885, in contrast to their abundance in Lake 255, was another indication of the relative instability of the former Lake. As Makrushin (1971) explained the Macrothricidae, Chydoridae and Bosminidae form primitive ephippia which are discarded only after a second moult, a disadvantage in highly variable situations like Lake 885. Daphnidae, on the other hand, form true ephippia which develop rapidly and are released immediately upon the first moult thus accounting for their dominance in ponds and small lakes noted for their instability. In agreement with Dickman (1968), Lake 885's low diversity was associated with high crustacean abundance and biomass.

A basic group of ten species were common to all three lakes (Table 6) and they contributed from 85 to $99 \%$ of community abundance and biomass. Of the eight species common in Loadmans' (1980) prairie lakes, all but Daphnia galeata mendotae were represented in the basic Erickson group. Of the 27 species identified by Patalas (1971) in shield lakes of the Experimental Lakes Area, northwestern Ontario (ELA), only 11 were found in the present study. Five of these, C.b. thomasi, C. vernalis, D. leptopus, D. schoedleri and B. longirostris were included in the basic Erickson group. ㅁ. schoedleri, however occurred in only two small ELA lakes both with extremely high, for this region ( 21.0 and $250 \mu \mathrm{~g}^{-1}$ ) chlorophyll-a
values. D. leptopus was found only in small ELA lakes while C. vernalis showed a tendency to smaller shallower lakes. Patalas (1964) also found D. leptopus common in shallow lakes and ponds in Colorado. One obvious distinction between shield and prairie lakes was the lack in ELA of D. siciloides. This species is usually associated with eutrophic (Comita 1972, Torke 1974), saline plains lakes (Reed and 0live 1958). It was not detected in 696 lakes in glaciated eastern North America by Carter et al. (1980). Of the 40 crustacean species occurring in the latter lakes, only C. ㄹ. thomasi, ․ vernalis, ․ leptopus, ․ rosea, ․ parvula and B. longirostris were found in prairie lakes. Of these six, ㄷ. ㅎ. thomasi, ㄷ. vernalis and B. longirostris were widely distributed and tolerated all extremes of lake morphometry temperature and water chemistry. Also, ㅁ. leptopus was associated with smaller but deeper lakes and $\underline{D}$. parvula was usually found in small shallower lakes. Although ㅁ. rosea was considered essentially a shallow water form by Brooks (1957), Carter found it only in lakes of maximum depth 18 m or greater.

The relative annual abundance of cyclopoids (Fig. 9) appeared to be related to the severity of winter oxygen depletion with highest proportions in Lake 885 and lowest in Lake 019. This trend primarily reflected relative densities of $\underline{\mathbf{C}}$. $\underline{\text { b }}$. thomasi which accounted for $99.8,88.9$ and $56.4 \%$ of annual cyclopoid abundance in Lakes 885, 255 and 019 respectively. The remaining species of the cyclopoid group did not exhibit this trend. Also despite these large differences in abundance, relative cyclopoid biomass was similar in all three lakes.

Certain cyclopoids, including ․ . ․ . thomasi, are recognized for their. wide physiological tolerance (Hutchinson 1967, Anderson 1974). Elgmork (1973) reported Cyclops scutifer, Mesocyclops oithonoides and Mesocyclops
leukarti passing through anaerobic layers containing $\mathrm{H}_{2} \mathrm{~S}$ to enter the sediments. Cyclops varicans and other cyclopoids tolerate anoxia on or in the benthos by building up an oxygen debt which they recover during nightly migrations to oxygenated water layers (Chaston, 1969).

The proportion of calanoid abundance and biomass were inversely related to the frequency and intensity of oxygen depletion (Fig. 9). Others, such as Gannon (1972), Patalas (1972) and McNaught (1975) have associated decreasing proportions of calanoids with increasing eutrophication in large lakes. Smaller Lakes 255 and 885 also followed this trend but in Lake 019 calanoid percentages were higher than expected. Calanoids, as a group, generally prefer deeper lakes (Patalas 1971). Loadman (1980) described a positive relationship between D. siciloides abundance and mean depth. Probably the $2-3^{\circ} \mathrm{C}$ cooler mean summer temperatures in the lower region of Lake 019's oxygenated layer were more suitable to D. siciloides than warmer Lake 255. Overwinter survival of mature D. siciloides in Lake 019 also contributed to higher calanoid fractions than in winterkilled Lake 255. O'brien (pers. comm.) found calanoids less vulnerable than cladocerans to fish predation. Perhaps in Lake 019, the dominance of D. siciloides was also partially a response to intense planktivory.

The relative annual abundance of cladocerans also varied inversely with the frequency and severity of anoxia (Fig. 9). In Lake 019, high cladoceran abundance was associated with numerous $\underline{B}$. longirostris while in Lakes 255 and 885 larger species such as $\underline{D}$. schoedleri presided in lower densities. These species variations were related to the relative densities of planktivores and invertebrate predators. In Lake 885, summer anoxia reduced cladoceran densities even further than in Lake 255.

Relative annual cladoceran biomass displayed a positive relationship with oxygen depletion, a lower fraction occurring in non depleted Lake 019
and larger percentages in winterkilled Lake 255 and 885. Species responses to fish predation likewise influenced this trend. Higher cladoceran biomass in Lake 885 than in Lake 255 was associated with the solitary presence of D. schoedleri. The success of this filtrator may have been related to its large size with higher filtration efficiencies (Burns 1968) and reduced susceptibility to cyclopoid predation (Lampert and Schober 1978). It can also utilize bacteria associated with phytoplankton degradation (Peterson et al. 1978; Daborn et al. 1978). The intestines of preserved daphnids were filled with decaying algae and detritus during Aphanizomenon blooms.

Horizontal variation of annual zooplankton community abundance and biomass was influenced by a variety of factors (Fig.10). In Lake 255, higher total densities nearshore were associated with the diverse habitat created by abundant macrophytes. Smyly (1952) and Straskraba (1965) cited in Pittinger (1978) held that abundance of littoral zooplankton was directly dependent on macrofloral density. As Lake 255 was continuously mixed and the vertical distribution of plankton was probably random, concentrations were not likely affected by depth. In Lake 019, offshore plankton concentrations were higher despite inclusion of anoxic bottom layers in calculations. As mixing usually reached 4-5 m, lower crustacean densities nearshore were related to high fish densities. Moderate macrophyte development in Lake 019 was not solely responsible for lowered nearshore crustacean abundance. On the other hand, the uniform distribution of plankton abundance in Lake 885 reflected its poorly developed macrophytes. These similar crustacean totals, however, masked opposing spatial preferences by C. ․ . thomasi (offshore) and D. schoedleri (nearshore, Table 7) as well as seasonal variation in zonal abundance.

The spatial variation of annual biomass was governed by factors influencing zooplankton abundance and composition (Fig. 10). In Lake 019, higher abundance and advanced population maturity of D. parvula, associated with reduced planktivory, contributed to greater deep zone biomass (Table 7). In contrast, smaller and less vulernable I. p. mexicanus was more abundant near shore. Additionally, it achieved a more advanced population age structure than larger C. ㅁ. thomasi which consisted of more mature individuals only during winter when fish grazing was slowed by temperature. C. b. thomasi, more common in deeper ELA lakes (Patalas 1971), and B. longirostris preferred the deeper zone of Lake 019. Cooler temperatures in deeper layers of Lake 019, likely encouraged greater accumulations of D. siciloides offshore but greater maturity also indicated reduced predation. By comparison, D. siciloides maturity in Lake 255, where fish predation was minimal was always proportionally higher than in Lake 019. The offshore zone of Lake 019 lacked two of the ten common species, M. albidus and $\underline{D}$. leptopus, known to generally prefer shallow waters (RyTov. 1963, Hammer and Sawchyn 1968, Pennak 1978).

In Lake 255, a smaller zonal variation in biomass was related to fewer but larger ㅁ. siciloides offshore and more numerous but smaller forms near shore(e.g. C. sphaericus, A.rectangula and C. quadrangula) (Table 7). The rich supply of epiphytes on near shore submergent surface likely favoured smaller cladocerans (Fryer 1968 cited in Downing 1980). Of the two daphnids in Lake 255 , smaller D. rosea clearly preferred the shallow zone while $\underline{D}$. schoedleri was more uniformly distributed. It is generally recognized that larger copepods and cladocerans are usually capable of grazing a wider size range of food particles (McQueen 1970; Berman and Richman 1974; Bogdan and McNaught 1975; Gliwicz 1977). Higher biomass of D. siciloides offshore was likely associated with its preference for
relatively deeper water.
In Lake 885 , substantially higher shallow zone biomass was related to significantly more abundant, larger and older D. schoedleri near shore. Causes of this distribution were not obvious but the presence of deoxygenated deeper layers in the offshore zone may have been partially responsible for lower per litre concentrations offshore. A cyclopoid-daphnid interaction (Lampert and Schober 1978) also possibly contributed to these differences. The frequent occurrence of several C. ․ . thomasi copepodids in the brood chambers of large D. schoedleri hinted of a close relationship between these species. This phenomenon was not observed in Lake 255 and Lake 019 daphnids. Whether or not a preservation artifact (Comita 1972, Edmondson 1974) or some form of parasitism was involved could only be determined by examining live material.

Seasonal Dynamics of Crustacean Zooplankton Communities
Seasonal changes in community abundance, biomass and species composition were influenced by varations in water temperature, dissolved oxygen and chemical concentrations, phytoplankton and predation. Detritus was also likely of some importance to zooplankton development but was not examined in this study. In spring, the initial rate of community development was primarily a function of water temperature (Fig. 12). Lake 255, warming most rapidly, was first to reach peak abundance in mid May, followed by slightly cooler Lake 885 in late May and coolest Lake 019 attaining an initial plateau in early June. The magnitude of this spring development, dominated in all three lakes by cyclopoids, mainly ㄷ. ․ . thomasi was basically related to the severity of winter oxygen depletion. In Lake 885 , with substantial nutrient regeneration (Srisuwantach 1978), high algal biomass developed during March and April (Fig. 8). The large cohort of emerging ClV-V, likely utilizing protozoans and bacteria (Monakov and Sorokin 1972 cited in Adalsteinsson 1979), matured and rapidly increased. Fewer gammarids plus delayed and restricted de-
velopment of other cyclopoids as a result of winter anoxia, $\mathrm{H}_{2} \mathrm{~S}$ and $\mathrm{NH}_{4} \mathrm{OH}$, also possibly favoured extreme $\underline{\mathrm{C}}$. b. thomasi densities.

In moderately depleted Lake 255 , a substantially smaller cohort of CIV-V emerged. Algal biomass under ice was lower but protozoan biomass was higher than in Lake 885. Relatively high densities of five other cooccurring cyclopoids, and higher gammarid densities, associated with milder winterkill, may have affected lower C. ㅁ. thomasi concentrations.

In Lake 019, several mature ㄷ. ․ . thomasi overwintered and were the main source of spring development rather than existing CIV-V. Spring algal biomass, similar to Lake 885 and abundant protozoans, did not positively effect C. b. thomasi. Relatively high densities of potentially predacious C. vernalis and $\underline{E}$. agilis may have contributed to restricted $\underline{C}$. b. thomasi densities. Loadman (1980) also found cyclopoids dominant in spring with a maximum of $544 \underline{\text { C.b. }}$. thomasi $L^{-1}$ in Lake 1 compared to 68 ind $L^{-1}$ in Lake 019. At the same time, C. vernalis and M. edax were virtually absent in Loadman's lake, predominating only when C. b. thomasi was scarce. Patalas (1972) found C. vernalis abundant in the Great Lakes only when C. b. thomasi was not. It is difficult to precisely determine the nature of these cyclopoid interactions. Anderson (1970c) suggested that predaceous species, both cyclopoid and diaptomid, are potential predators on each other, where the role of predator or prey is determined by the relative size or instar of each species. In the Erickson lakes, E. agilis, C. vernalis, M. edax and M. albidus were all larger than C. ㅂ. thomasi.

Another suggestion of cyclopoid interaction was provided by variation in the start of egg production. In Lake 885, numerous C. b. thomasi gravid females were first noted on April 27. Only a few $\mathbb{C}$. vernalis females carried eggs at the time. Half as many gravid C. ․ thomasi females appeared simultaneously in Lake 255 accompanied by considerably more ovi-
gerous C. vernalis females and several M. edax adults. In Lake 019, C. vernalis and E. agilis were producing eggs earlier in March while low numbers of gravid $\underline{C}$. b. thomasi females were not seen until mid May.

In response to warming temperatures, community abundance and composition began to change. Maximum C. b. thomasi egg production in each lake occurred between $12-14^{\circ} \mathrm{C}$, temperatures achieved approximately in early and mid May and early June in Lakes 255, 885 and 019 respectively. Subsequent respective total copepodid densities peaked about two weeks later in mid and late May and mid June, the timing of this sequence influenced by several factors including temperature, competition and predation.

With the shift to cladocerans $\underline{B}$. longirostris and $\underline{D}$. parvula and to D. siciloides, Lake 019 community abundance and biomass increased through June and into July. At that time, maximum diversity, 13 species, was also reached. Despite increasing numbers of herbivores, algal biomass rose during this period and phytoplankton - zooplankton biomass ratios ( $P / Z$ ), a rough measure of the grazing intensity of filtrators (Ruttner 1938 cited in Adalsteinsson 1979) averaged 1.0. Presumably smaller algae were eaten while larger forms accumulated.

In Lake 255 during the same period, lowest zooplankton community abundance and biomass was associated with highest diversity, 18 species, principally including $\underline{D}$. siciloides, the dominant mid summer species, D. schoedleri and several cyclopoids of which M. edax was most important. Summer substitution of the genus Cyclops by Mesocyclops is well documented (Hutchinson 1967). Lowest algal biomass in Lake 255 during June - July, resulting in an average $P / Z=.28$, indicated heavy grazing pressure by dominant D. siciloides.

In Lake 885, although community abundance declined, through June and July, and diversity was moderate with 10 species, ㄷ. ㅁ. thomasi remained
the dominant species with E. agilis, C. vernalis, M. albidus, present only in very low numbers. Gammarus was also relatively scarce during mid summer. The continued prevalence of $\underline{C}$. b. thomasi, in spite of high summer temperatures, indicated that its abundance was determined by a complex of factors including invertebrate predation, considered by Anderson (1974) as most crucial to its dispersal. Whereas D. schoedleri accounted for only $14 \%$ of community abundance during this period it was responsible for more than $80 \%$ of the total biomass. With algal biomass fluctuating two orders of magnitude during June and July, P/Z varied from a low value of .03 in mid June to a high of 11.45 in mid July. Kajak and Hilbricht Ilkowska (1972) cited in Adalsteinsson (1978), reported P/Z ratios ranging from 0.3 for oligotrophic Lake Krugloe to 7.1 for the Rybinsk reservoir. The striking low values in Lake 885 were associated with intense daphnid grazing on relatively abundant chlorophytes and cryptophytes (Appendix E) producing a clarification of the water column in latter June. A similar change was observed by Daborn et al. (1978) who calculated that 932 D. pulex $L^{-1}$ in sewage oxidation ponds without predators could filter all phytoplankton within 24 hours. As Lake 885 stratified in early July and nitrogen became deficient (Srisuwantach 1978), large Aphanizomenon accumulations, of little direct food value to D. schoedleri (Sorokin 1968; Edmondson 1974; Andersson et al. 1975), resulted in the high $P / Z$ values of mid July.

During August, total abundance and biomass declined in both Lakes 885 and 019 but for different reasons. In Lake 885, D. schoedleri was severely affected by decreasing oxygen concentrations evidenced by the large drop in total biomass (Fig. 12). Also a major evacuation from and cessation of egg production within the deoxygenated offshore zone was noted. Abundance declined from over 200 to less than 10 ind $L^{-1}$ during late August anoxia
(Fig. 18). Daborn et al. (1978) noted a similar decline of D. pulex when aeration of sewage ponds was discontinued. With algae biomass decreasing an order of magnitude during August, $P / Z$ also dropped from 80.0 to 12.0 , still high and indicating little direct daphnid grazing.
C. ․ . thomasi, unlike ․ . schoedleri, remained offshore and produced eggs throughout anoxia. Relatively low copepodid densities in Lake 885 during August were, as in Lakes 255 and 019, a normal cyclical feature of $\underline{C}$. $\underline{\text { b }}$. thomasi rather than a response to anoxia. Similar patterns for this species were found by Loadman (1980). However, high nauplii mortality occurred in Lake 885 during August in contrast to their sustained survival in Lake 255, 019 and Fort White lakes. Perhaps either a lack of proper food, toxic algal exudates (Gentile and Maloney 1968, Pennak 1973) or canabalism by CIV-V and adults (Anderson 1970b) deterred nauplii survival during this period. Although species diversity was moderate through the first half of August, only three species, ㄷ. ․ . thomasi, D. schoedleri and D. leptopus persisted without interruption through summerkill (Fig. 14).

In Lake 019 during late July and August, rapidly declining total densities, primarily of $\underline{B}$. longirostris and $\underline{D}$. siciloides were not associated with any significant, sharp perturbations in water temperature, transparency, dissolved oxygen or nutrient concentration. Community diversity remained fairly high with 12 species, their occurrences uninterrupted. As crustacean biomass descreased substantially, algal biomass increased slightly with $P / Z$ climbing from 1.5 in late July to 30.3 by mid August. No significant changes in phytoplankton composition were apparent during this period (Srisuwantach 1978). Rather, the decline of both grazers, B. Iongirostris and D. siciloides, was a function of invertebrate predation.

Despite moderate and consistant fecundities, B. longirostris densities dropped, particularly the proportions of ovigerous females. Similarly D. siciloides produced substantial amounts of eggs and nauplii through July and August, but transformation to CI-III was relatively unsuccessful (Fig. 33). In Lake 255 by comparison, further advancement of D. siciloides nauplii during August was much more successful (Fig. 25). Favourable growth of $\underline{D}$. siciloides was also noted by Comita (1972) and Loadman (1980). The high mortality of Bosmina and diaptomid nauplii was most likely related to predatory Chaoborus resident offshore in Lake 019 (Fig. 20). Federenko (1975) determined B. longirostris to be the major prey of C. americanus and C. trivittatus larval instars II to IV. An absence of B. longirostris in two fishless lakes containing high amounts of Chaoborus was reported by von Ende (1979). Anderson and Raasveldt (1974) identified diaptomid nauplii as common prey of Chaoborus instar IV. Chaoborus may have also contributed to the paucity of B. longirostris in Lake 885.

In Lake 255, August increases in total abundance and biomass, mainly related to cladocerans D. rosea, C. quadrangula, C. sphaericus, A. rectangula and a second pulse of ㅁ. schoederli, contrasted with Lake 885 declines. High diversity, $16-17$ species, persisted through August and into September. Although algal biomass reached its summer maximum during August, the low average $P / Z=.30$ suggested continued grazing pressure.

The increases in Lakes 885 community diversity, abundance and biomass immediately following summerkill were responses to rapidly improving oxygen conditions initiated by cooler, windy, wet weather. The dramatic rise in $\underline{C}$. $\underline{\text { b }}$. thomasi and ㅁ. schoedleri juvenile densities in September were related to the significantly larger broods carried by surviving females as well as reduced nauplial and immature daphnid mortality. A postkill increase in protozoan and algae biomass (Fig. 8) may have contributed to
improved recruitment. Summerkill in Lake 885 was obviously not as catastrophic as that observed by Dunn (1970) in a tropical pond where crustaceans finally reappeared after 18 days. Because of adult survival in refugia throughout the lake, repopulation of Lake 885 was not primarily dependent on resistant stages as in rotenone treated lakes (Anderson 1970a).

In September, the replacement of C. ․ . thomasi by I.p. mexicanus in Lake 019 was possibly related to fish predation. In the absence of intense planktivoryin Lakes 885 and 255 , C. b. thomasi developed a fall peak. I. P. mexicanus was absent from all four of Loadman's (1980) lakes where fish grazing was minimal.

In Lake 255, the late September abundance maximum was basically related to an increase of C. b. thomasi although several species including E. agilis, M. albidus and $\underline{C}$. varicans among cyclopoids and several cladocerans $\underline{D}$. rosea, $\underline{C}$. sphaericus and $\underline{A}$. rectangula also became abundant. In all, 17 species occurred during this period. Community succession during the fall was related to decreasing water temperature and changing phytoplankton composition. D. schoedleri, predominant during July and August when cyanophytes were abundant, was displaced by $\underline{D}$. rosea in the fall when smaller flagellated algae prevailed (Appendix E). Examining a similar interaction between Daphnia pulex and Ceriodaphnia reticulata, Lynch (1978) concluded that factors such as seasonal temperatures, cladoceran age structure and positive enhancement of algal resources by each co-exploiter were involved. For example, shifts in the competitive ability of daphnid species were related to the effect of declining water temperature on maximum feeding efficiencies. Lynch also held evidence of the maintenance of Aphanizomenon blooms in Minnesota ponds by daphnid grazing of algal
competitors. Donald (1971) described the succession of D. magna by D. rosea in a temporary pond in Alberta. Frank (1957) demonstrated a competitive exclusion of $\underline{D}$. magna by $\underline{D}$. pulicaria, the latter species inducing a shift from parthenogenesis to male and ephippial production in the former. However, he could not rule out oxygen and food as limiting factors.

The general decline of crustacean abundance and biomass in each lake during late fall and winter 1976-77 reflected the slowing of physiological activity in cooler temperatures. Abundance and duration of each community was governed by the rate of oxygen depletion. Earliest crustacean depletion occurred by January in Lake 885 where oxygen, disappeared most rapidly, likely a consequence of Lake 885's lower fall oxygen content and largest decomposing algal biomass. A month later, Lake 255's community was substantially depressed. In contrast, crustaceans consistantly increased in Lake 019 through winter in the presence of sufficient oxygen. Slightly warmer temperatures may have also enhanced growth. Lowest abundance during mid to late winter in Lake 885 was associated with the largest oxygen deficit and highest $\mathrm{H}_{2} \mathrm{~S}$ and $\mathrm{NH}_{4} \mathrm{OH}$ concentrations. Highest abundance and biomass persisted in non winterkilled Lake 019 while moderate abundances occurred in Lake 255.

The total number of species surviving through winter reflected the severity of anoxia in each lake. In March, only two species were found in Lake 885, five in Lake 255 and as many as seven in Lake 019.

From fall until ice out 1977, cyclopoids, primarily C. b. thomasi numerically dominated each community. With a few exceptions they also dominated biomass. Only in Lake 019 were calanoids, represented by D. siciloides, able to overwinter actively. In addition, 3 cladocerans D. parvula, A. rectangula and M. laticornis were present until mid March
in Lake 019 whereas C. sphaericus and A. rectangula endured only until mid January in Lake 255. No cladocerans existed beyond December in Lake 885.

As in 1976, the rate of community spring development in 1977 was dependent on the date of ice out and water temperatures with most rapid heating contributing to advanced growth in Lake 255.

Selected Seasonal Aspects of Major Species
Perhaps one of the most interesting facts revealed by this study was the remarkable adaptability of certain zooplankton species to particular trophic, morphologic and biotic constraints. Apart from obvious distinctions in amplitude, periodicity and age structure, the seasonal dynamics of $\underline{C}$. b. thomasi in each lake were marked by differences in reproduction and diapause. Only in Lake 019, where oxygen was available during winter, did C. ́. thomasi reproduce continuously under ice. Reproduction did not occur in Lakes 885 and 255 during winter. Instead, reproduction was sustained in Lake 885 throughout the entire ice-free period but was interrupted for one month (late June to late July) in Lake 255. On the other hand, during the open water season Lake 019 egg production occurred only from mid May to mid July.

In addition to this reproductive flexibility, ㄷ. b. thomasi exhibited the ability to overwinter primarily either as diapausing CIV-V or actively swimming copepodids depending on environmental conditions. In Lakes 885 and 255, fall and early winter C. b. thomasi did not advance beyond CIV-V prior to their disappearance from the plankton in January and February 1977 respectively. Copepodids IV-V were also the first instars to reappear in late winter in both lakes. In Lake 019, on the other hand, a significant portion of the population matured and reproduced with all
developmental stages present during winter, perhaps in response to warmer winter temperatures and higher oxygen levels. Thus, ㄷ. b. thomasi in Lakes 255 and 885 appeared to depart from the planktonic overwintering patterns of $\underline{C}$. $\underline{b}$. thomasi reported by Elgmork (1967).

More recently, Elgmork et al. (1978) proposed that cyclopoid diapause may be related to lake morphology, those species not displaying diapause occurring in largest and deepest lakes. This appeared to be the case of $\underline{C}$. $\underline{\text { b }}$. thomasi in Lake 019, the deepest study lake. Loadman (1980) also found overwintering, reproducing C. b. thomasi populations in adequately oxygenated Fort White lakes. All of the above findings support the contention of Wierzbicka (1962) that the initiation of diapause is controlled by oxygen concentration.

No convincing evidence of summer diapause by C. b. thomasi was found in the Erickson lakes. Substantial densities of C. b. thomasi adults and CIV-V were observed throughout the entire summer in Lake 885 despite summer anoxia. In Lakes 019 and 255, although lower summer C. b. thomasi abundances made it more difficult to draw conclusions regarding the possible initiation of diapause, no emergences of CIV-V were observed in late summer or fall to indicate a termination of diapause. ․ b. thomasi has generally been considered a "summer resting" cyclopoid (Elgmork 1967). Apparently, in eutrophic, shallower prairie lakes subject to winter anoxia, this species alters its period of dormancy.

Nilssen (1977) and Elgmork et al. (1978), finding no regularity in the control of diapause by abiotic factors, suggested biotic (fish and invertebrate predation) regulation. Diapause in the sediments could be regarded as a means of reducing or eliminating exposure of larger susceptible instars to predation. Despite numerous fish and Chaoborus predators in Lake 019, C. b. thomasi did not apparently diapause to avoid
predation.
The life cycle of $\underline{D}$. schoedleri, not featuring a summer resting phase, revealed the effects of summer anoxia in Lake 885. Whereas daphnid densities fell on order of magnitude during latter August in Lake 885, in Lake 258 they remained relatively constant near 25 ind $L^{-1}$ through this period. D. schoedleri population age structures and reproductive patterns were also dissimilar in these lakes. While mature to immature abundance ratios were relatively stable, from .8 to 1.2 , between August 17 to September 9 in Lake 255, those in Lake 885 concurrently fluctuated widely from .2 to 18.2. The changing ratios in Lake 885 indicated high immature mortality during anoxia and high juvenile recruitment following anoxia. Whereas egg production remained consistent during August in Lake 255, a sharp, mid August drop was observed in Lake 885. Through July and August, numerous ephippia were continuously produced in Lake 885 (Fig. 27) but very few in Lake 255. The high incidence and abundance of $\underline{D}$. schoedleri males and ephippial females in Lake 885 was a departure from normal daphnid development perhaps related to the omnipresent threat of algal collapse and anoxia. The appearance of males is usually restricted to shorter periods late in spring reproduction. Pennak (1978) suggests a probable complex of factors responsible for male daphnid development including (1) crowding (2) reduction of available food (3) water temperatures of $14^{\circ} \mathrm{C}$ to $17^{\circ} \mathrm{C}$, and (4) light intensity. Seasonal maximum male densities, 13.0 ind $\mathrm{L}^{-1}$, occurred in Lake 885 on September 16, coincidentally with a fall daphnid peak. High male densities were also associated with population pulses on June 29, July 10 and August 2. Mid summer ephippial female densities were higher during periods of increased algal biomass in Lake 885. In fall, ephippial densities remained high despite declining algal biomass and increasing to transparency. Declining
light intensity, as Pennak (1978) suggested was possibly influencing bisexua? reproduction in autumn.
D. siciloides in Lakes 019 and 255 reflected the environmental differences between these lakes. Although mean annual densities were similar in both lakes, the pattern of uniformly low abundance in Lake 255 (Fig. 24) contrasted with the very high mid summer pulse in Lake 019 (Fig. 28). Higher maximum abundance in Lake 019 was associated with eutrophy while brevity of the pulse was influenced by Chaoborus predation on nauplii recruits. In Lake 255, lower trophy contributed to lower D. siciloides densities. Seasonal D. siciloides abundance in Lake 255 was comparable to that found by Loadman (1980) but the apparent development of five generations in Lake 255 was closer to Comita's (1972) findings for Severson Lake.
D. siciloides egg production was continuous in non winterkilled Lake 019 except for a brief period on March 1977. In winterkilled Lake 255, gravid females were observed for a shorter period, between May 25 and December 16, 1976. Quantities of subitaneous eggs, produced in both lakes between late May and early September, averaged 14.8 and 13.3 eggs $L^{-1}$ in Lakes 019 and 255 respectively. However, substantially greater amounts of eggs were produced after September in Lake 255 (55.7 eggs $L^{-1}$ mean, Sept. 9 to Dec. 16) than in Lake 019 ( 1.4 eggs $L^{-1}$ mean Sept. 9 to March 25, 1977). In Lake 255 , most if not all of these were resting eggs produced before anoxia. In Lake 019 during winter, the majority of eggs carried by females were also likely resting eggs as nauplii were absent despite relatively high levels of oxygen.

Trophy and morphometry influenced oxygen conditions and were the main factors regulating biological production in Lakes 019, 255 and 885.

Local terrain strongly influenced lake trophy, stratification, snow depth and hydrology, consequently affecting thermal, oxygen and nutrient regimes. Annual zooplankton community abundance and biomass were correlated with lake productivity, although planktivorous fish had a considerable impact on crustacean biomass in Lake 019. Community diversity was inversely related to trophy while species composition was basically typical of shallow lakes. In Lake 019, however, community composition was also altered by severe fish predation. With increasing frequency and severity of anoxia among lakes, cyclopoids assumed greater importance but calanoid and cladoceran relative densities decreased. Relative biomass of cladocerans, however, was largest in hypertrophic Lake 885 and smallest in eutrophic Lake 019. Differing horizontal variation of plankton in each lake was associated with macrophyte development, fish predation and morphology.

The seasonal patterns of community abundance and species succession varied in each lake and were regulated by water temperature, dissolved oxygen, chemistry, phytoplankton and predation. Spring densities of C. b. thomasi were influenced by the severity of winter anoxia and the intensity of invertebrate predation. No evidence of summer diapause by C. b. thomasi was found in the Erickson lakes. Summer anoxia in Lake 885 inflicted heavy mortality on all ㅁ. schoedleri stages but nauplii were the
only C. b. thomasi instars to be severely affected. Polycyclic production of ephippia by $\underline{D}$. schoedleri in Lake 885 was a response to the continual threat of algal collapse and anoxia.

Fewest species were present in severely winterkilled Lake 885 while the winter community of oxygenated Lake 019 was most diverse. Winter diapause by C. ㅎ. thomasi was observed in both winterkilled lakes but not in Lake 019. ㄷ. ㅎ. thomasi and D. siciloides reproduction was continuous through winter in non winterkilled Lake 019. The pattern of C. b. thomasi summer reproduction varied in each lake.

Although differences in trophy and morphology among the lakes were rather small, they led to large differences in oxygen conditions and had a significant effect on crustacean plankton community composition and abundance and particularly seasonal population dynamics.

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Appendix A. Secchi disc visibility (m) at shallow and deep zone stations of Lake 019 during the open water seasons of 1976 and 1977. Zone means on date, deep zone station means during the period 28.6 to 24.9 and shallow zone station means during the period 28.6 to 9.9 provided.

|  |  |  |  | Stations |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Date | 1 | II | III | IV | $v$ | VI | $\bar{x}$ |

Lake 019

|  | 20.2 | - | - | - | - |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 22.3 | - | - | - | - 30 |  |  |  |
|  | 29.4 | - | - |  | 1.30 |  |  | 1.30 |
|  | 12.5 | . 60 | - | . 70 | - |  |  | . 65 |
|  | 27.5 | 1.42 | - 65 |  | - |  |  | 1.42 |
|  | 2.6 | - | 1.65 |  | - |  |  | 1.65 |
|  | 9.6 | 1.10 | 1.00 | - | - |  |  | 1.05 |
|  | 16.6 | - | - | 1.40 | - | - |  | 1.40 |
|  | 23.6 | - | 1.75 | 1.40 | - 70 |  |  | 1.58 |
|  | 28.6 | 1.60 | 1.40 | 1.75 | 1.70 | 1.00 | 1.60 | 1.51 |
| D | 5.7 | 1.45 | 1.45 | 1.55 | 1.55 | 1.00 | 1.45 | 1.41 |
| E | 12.7 | 1.10 | 1.20 | 1.20 | 1.35 | 1.00 | 1.40 | 1.21 |
| E | 19.7 | 1.10 | 1.00 | - | 1.10 | 1.10 | - | 1.08 |
| P | 26.7 | 1.00 | 1.10 | 1.05 | 1.30 | 1.10 | 1.30 | 1.14 |
|  | 3.8 | . 95 | . 95 | . 90 | . 95 | . 95 | . 95 | . 94 |
| 2 | 10.8 | . 85 | . 85 | . 95 | . 90 | . 75 | . 90 | . 87 |
| 0 | 19.8 | - | - | . 90 | . 90 | . 85 | - | . 88 |
| N | 26.8 | 1.10 | 1.10 | 1.10 | 1.15 | . 90 | 1.20 | 1.09 |
| E | 9.9 | . 90 | . 90 | - | - | . 90 | . 90 | . 90 |
|  | 24.9 | 1.20 | 1.25 | 1.20 | 1.15 . | 1.35 | 1.45 | 1.27 |
|  | 15.10 | . 90 | - | - | - | - | - | 90 |
|  | 19.11 | - | - | - | - |  |  |  |
|  | 17.12 | - | - | - | - | - |  |  |
|  | 18.1 | - | - | - | - | - |  |  |
|  | 18.2 | - | - | - | - |  |  |  |
|  | 10.3 | - | - | - | - |  |  |  |
|  | 25.3 | - | - | - | - | - |  |  |
|  | 12.4 | - | - | - | - | - |  | 70 |
|  | 26.4 | . 70 | - | - | - | - | - | . 70 |
|  | $\begin{gathered} \stackrel{\bar{x}}{(28.6-24.9)} \end{gathered}$ | 1.10 | 1.10 | 1.15 | 1.18 | . 99 | 1.20 | 1.12 |
|  | 20.2 | - | - | - | - | - | - |  |
|  | 22.3 | - | - | - | - | - | - |  |
|  | 29.4 | 1.20 | -75 | - | - |  |  | 1.20 |
|  | 12.5 | - | . 75 | 0 | - | . 75 |  | . 75 |
|  | 27.5 | - | - | 1.42 | - | 1.42 | - | 1.42 |
|  | 2.6 | 1.65 | - | - | - - | - | - | 1.65 |
|  | 9.6 | - | - | - | - | - |  |  |
|  | 16.6 | 1.40 | 1.40 | - | - | - | - | 1.40 |
| S | 23.6 | 1.60 | - 3 | , |  |  |  | 1.60 |
| H | 28.6 | 1.50 | 1.35 | 1.30 | 1.20 | 1.30 | 1.50 | 1.36 |
| A | 5.7 | 1.45 | 1.45 | 1.35 | 1.10 | 1.15 | 2.00 | 1.42 |
| $L$ | 12.7 | 1.40 | 1.05 | 1.25 | 1.20 | 1.10 | 1.25 | 1.21 |
| $L$ | 19.7 | 1.10 | - | 1.10 | - | 1.10 | 1.10 | 1.10 |
| 0 | 26.7 | 1.10 | 1.15 | 1.10 | 1.10 | 1.05 | 1.15 | 1.11 |
| W | 3.8 | . 95 | . 95 | . 95 | 1.00 | . 95 | . 90 | . 95 |
|  | 10.8 | . 75 | . 85 | . 80 | 1.00 | . 98 | . 95 | . 89 |
| 2 | 19.8 | . 80 | - | - | . 85 | . 80 | - | . 82 |
| 0 | 26.8 | 1.10 | 1.00 | 1.05 | 1.05 | 1.00 | 1.00 | 1.03 |
| $N$ | 9.9 | . 90 | . | - | - | . 85 | . 85 | . 87 |
| E | 24.9 | 1.15 | - | 1.30 | 1.25 | - | 1.20 | 1.23 |
|  | 15.10 |  | - | - | - | - | 1.00 | 1.00 |
|  | 19.11 | - | - | - | - | - | - |  |
|  | 17.12 | - | - | - | - | - | - |  |
|  | 18.1 | - | - | - | - | - | - | - |
|  | 18.2 | - | - | - | - | - | - | - |
|  | 10.3 | - | - | - | - | - | - |  |
|  | 25.3 | - | - | - | - | - | - |  |
|  | 12.4 | - | - | - | - | - | - | - |
|  | 26.4 | - | - | - | - | - | - | - |
|  | $\underset{(28.6-9.9)}{\bar{x}}$ | 1.11 | 1.08 | 1.06 | 1.05 | 1.03 | 1.15 | 1.08 |

Appendix B. Secchi disc visibility (m) at shallow and deep zone stations of Lake 255 during the open water seasons of 1976 and 1977. Readings to lake bottom indicated as B. Zone means on each date provided.

|  | Date | I | II | Stations III | IV | $V$ | $\bar{\chi}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Lake 255 |  |  |  |  |  |  |  |
|  | 19.2 | - | - | - | - | - | - |
|  | 21.3 | - | - |  |  |  | 90 |
|  | 26.4 | - | - | .90 | - | - | . 90 |
|  | 30.4 | - | - | - | - |  | 70 |
|  | 12.5 | - | - | $\bar{B}$ | $\bar{\square}$ | . 70 | . 70 |
|  | 25.5 | B | B | B | B | 2.65 | 1 |
|  | 31.5 | B | 8 | B | B | 2.50 |  |
|  | 8.6 | B | B | 8 | B | 2.60 |  |
|  | 17.6 | B | B | B | B | 2.80 |  |
|  | 22.6 | B | B | B | B | 2.75 | >2.50 |
|  | 28.6 | 8 | 8 | B | B | 2.85 | (To Bottom) |
| D | 6.7 | B | B | B | B | 2.80 |  |
| E | 13.7 | B | 8 | B | B | 2.80 |  |
| E | 20.7 | B | B | 8 | B | 2.75 |  |
| P | 26.7 | B | B | B | B | 2.78 |  |
|  | 3.8 | B | B | B | B | 2.75 |  |
| 2 | 9.8 | B | 8 | B | B | 2.75 |  |
| 0 | 17.8 | B | B | B | B | 2.80 |  |
| N | 22.8 | - | 2.10 | 2.10 | 2.00 | 2.45 | 2.22 |
| E | 9.9 | $\bar{\square}$ | - | - | - | 2.20 | 2.20 -250 |
|  | 17.9 | B | B | 8 | B | 2.65 2.70 | ( 70.50 |
|  | 24.9 | B | B | B | B | 2.70 | (To Bottom) |
|  | 14.10 | B | B | B | B | 2.65 |  |
|  | 19.11 | - | - | - | - | - |  |
|  | 15.12 | - | - | - | - | - | - |
|  | 16.1 | - | - | - | - | - | - |
|  | 16.2 | - | - | - | - | - | - |
|  | 9.3 | - | - | - | - |  |  |
|  | 25.3 | - | - | - | - | - |  |
|  | 12.4 | - | - | - |  | 1.00 | 1.00 |
|  | 25.4 | - | - | - | - | 1.00 | 1.00 |
|  | $\bar{\chi}$ | - | - | - | - | - | >2.4 |
|  | 19.2 | - | - | - | - | - | - |
|  | 21.3 | - | - | - | - | - | - |
|  | 26.4 | - | - | - | - | $\cdots$ | - |
|  | 30.4 | - | - | 70 |  | - |  |
|  | 12.5 | .$^{70}$ | B | .$^{70}$ | .$^{70}$ | 8 | .$^{70}$ |
|  | 25.5 | B | B | B | B | 8 |  |
|  | 31.5 | B | B | B | B | B |  |
|  | 8.6 | 8 | 8 | 8 | B | B |  |
|  | 17.6 | B | B | B | B | B |  |
| H | 22.6 28.6 | B | B. | B | B | B |  |
| A | 6.7 | B | B | B | B | B |  |
| 1 | 13.7 | B | B | B | 8 | B |  |
| 1 | 20.7 | B | B | B | B | B | (To Bottom) |
| 0 | 26.7 | B | B | B | B | B |  |
| W | 3.8 | B | B | B | ${ }^{8}$ | B |  |
|  | 9.8 | B | B | B | ${ }_{8}^{B}$ | 8 |  |
| 2 | 17.8 | B | B | 8 | ${ }_{8}^{8}$ | B |  |
| 0 | 22.8 | B | B | 8 | ${ }^{\text {B }}$ | ${ }_{8}$ |  |
| $N$ | 9.9 | B | B | B | B | B |  |
| E | 17.9 24.9 | ${ }^{\text {B }}$ | B B | 8 | B | B | 1 |
|  | 14.10 | B | 8 | B | B | B | B |
|  | 19.11 | - | - | - | - | - |  |
|  | 15.12 | - | - | - | - |  |  |
|  | 16.1 | - | - | - | - | - |  |
|  | 16.2 | - | - | - | - | - |  |
|  | 9.3 | - | - | - | - | - |  |
|  | 25.3 | - | - | - | - | - | - |
|  | 12.4 | - | - | - | - | - | - |
|  | 25.4 | - | - | - | - | - | - |

Appenaix
Lake 885 during the open water seasons of 1976 and 1977. Readings to lake bottom indicated as $B$. Zone means on each date and deep zone station means during the period 6.7 to 23.9 provided.

Stations
Dat

|  | 19.2 | - | - | - | - |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 21.3 |  |  |  |  |  | 60 |
|  | 27.4 | . 60 | - | - |  | 30 | . 30 |
|  | 13.5 | - | - |  |  | . 32 | . 32 |
|  | 26.5 | - |  |  |  | . 50 | .50 |
|  | 1.6 | - |  |  |  |  |  |
|  | 10.6 | - | - | - |  | 70 | . 70 |
|  | 17.6 | - | - |  |  | 2.25 | 2.25 |
|  | 23.6 | - | 3.15 |  | - |  | 3.15 |
|  | 29.6 | B | 3.15 | 90 | . 90 | . 90 | . 89 |
|  | 6.7 | . 85 | . 90 | . 90 | . 90 |  | . 70 |
| 0 | 13.7 | . 70 | . 30 | . 40 | . 40 | . 45 | . 38 |
| E | 20.7 | . 35 | . 30 | . 50 | . 55 | . 50 | . 49 |
| E | 27.7 | . 45 | . 45 | . 85 | . 85 | . 80 | . 78 |
| P | 4.8 | .60 .05 | .80 1.10 | 1.10 | 1.18 | 1.10 | 1.11 |
|  | 10.8 | 1.05 | 1.10 | 1.10 | 1.25 | $\underline{-}$ | 1.40 |
| 2 | 17.8 | 1.55 | 2.05 | 1.95 | 1.80 | 1.95 | 1.94 |
| 0 | 22.8 | 1.95 | 2.05 | 1.95 | 1.80 | - | 1:85 |
| $N$ | 26.8 | 1.85 | 1.85 1.30 | 1.30 | 1.40 | 1.50 | 1.36 |
| E | 29.8 | 1.30 | 1.30 | 2.50 |  | 2.20 | 2.42 |
|  | 1.9 | 2.55 | 2.15 | 2.50 | - | . 2 | 2.13 |
|  | 10.9 | 2.00 | 2.15 | 2.25 | - | 2.10 | 2.20 |
|  | 16.9 | 2.30 | 2.25 | 2.15 | 1.35 | 1.50 | 1.30 |
|  | 23.9 | 1.30 | 1.30 | 1.05 | 1.35 | 1.50 | . 50 |
|  | 14.10 | . 50 | . 50 | - | - | - |  |
|  | 18.11 | - | - | - | - | - | - |
|  | 15.12 | - | - |  |  |  |  |
|  | 18.1 | - | - | - |  |  |  |
|  | 17.2 | - | - | - |  |  |  |
|  | 9.3 | - | - | - |  |  |  |
|  | 24.3 | - | - | - |  |  |  |
|  | 13.4 | - | - | - |  | 40 | 40 |
|  | 26.4 | - | - | - | - | . 40 |  |
|  | $\begin{gathered} \bar{x} \\ (6.7-23.9) \end{gathered}$ | 1.34 | 1.36 | 1.35 | 1.36 | 1.36 | 1.35 |
|  | 19.2 | - | - | - | - | - |  |
|  | 21.3 | - | - | - | - | - |  |
|  | 27.4 |  | - |  |  | - | . 35 |
|  | 13.5 | . 35 | - | . 35 | - | - | . 40 |
|  | 26.5 | . 40 | - | . 40 | - | - | . 50 |
|  | 1.6 | - | - | .50 | - | - |  |
| S | 10.6 | 70 | - | . 70 | - | - | . 70 |
| H | 17.6 | .$^{70}$ | B | .$^{.70}$ | B | $\bar{B}$ | B |
| A | 23.6 | B | 8 | B | B | B | B |
| $L$ | 29.6 | B | ${ }^{\text {B }} 75$ | ${ }_{1}{ }^{\text {B }}$ | 85 | . 95 | . 91 |
| $L$ | 6.7 | . 85 | . 75 | 1.15 | . 85 |  | . 70 |
| 0 | 13.7 | . 70 | - 35 |  | . 35 | . 55 | . 39 |
| W | 20.7 | . 35 | .35 | . 35 | . 35 | . 50 | . 48 |
|  | 27.7 | . 50 | . 85 | . 45 | . 85 | . 80 | . 84 |
| Z | 4.8 10.8 | . 85 | .85 1.24 | 1.25 | 1.05 | 1.15 | 1.13 |
| $N$ | 17.8 | B | B | B | B | B | 1 |
| E | 22.8 | B | B | B | B | B |  |
|  | 26.8 | B | B | B | B | B |  |
|  | 29.8 | B | B | B | B | B | (To Bottom) |
|  | 1.9 | B | B | B | B | B |  |
|  | 10.9 | B | B | B | B | ${ }_{8}^{8}$ |  |
|  | 16.9 | B | B | B | B | 8 | $t$ |
|  | 23.9 | B | B | B | B | B |  |
|  | 14.10 | - | - | - | - | - |  |
|  | 18.11 | - | - | - | - | - |  |
|  | 15.12 | - | - | - | - |  |  |
|  | 18.1 | - | - | - | - |  |  |
|  | 17.2 | - | - | - | - |  |  |
|  | 9.3 | - | - | - | - |  |  |
|  | 24.3 | - | - | - | - | - | - |
|  | 13.4 | - | - | - | - | - | - |
|  | 26.4 | - | - | - | - |  |  |

Appendix D. Precipitation ( mm ) receipts in the vicinities of lakes 019 (Minnedosa AES station),

 6.Cryptophceae 7. Peridineae

Appendix F. Seasonal abundance (ind./L) of the life history stages of crustacean zooplankton species in the shallow ( $z \leq 1.5 \mathrm{~m}$ ) zone of Lake 019, April 1976 to April 1977. Numbers represent means of counts of two composite samples each consisting of 6 subsamples taken in the shallow zone. Weighted shallow total abundance obtained from comununity totals (excluding harpacticoids, chaoborids and gammarids) x. 06 ( shallow zone share of lake volume). For copepods : $\mathcal{T}=$ exovigerous adult females; $\mathscr{O}=$ ovigerous females; $O^{\circ}=$ adult males; CIV-V $=$ copepodid stages IV and V (or older immatures) . CI-II $=$ copepodid stages I and II and III (or younger immatures). For cladocerans: $\mathscr{q}=$ exovigerous adult femates; $\mathscr{A}_{\mathscr{O}}=$ ovigerous females; $\varphi=$ ephippial females; $\mathcal{O}=$ total males.


Appendix G. Seasonal biomass (mg wet weight $\mathrm{L}^{-1}$ ) of the life history stages of crustacean zooplankton species in the shall gw (z 1.5 m ) zone of Lake 019, April 1976 to April 1977. Biomass values from corresponding abundances and cold ( $\leqslant 20^{\circ} \mathrm{C}$ ) or warm ( $>20^{\circ} \mathrm{C}$ ) period mean lengths converted to weight using formulae of Klekowski and Shushkina (1966 in Edmondson 1971). Total numbers and biomass generated during cold, warm or entire study periods presented at right. Other explanations as in Appendix F.


Appendix H. Seasonal abundance (ind. $/ L^{-1}$ bf the life history stages of crustacean zooplankton species in the deep ( $z>1.5 \mathrm{~m}$ ) zone of Lake 019, February 1976 to April 1977. Numbers represent means of counts of two composite samples each consisting of 6 subsamples taken in the deep zone: Weighted deep total abundance obtained from community totals ( excluding harpacticoids, chaoborids and gammarids) x 94 ( deep zone share of lake volume). Other explanations as in Appendix F.

| species | Date | 20.2 .36 | 22.3.16 | 29.4.76 | 12.5.76 | 27.5.76 | 2.6.16 | 9.6.76 | 16.6.76 | 23.6.76 | 29.6.76 | 5.7.16 | 12.1.16 | 19.1.16 | 26.1.16 | 3.8.7 | 10.8.86 | 19.8.76 | 26.8.76 | 9.9.76 | 24.9.76 | 15.10.76 | 19.11.76 | 12.12 .36 | 18.1.17 | 18.2 .71 | 10.3.n | 25.3.17 | 12.4 .11 | 26.4.11 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Eucyclops | \% | . 4 | . 21 |  |  | . 02 |  |  | . 54 |  | . 02 | .02 |  |  |  | : | : | : | : | : | : | : |  | : | : | : | : | : | : | : |  |
| \{ (10ch) | 8 | . 13 | . 03 | : |  | . 30 |  |  | . 54 | 2.15 | . 24 |  | !.11 | : | : | : | : | : |  |  |  | : |  |  |  |  |  |  |  |  |  |
|  | $\mathrm{Clv}_{\text {ci- }}^{\text {cil }}$ | . 17 | . 11 | . 26 | .15 | : | . 53 | . 55 | :54 | : |  |  | : | : | : | : | : | : | : | : | : | : | : | : |  |  | : | : | : | . 3 |  |
|  | toial | 1.08 | . 30 | . 26 | . 30 | . 32 | . 53 | . 55 | 2.26 | 2.15 | . 31 | . 01 | 1.11 | - |  | - | - |  | - |  |  |  |  |  |  | - | , |  | - | . 3 |  |
| Inopocrclops | $\bigcirc$ | 3.60 | 1.90 | . 19 | : | : | : | - 07 | . 54 | . 3 | 1.09 | ${ }^{2} .49$ | ${ }_{\text {1.03 }} .26$ | . 71 | . 20 | 1.04 | . 68 | ${ }^{1.26}$ | ${ }^{1.75}$ | ${ }^{4.58}$ | ${ }^{11.66}$ | 10.02 | 4.56 | 1.13 | 1.48 | ${ }^{1.16}$ | . 30 | : | - | : |  |
| (tansimus | 8 | : | : | : | : | : | : | 1.09 | 1.64 | 1.30 | . 893 | 3.32 | .$^{.03}$ | . 31 |  | 2.04 | . 42 | 4.5s | 3.26 | ¢.73 | 7.18 | ${ }^{\text {a }}$. 43 | 1.18 | . 11 |  |  |  |  | . 13 |  |  |
| KiEFFER | $\xrightarrow{C 10}$ | : | : | : | : | ; | : | : | ${ }^{3.25}$ | $\underline{1.07}$ | ${ }^{3.26}$ | i.09 | i.n | : | 1.180 | 4.15 | ${ }_{1}^{2.83}$ | ${ }^{\text {c }}$ 2.39 | ${ }_{4}^{2.22}$ | ${ }_{6} 8.818$ | ${ }^{4.188}$ | $\begin{array}{r}1.43 \\ \hline 0.3\end{array}$ | . 06 |  |  | . 08 | - | : |  | : |  |
|  | sotal | 3.60 | 1.90 | . 19 | - | . | - | 1.16 | 5.92 | 2.45 | 5.31 | 1.16 | 2.60 | 1.12 | 3.60 | 6.15 | 6.28 | 13.21 | 12.01 | 25.22 | 29.82 | 20.13 | 5.80 | 1.24 | 1.48 | 1.44 | . 30 | - | 13 | - |  |
| Crctops | 8 | . 0 | . 03 | - 00 | : | , 2 | . 03 | : | . 01 | . 73 | . 03 | : | : | : | 1.06 | : | : | : | : | : | : | : | : | : | : | : | : | : | : | : |  |
| Yefinchilis | \% | . ${ }^{\text {d }}$ | . 017 |  |  | . 15 | . 03 |  | 1:07 | \% 20 | 1.40 | : | . 75 | : | 1.05 | . 01 | . 01 |  |  |  | : | : | : | : | : | : | : | : | : |  |  |
|  | $\xrightarrow{\text { ciow }}$ | . 31 | .17 | : | 2.82 | +. ${ }^{\text {. } 78}$ | 2.13 | ${ }_{9}^{1.84}$ | ${ }_{5}^{5.91}$ | . 7 | : | : | 3.35 | i..11 | 2.05 | . 01 | . 01 | : | : | : | : | : | : | : | : | : | : | : | : | . 31 |  |
|  | toral | . 10 | . 29 | . 003 | 2.82 | 4.ss | 2.19 | 13.4 | 12.95 | 1.66 | 1.43 | - | 4.22 | 1.11 | 2.11 | .01 | . 01 | - | - | - | - | - |  |  | ; |  |  |  |  | . 3 |  |
| CYCLops | 8 | . 005 | . 04 | . 03 | . 125 | . 73 | . 68 | . 02 | ${ }^{1.07}$ | ${ }^{3.22}$ | -08 | . 315 | . 31 | . 10 | : | : | . 01 | : | : | : | : | .083 | . 06 | . ${ }^{\text {a }}$ | ${ }^{2 .} 89$ | ${ }^{2} .42$ | ${ }^{2.08}$ | 1.815 | ${ }^{1.95}$ | . 01 |  |
| cicuspianios | 8 | . 10 S | - 11 | . 03 | . 82 | 2.83 | : 13 | - 55 | ${ }^{2} \cdot 1.45$ | - 1.02 | . 29 | -45 | 1.26 |  |  | , 30 | . 03 | . 24 |  |  |  | . 39 |  | 1.47 | 2.21 | ci.37 | ${ }_{\text {a }}^{4.003}$ |  | 2.24 | 4.81 |  |
| foants | $\mathrm{civ}_{\text {cill }}$ | .06 | $\bigcirc$ | .18 | \% 1.23 | 19.38 | ${ }^{10.65}$ | ${ }^{19.98}$ | $\substack{10.21 \\ 1.07}$ | 3.22 1.07 | $\overline{6.57}$ | ${ }^{5} 5.41$ | ${ }^{6.62}$ | 4.8 | ${ }_{3}^{2.116}$ | 1.04 | . 05 |  | : | . 27 | . 41 | :993 | 1.43 | 1.93 | ${ }_{3}{ }^{1.89}$ | 2.04 | 2.9 | 1.55 | 16.49 | 16.48 |  |
|  | rotal | . 29 | . 21 | 1.14 | 2.38 | 25.80 | 30.39 | 36.62 | 14.90 | 2.60 | 1.80 | 22. | 17.07 | 10.33 | 5.27 | 1.3 | . 09 | . 6 | - | . 21 | . 6 | 2.01 | 2.43 | 5.42 | ${ }^{13.23}$ | 11.55 | 9.15 | 12.55 | ${ }^{22.31}$ | 19.22 |  |
| Crclopoider mupili |  | . 16 | 1.80 | 1.4 | 16.61 | 29.27 | 30.6 | 19.12 | 18.26 | 36.41 | 42.33 | 33.11 | 35.31 | 11.69 | 1.05 | 4.67 | 3.91 | 1.81 | c. 55 | 10.91 | 3.25 | 2.33 | 6. 38 | 4.46 | 3.06 | 14.25 | 31.15 | 37.97 | 25.32 | 19.02 |  |
| Diaptowes siclloides | 8 | . 6 | .2303 | . 05 | . 09 | . 18 | 2.21 | 1.40 | ${ }^{3.12}$ | 0.57 | ${ }^{13.02}$ |  | ${ }^{23.17} 3$ | 24.44 | ${ }^{39} 9.93$ | 31.85 | ${ }^{1.01}$ | 4.07 | 1.05 | . 54 | 1.58 | 3.22 | 2.20 | 1.15 | ${ }^{3} .62$ | $\stackrel{3.09}{3.03}$ | 2.4 | ${ }^{1.7}$ | ${ }^{1.17}$ | 1.68 |  |
| LILLECDK |  | . 21 | : 73 | . 01 | . 13 | .15 | 1.19 | 9.920 |  | ${ }_{\text {12,91 }}^{13}$ | 551.32 | $\underset{ }{23} 5$ |  | 716.57 | ${ }^{50.45}$ | ${ }_{\text {20.36 }}^{35}$ | 7.53 | ${ }^{3} .51 .51$ | 1.11 | ${ }_{2} \mathbf{4} \mathbf{4} 0$ | ${ }_{4.88}^{2.4}$ | ${ }^{4.4} 8$ | ${ }^{\text {4. }}$. 6 | ${ }^{2.15}$ | 2.8 | 3.10 | ${ }^{3.28}$ | 2.79 | 1.69 | ${ }^{3.8}$ |  |
|  | ${ }_{\text {civelil }}$ | : | : |  | . 08 | 2.n | ${ }_{2} 1.67$ | 24.03 | ${ }_{92}^{29} 3$ | 109.25 | ${ }_{67} 513$ | 12.61 | ${ }^{14.34}$ | 15.94 | ${ }^{26.13}$ | ${ }^{26}$ | 3.65 | ${ }^{21.23}$ | : | 6.18 | 3.66 | $\cdots$ |  |  | - | - |  | - |  |  |  |
| Diaptown siciloides | TOIAL | . 9 | .97 | . 28 | 4.18 | 8.108 | ${ }_{21.26}^{10.20}$ | 33.18 100.18 | 124.67 126.80 | ${ }_{\substack{162.28 \\ 4.28}}$ | ${ }^{153.06}$ | 145.52 | ${ }_{\substack{152.69 \\ 36.40}}$ | 117.417 | ${ }^{202.17}$ | 140.\% | 29.148 | ${ }^{10.59} 1.6$ | 13.60 | \%.29 | ${ }_{1}^{2.82}$ | 11.00 | 7.4 | 8.15 | 6.59 | 6.12 | 6.1 | 4.53 | ${ }^{3} .106$ | 2. 2.54 |  |
| Diaphanosom | timurune to | - | - | - | - | - | - | - | - | : | 03 | : | 3.31 | 4:36 | 4.82 | : | : | : | : | : | : | : | : | : | : | : | : | : | : | : |  |
| Lefochteamenginum | toral 8 |  | $:$ | $\stackrel{\square}{\square}$ | - | : | $\stackrel{\square}{-}$ | $:$ |  | : | . 03 | : | 4.26 | 6.11 | 4.82 | - | - | - | . | . | - | . | . | - | - | . | - | - | - | . |  |
| Datheia rosea seas |  |  |  | - |  |  |  |  |  | - | - | - | - | ; | ; | - | - | - | - | - | - | . 01 |  |  | - |  |  |  |  |  |  |
|  | 8 | .00s | .003 | : | . 38 | 1.40 | ${ }_{12}^{23.96}$ | ${ }^{1.104}$ | 1.61 | ${ }^{2.4 .48}$ | ${ }^{31.48}$ | 22.35 | ${ }^{4.42}$ | 3.54 | ${ }^{2.31}$ | 4.15 | .06 | . 01 | : | .02 | . 54 | . 08 | . 78 | . 54 | :28 | .19 | . 10 | : | : |  |  |
|  |  |  | : |  |  |  | 3.55 | 0.03 | i.0 | is | - ${ }^{\text {. }}$ 799 | . 027 | $\cdot$ |  | : |  |  | : | - |  |  | 1.28 | - ${ }_{16}$ | . ${ }^{12}$ | : | : | : | - | : |  |  |
|  | amaruex |  | : | .89 | . 30 | ${ }^{16} 515$ | ${ }^{36.20}$ | 4.92 | 15.04 | 42\% | ${ }^{22.80}$ | 32.61 | 2.81 | 1.42 | 2.11 | i.s6 | . 22 |  | - | . 4 | . 27 | . 27 | .02 | : | - | - | - |  |  | . 16 |  |
|  | rotal | .07 | . 01 | . 6 | . 4 | 25.36 | 122.41 | 13.6 | 22.56 | 0.69 | 12.45 | 65.14 | 6.73 | 5.69 | 9.50 | 5.71 | . 29 | . 01 | - | . 31 | 1.6 | 2.51 | 1.26 | 6 | 3 | . 19 | 10 |  |  | 16 |  |
|  |  | - | - | - | - | . | . | - | - | - | - | - | - | 01 | - | - | ¢. 01 | - | - | - | - | - | - | - | - | - | . |  |  | . 01 |  |
| Ceriopaphuide | imuture to | : | : | : | : | : | : | . 51 | . 01 | ${ }^{3.07}$ | 9.17 | ${ }^{16.30}$ | 3.14 | ${ }_{\substack{10.22 \\ 1.22}}$ | ${ }_{6} 6.33$ | ${ }^{1.00}$ | - ${ }^{4}$ | . 000 | : | . 27 | $\square^{-14}$ | . 09 | : | $:$ | : | : | : | : | : | : |  |
|  | toras |  |  | - | - | - |  | . 56 | . 55 | 4.28 | 12.88 | 17.55 | 4.58 | 11.44 | 6.73 | 1.05 | .4. 6 | . 01 | - | . 21 | . 14 | .11 | - |  |  |  |  |  |  |  |  |
| (oshim Lomg mostals | imarume +8 | . 31 | $\stackrel{1.06}{.22}$ | . 23 | . ${ }_{\text {. }}^{3}$ | ${ }_{1}^{13.88}$ | ${ }_{1}^{16.51}$ | $\begin{aligned} & 31.14 \\ & 10.92 \end{aligned}$ | $\begin{aligned} & 167.55 \\ & 64.04 \end{aligned}$ | $\begin{gathered} 282.15 \\ 25.71 \\ \hline 102 \end{gathered}$ | $\begin{gathered} 370.15 \\ 39.07 \\ 2.17 \end{gathered}$ | $\begin{gathered} 222.06 \\ \substack{23.15 \\ 1.09} \end{gathered}$ | ${ }_{\text {230, }}^{13.50}$ | $\begin{gathered} 250.16 \\ 99.16 \end{gathered}$ | $\begin{array}{r} 141.23 \\ 6.32 \end{array}$ | 25.93 | 1.67 | .4 | . 12 | . 4 | . 14 | . 54 | . 42 | $\begin{aligned} & .02 \\ & .05 \\ & .05 \end{aligned}$ | :04 | . 38 |  | . 80 |  | . 81 |  |
|  | total | . 43 | 1.28 | .sb | 1.15 | 1s.09 | 23.43 | 42.61 | 211.59 | 309.19 | 111.39 | 27.30 | 335.39 | 49.52 | 14.55 | 25.97 | 1.67 | . 4 | . 12 | . 4 | . 14 | . 54 | .4 | . 09 | . 16 | . 46 | . 6 | . 65 | 15 | . 31 |  |
| Macrothilix (unice | imuruam yo | : | : | . ${ }^{3}$ | . 23 | : | : | = | : | : | : | : | : | .$^{10}$ | : | : | : | : | : | : | : | . 09 | : | : | : | : | : | . | : | : |  |
| - | rotal. |  | . | . 03 | 4 | - | - | - | - | - | - | - | - | . 10 | - | - | - | - | - | - | - | . 09 | - | - | - | . | - | - | - | - |  |
| Mom nectamana | tmutuat ${ }^{\text {\% }}$ | . 05 | : | : | - | : | -.31 | : | . ${ }^{4}$ | : | : | : | $!11$ | : | : | . 10 | . 16 | . 28 | : | - | : | . 02 | - | - | : | : | : | - | : | - | r |
|  | total 8 | .0s | - | - |  |  | . 3 | - | . 54 | - | - | - | 1.11 | - | - | . 10 | . 16 | . 28 | - | - | - | .02 | - | - | - | - | . | - | - | - |  |
| Coryonus spheticus | Torn | - | - | - | . 04 | - | - | - | - | - | - |  | - |  |  | - | - | - | - | - | - | - | - |  |  |  |  |  |  |  |  |
| Herpacticolda muplil |  | 1.4 | 2.07 | . ${ }^{\text {d }}$ | .3] | 1.61 | 6.92 | 3.28 | . 54 | - | - | 1.09 | . 16 | . 10 | - | - | - | - | - | - | - | - | - | . 21 | . 10 | . 08 | - | - | - | - |  |
| Cranoorus sp |  | - | - | . 03 | - | .03 | - | - | . | . 03 | . 17 | . $\mu$ | . 28 | . 6 | . 16 | . 01 | . 10 | .05 | - | . 014 | - | - | . 12 | .004 | .00s | .008 | * | . 82 | - | - |  |
| Gumatus ip |  | . | - | . |  | . | - | - | $\cdot$ | - | - | - | - | $\cdot$ | $\cdot$ | - | - | - |  | - | - | $\cdot$ | - | - | - | - | . 004 |  | - | $\cdot$ |  |
| Comemiry torat ma/l |  | 6. 41 | - 11 | 6.\% | 23.42 | 112.81 | 251.45 | 27.11 | 540.98 | 614.02 | 23.05 | 569.30 | \$01.45 | 626.54 | 655.16 | 215.16 | 59.14 | 29.13 | 37.37 | 55.14 | 49.84 | 39.16 | 23.01 | 16.36 | 28.98 | 3.40 | 41.71 | 55.73 | 51.55 | 67.00 |  |
| (MGigited deep toral TMOL |  | 8.38 | 8.6 | 8.60 | 27.56 | 105.53 | 24.20 | 281.6 | 500.39 | ${ }^{313.58}$ | 67.19 | 554.09 | 567.47 | 588.95 | 427.65 | 203.26 | 53.63 | 27.38 | 35.13 | 52.41 | 4.ess | 3.18 | 22.60 | 15.18 | 25 | 3.71 | \% | \$2.4 | 6 | 6.m |  |
|  |  | 1.12 | 8. 6 | 6.06 | 8.11 | 113.60 | 238.12 | 27.6 | 523.0. | 63.19 | 705.65 | 579.10 | cos.cr | c01.41 | 43.44 | 205.23 | \$.\%.\% | 20.38 | 3.63 | 55.33 | 48.12 | 38.93 | 33.17 | 16.11 | 21.0 | 33.3 | 45.23 | 50.26 | 51.12 | 4.36 |  |

Appendix I. Seasonal biomass ( mg wet weight $\mathrm{L}^{-1}$ ) of the life history stages of crustacean zooplankton species in the deep $(z>1.5 \mathrm{~m})$ zone of Lake 019, February 1976 to April 1977. Other explanations as in Appendices $G$ andH.


Appendix J. Seasonal abundance (ind $L^{-1}$ ) of the life history stages of crustacean zooplankton species in the shallow ( $z \leqslant 1.5 \mathrm{~m}$ ) zone of Lake 255, April 1976 to April 1977. Numbers represent means of counts of two composite samples each consisting of 5 subsamples taken in the shallow zone. Weighted shallow total abundance obtained from community totals (excluding harpacticoids, chaoborids and gammarids) x. 20 (shallow zone share of lake volume). Other explanations as in Appendix F.


Appendix K. Seasonal biomass ( mg wet weight $L^{-1}$ bf the life history stages of crustacean zooplankton species in the shallow ( $z \leqslant 1.5 \mathrm{~m}$ ) zone of Lake 255, April 1976 to April 1977. Other explanations as in Appendices


Appendix $L$. Seasonal abundance (ind $L^{-1}$ ) of the life history stages of crustacean zooplankton species in the deep ( $z>1.5 \mathrm{~m}$ ) zone of Lake 255, February 1976 to April 1977. Numbers represent means of counts of two composite samples each consisting of 5 subsamples taken in the deep zone. Weighted deep total abundance obtained from community totals (excluding harpacticoids, chaoborids and gammarids) x. 80 (deep zone share of lake volume). Other explanations as in Appendix $F$.


Appendix M. Seasonal biomass ( mg wet weight $t^{-1}$ ) of the life history stages of crustacean zooplankton species
in the deep ( $z>1.5 \mathrm{~m}$ ) zone of Lake 255, February 1976 to April 1977. Other explanations as in Appendices $G$ and $L$


Appendix N. Seasonal abundance (ind $\mathrm{L}^{-1}$ ) of life history stages of crustacean zooplankton species in the shallow ( $z \leqslant 1.5 \mathrm{~m}$ ) zone of Lake 885, April 1976 to April 1977. Numbers represent means of counts of two composite samples each consisting of 5 subsamples taken in the shallow zone. Weighted shallow total abundance obtained from community totals (excluding harpacticoids, chaoborids and gammarids) $x .15$ (shallow zone share of the lake volume). Other explanations as in App. F.


Appendix 0 . Seasonal biomass (mg wet weight $\left[^{-1}\right.$ ) of the life history stages of crustacean zooplankton species in the shallow ( $\mathrm{z} \leqslant 1.5 \mathrm{~m}$ ) zone of Lake 885 , April 1976 to April 1977. Other explanations as in Appendices $G$ and $N$.


Appendix P. Seasonal abundance (ind $L^{-1}$ ) of the life history stages of crustacean zooplankton species in the deep ( $\mathrm{z}>1.5 \mathrm{~m}$ ) zone of Lake 885, February 1976 to April 1977, Numbers represent means of counts of two composite samples each consisting of 5 subsamples taken in the deep zone. Weighted deep total abundance obtained from community totals (excluding harpacticoids, chaoborids and gammarids) x. 85 (deep zone share of lake volume). Other explanations as in Appendix F.


Appendix $Q$ Seasonal biomass (mg wet weight $L^{-1}$ ) of the life history stages of crustacean zooplankton species in the


| Coghemity total | .42 | 1.936 | J. 160 | 3.03 | 13.532 | 12.028 .804 | . 031 | 28.169 | 11.630 | 24.322 | 16.3\% | 11.201 | 32.623 | 23.36 | 27.299 | 514.3 .1 | 3.626 | 1.091 | 7.888 | 10.40 | 13.637 | 11.651 .321 | 9.0 | 1.14 | . 01 | . 011 | .003.180 | U4 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | . 4 | 1.4 | 2.6 | 3.0\% | 11.0 | 10.24 . 15 | 2.\% | 28.42 | 14.00 | 13.90 | 14.11 | 10.42 | 19.31 | 19.13 | 3.21 | 16.534 .80 | 4.11 | 8.01 | 6.1 | 8.\% |  | 1.11 6.4 | $1 . n$ | 6.0s | .cos | . 01 | .003 .11 | . 181.4 |
|  | . 14 | 1.4 | 3.18 | 1.34 | 12.4 | 10.14 0.4 | 24.15 | 33.13 | 22.31 | 31.12 | 33.22 | 30.92 | 23.98 | 41.35 | 21.4 | 23.56 12.31 | 8.39 | 6.58 | 1.03 | 11.19 | 23.0 | 11.26 12.16 | 8.14 | 9.60 | .003 | . 04 | . 003 | .4 1.4 |

Appendix R. Seasonal mean total egg and ephippia abundance (eggs $t^{1}$ )for the major zooplankton species in the shallow and deep zones of Lake 885, February 1976 to April 1977. Mean fecundities (egg clutch determined from egg counts of 20 ovigerous females on each sampling date. $Q_{0}=$ ovigerous females; $\varphi_{\varphi}=$ ephippial cladocerans.


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Appendix S. Seasonal mean total egg and ephippia abundance (eggs $\left[^{1}\right.$ )for the major zooplankton species in the shallow and deep zones of Lake 255, February 1976 to April 1977. Other explanations as in Appendix R.

,Appendix T. Seasonal mean total egg and ephippia abundance (eggs $L^{-1}$ ) for the major zooplankton species in the shallow and deep zones of Lake 019, February 1976 to April 1977. Other explanations as in Appendix R.

\begin{tabular}{|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|c|}
\hline 19 Sranow Zore \& Date \& 20.2 \& 22.3 \& 329. \& . 4 \& 12.5 \& 27.5 \& 2.6 \& 9.6 \& 16.6 \& 23.6 \& $28.6 \quad 5.7$ \& 12.7 \& 19.7 \& 26.7 \& 3.8 \& 10.8 \& 19.826 .8 \& 9.9 \& 24.9 \& 15.10 \& 19.11 \& 17.12 \& 18.1 \& 18.2 \& 10.3 \& 25.3 \& 12.4 \& 26.4 <br>
\hline \& \& - \& - \& \& \& ${ }^{14}$ \& ${ }_{90} 0.01$ \& ${ }^{12} .04$ \& : \& $4{ }^{.04}$ \& 37.31 \&  \& 28.01 \& 22.06 \& - \& = \& - \& - : \& : \& - \& - \& \& : \& : \& \& : \& - \& : \& <br>
\hline YCLOPS \& avg cumtor \& $:$ \& - \& \& \& 3.0

0.022 \& 90.0
.9 \& ${ }_{1}^{42.68}$ \& - \& 1.64 \& . 37 \& $\begin{array}{rrr}33 & \\ .33 & 1.92\end{array}$ \& . 28 \& 1.32 \& - \& - \& - \& - - \& - \& - \& - \& - \& - \& - \& - \& - \& - \& - \& - <br>
\hline \& O/al \& - \& \& \& \& 10.2 \& $\square$ \& 2 \& ${ }_{23.93}{ }^{83}$ \& 16.40 \& : \& $11.67{ }^{12} 12.88$ \& 13.0 \& : \& 16.01 \& 18.01 \& 16.62 \& $17.464^{3} 18.9$ \& : \& : \& : \& : \& : \& : \& : \& : \& : \& : \& : <br>
\hline Rasinus \& afic cular \& - \& \& \& \& - \& - \& \& 23.93
19.86 \& $\underline{16.4}$ \& \& ${ }_{8.40}^{11.62}$ \& 4.42 \& - \& . 16 \& . 18 \& . 33 \& 5.943 .42 \& - \& - \& - \& - \& - \& - \& - \& - \& - \& - \& - <br>
\hline \& Total \& \& \& \& \& \& \& \& \& . 01 \& . 88 \& ${ }_{\text {. }} .5$ \& - \& - \& - \& - \& - \& : : \& $:$ \& : \& : \& : \& : \& : \& - \& : \& : \& : \& - <br>
\hline YCLLops
ERNALIS \&  \& - \& - \& \& : \& : \& : \& - \& - \& 48. \& 58. \& 20. \& \& \& \& - \& \& - - \& $\square$ \& - \& - \& - \& - \& \& - \& \& \& \& <br>
\hline \& Total \& - \& - \& \& - \& - \& - \& - \& - \& . 48 \& 51.04 \& 1.0 \& - \& \& \& - \& - \& - \& - \& : \& - \& - \& $:$ \& - \& - \& - \& $:$ \& - \& . 07 <br>
\hline UCYCLLOPs \&  \& : \& : \& \& ${ }^{.02}$ \& $46.0{ }^{\text {a }}$ \& 34.05 \& 26.09 \& : \& : \& : \& 16. \& - \& - \& 26. \& - \& - \& - - \& - \& - \& - \& \& - \& \& \& \& \& \& 4.76 <br>
\hline \& rotal \& - \& \& \& . 04 \& . 46 \& 1.70 \& 2.44 \& $\bigcirc$ \& \& \& . 64 \& \& \& 1.56 \& \& . 06 \& . 91 \& . 19 \& - \& . 63 \& . 18 \& . 27 \& - \& - \& . \& - \& . 12 \& 1.04 <br>
\hline laptomus \& $8 / 2$ \& : \& \& \& ${ }^{3.01}$ \& : \& 13.00 \& ${ }_{25.20} .27$ \& 23.25 \& (8.12 \& ${ }_{8.05}^{1.45}$ \& $\begin{array}{ll}\text { 1.78 } \\ 5.94 & 4.25\end{array}$ \& 3.80 \& 3.55 \& 3.05 \& 2.29 \& \& 5.67 \& 4.67 \& - \& 13.50 \& 23.5 \& 8.40 \& - \& \& \& \& \& <br>
\hline ICILOIDES \& avg cintan Total \& $:$ \& \& \& . 13 \& - \& 13 \& 6.80 \& 13.72 \& 58.35 \& 11.35 \& $10.57 \quad 2.76$ \& 19.27 \& 15.90 \& 3.17 \& 0.92 \& - \& 5.16 \& 0.69 \& - \& 8.51 \& 4.23 \& 2.27 \& \& $\because$ \& \& \& 1.68 \& 16.72 <br>
\hline Japhila \& 8/L \& : \& : \& \& : \& 2.01 \& 3.60 \& 1.5 \& 1.83 \& 1.06 \& 2.5 \& 2.08 \& 2.05 \& : \& - \& : \& - \& - \& : \& : \& : \& : \& - \& \& $:$ \& $:$ \& \& \& - <br>
\hline ARVULA \& Total \& - \& - \& - \& - \& . 02 \& 1.04 \& . 20 \& . 57 \& . 06 \& . 25 \& 1.14 \& . 10 \& $\cdots$ \& $\cdots$ \& - \& 14 \& - \& : \& - \& \& \& - \& \& - \& \& \& \& <br>

\hline osmina \& Pl/ \& - \& : \& \& 2.05 \& 3.3 \& $\stackrel{.20}{2.92}$ \& ${ }^{4.22}$ \& ${ }_{1}^{5.85}$ \& | 14.10 |
| :--- |
| 2.15 |
| 1.15 | \& ${ }_{18.5}^{18.27}$ \&  \& ${ }^{79} 1.05$ \& $\underset{1}{12.15}$ \& ${ }^{2.08}$ \& :- \& 1.4 \& : \& : \& $:$ \& - \& - \& - \& \& \& \& \& \& ${ }_{1.85}$ <br>

\hline ongirostris \& Total \& . \& . \& \& . 10 \& . 13 \& . 58 \& 8.65 \& 10.42 \& 30.32 \& 27.41 \& $\begin{array}{llll}13.10 & 23.39\end{array}$ \& 83.98 \& ${ }^{14.08}$ \& 2.18 \& - \& . 14 \& - - \& - \& $:$ \& \& $:$ \& - \& \& - \& \& - \& : \& <br>
\hline Cerlodaphnia
Lacusiris \& 9AVG B8000 \& \& : \& - \& : \& - \& : \& : \& ${ }_{13.01}{ }^{.01}$ \& 3. ${ }^{\text {a }}$ \& 5.67 \& $\begin{array}{ll}1.08 \\ 4.8 & 1.47 \\ 3.15\end{array}$ \& 3.10 \& 3.27 \& 1.0 \& $:$ \& \& - - \& \& - \& \& $:$ \& - \& \& \& \& \& - \& <br>
\hline Diaphanosoma Leuchtengerg lanum \& 8/L \& \& \& - \& : \& . \& - \& - \& \& : \& .01
0
1.02 \& . 06 \& 4.50 \& - 5 \& \& \& $:$ \& . 11 - \& - \& - \& : \& - \& - \& - \& - \&  \& - \& $:$ \& <br>
\hline Microthrix dinticornis \& Al/ \& \& \& \& : \& - \& 4.40 \& ${ }^{\text {: }}$ \& - \& - \& \& \& 45 \& \& 2.0
.88 \& . 40 \& \& - \& - \& $\because$ \& $:$ \& - \& - \& - \& - \& - \& - \& - \& ${ }^{8 .} 35$ <br>
\hline ALONA RECTANGULA \&  \& - \& - \& \& : \& : \& : \& - \& - \& - \& - \& : : \& \& \& 1.25 \& \& \& - - \& - \& \& - \& \& \& \& \& \& \& \& <br>
\hline 019 Deep zone \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& \& <br>
\hline \& \& \& \& \& \& \& \& \& \& \& \& ${ }^{.05}$ \& \& : \& - \& \& \& . - \& - \& - \& 74.003 \& : \& : \& 85.85 \& 72.43 \& 62.31 \& 60.25 \& 63.29 \& : <br>
\hline Crclops \& Avocurar \& - \& \& \& \& 65. \& 50.63 \& ${ }^{47.8}$ \& \& \& \& \& ${ }^{28} 1.40$ \& \& \& \& \& \& \& \& . 22 \& \& \& 1.73 \& 5.07 \& 2.49 \& 9.03 \& 18.4 \& <br>
\hline \& Total \& \& \& , \& - \& 2.30 \& 11.64 \& 5.74 \& \& \& \& \& \& \& \& \& \& \& \& - \& - \& - \& - \& \& : \& : \& : \& : \& : <br>
\hline Tropocyclops \& \& : \& \& : \& . \& - \& - \& : \& 23.00 \& ${ }_{41.92}^{\text {24 }}$ \& $17.0{ }^{1.31}$ \& 14.03 15.7 \& 12.5 \& 12. \& \& 15.5 \& 17.3 \& 17.506 .90
4.905 .92 \& 13.25
1.86 \& \& \& \& \& \& \& - \& - \& : \& <br>

\hline Prasinus \& $$
\begin{aligned}
& \text { AVG C } \\
& \text { Total }
\end{aligned}
$$ \& \& \& \& - \& \& \& - \& 1.61 \& 22.64 \& 5.27 \& . 424.87 \& 0.38 \& 8.52 \& \& \& \& 4.905 .92 \& 1.86 \& $\stackrel{\square}{-}$ \& - \& \& \& \& - \& - \& : \& - \& : <br>

\hline $\underset{\text { VERCLAPLI }}{\substack{\text { CYe }}}$ \&  \& \& \& .$_{68} 12$ \& ${ }_{22} .003$ \& : \& $\stackrel{0}{ }{ }^{2}$ \& 2 : \& : \& 52.01 \& 55.73
40.37 \& 56.0
1.68 \& - \& \& \& \& \& - - \& - \& $:$ \& - \& $:$ \& - \& \& - \& $:$ \& $:$ \& $:$ \& <br>
\hline \& Total \& \& \& . 03 \& \& \& - \& \& \& \& - \& \& - \&  \& \& \& . \& : : \& : \& : \& : \& - \& : \& \& : \& : \& - \& - \& - <br>
\hline Eucyclops \& Ariscura \& : \& 25. \& . \& - \& - \& - \& \& \& \& \& 18. ${ }^{14 .}{ }^{14}$ \& \& \& \& \& \& \& - \& \& - \& - \& \& - \& - \& \& - \& - \& ${ }^{-}$ <br>
\hline \& rotal \& \& \& . 75 \& \& \& \& \& \& \& \& $\begin{array}{r}.36 \\ 4.35 \\ \hline 2.02\end{array}$ \& \& \& \& \& \& . 121.17 \& . 54 \& . 27 \& . 27 \& . 12 \& . 01 \& 10.01 \& . 03 \& . \& 6.03 \& ${ }_{13.32}$ \& ${ }_{17}{ }^{.30}$ <br>

\hline Diaptomus \& Q/L \& : \& $$
11
$$ \& \[

4_{1}^{.003}
\] \& 12.85 \& 17.5 \& 15.40 \& 404.65 \& 526.0 \& 18.75 \& 8. 25 \& 5.905 .05 \& 4.10 \& 3.60 \& \& 763.50 \& 3.60 \& 2.906 .10 \& 6.5 \& ${ }^{13.50}$ \& 14.83

4.00 \& 12.93
1.55 \& 8.80 \& 0.11 \& 8. 0.24 \& \& 0.18 \& 2.66 \& ${ }^{17.16}$ <br>
\hline \& Total \& \& \& . 033 \& . 64 \& 1.23 \& 31.54 \& 4 24.40 \& 0 \& 21.00 \& 3.80 \& 25.6710 .20 \& 16.15 \& 545.94 \& \& 3410.89 \& 94.43 \& . 357.14 \& 3.51 \& 3.65 \& \& \& \& . 06 \& . \& - \& - \& - \& <br>

\hline Daphmia \&  \& \& \& : \& : \& ${ }_{6.81}{ }^{\text {. }}$ \& | 6 | 1.51 |
| :--- | :--- |
| 6.35 |  | \& 5154.12 .25 \& 15 ${ }^{5} 3.10$ \& ${ }_{3.8}^{1.61}$ \& 8.58

2.40 \& 8.69
1.60
1.409
1.40 \& 1.10 \& ${ }^{0} 2.20$ \& \& 02 \& 1.5 \& - \& 3.5 \& 5.94 \& 5.0 \& - \& - \& \& \& \& \& \& <br>
\hline parvula \& Aratal \& \& \& \& \& 6, \& 17.86 \& 86
50.23

3.75 \& $5^{3} 8.84$ \& 6.12 \& 20.59 \& | 13.90 |  |
| ---: | ---: |
| .79 | 3 |
| 02 |  | \& \& 21.61 \& \& : \& . 02 \& - : \& : 11 \& 3.21 \& . 18 \& . 30 \& . 02 \& \& \& \& \& \& <br>

\hline \&  \& ¢ $\mathbf{L}^{-}$ \& \& \& \& \& 1.21 \& \& 92 10.92 \& ${ }^{44.04}$ \& 25.71 \& .09
39.07
1.254 .35

1.30 \& | 101.50 |
| :--- |
| 1.05 | \&  \& \& 32 0.04 \& . 04 \& : \& : \& : \& : \& 1. ${ }^{\text {a }}$ \& 1.05 \& 1.04 \& 1.08 \& : \& 1.20 \& 1.02 \& <br>

\hline Boskilat
LONGIROSTRIS \& AVG brocos \& \& \& 1.2 \& 2.0 \& 4.6 \& 4.38 \& 382.50 \& 50 2.00 \& 1.68 \& 81.45 \& \& 1.06 \& \& \& \& \& \& \& \& \& 0.09 \& . 05 \& . 04 \& . 08 \& - \& . 32 \& . 02 \& - <br>
\hline \& Total \& \& \& . 26 \& . 46 \& 1.4 \& 44.09 \& . 0917.3 \& 3021.84 \& 73.99 \& 937.28 \& 48.8470 .66 \& 106.58 \& + \& \& \& \& \& \& \& \& \& \& . \& \& - \& \& - \& <br>

\hline Ceriodaphila \& $8 /$ \& \& \& : \& : \& - \& : \& : \& 4.01 \& 4.01 \& [ 1.07 \& | 3.71 |
| :--- |
| 3.75 | \& ${ }_{3.60}$ \& 3.30 \& \& 40 . 0 \& \& : : \& \& - \& - \& - \& - \& - \& \& $:$ \& - \& $:$ \& $:$ <br>

\hline Lacustris \& \& \& \& \& \& \& \& \& \& \& \& \& \& $5 \quad .31$ \& \& \& \& - \& - \& \& \& \& \& : \& : \& \& - \& - \& <br>
\hline Diaphanosoma \& a ats broon \& - \& \& : \& - \& - \& - \& - \& - \& - \& - \& - - \& 2.70 \& 02.20 \& \& - \& \& - - \& \& \& \& \& \& \& \& \& \& \& <br>
\hline
\end{tabular}



## PERIOD

|  | Lake | Tax. Group | Feb 76 Mar | Apr May | June July | Aug | Sept Oct Nov | $\begin{aligned} & \text { Dec } 76 \\ & \text { Jan } 77 \end{aligned}$ | Feb Mar | Apr | Annual Apr 76 Apr 77 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 019 | Cyclopoids | 5.04 | 22.65 | 50.18 | 15.24 | 24.91 | 15.98 | 35.02 | 44.55 |  |
| A |  | Calanoids | . 78 | 3.99 | 187.91 | 57.61 | 11.19 | 5.24 | 5.85 | 15.51 |  |
| B |  | Cladocerans | . 87 | 11.37 | 280.73 | 9.25 | 2.25 | . 62 | . 65 | . 37 |  |
| U |  | Total | 6.69 | 38.01 | 518.82 | 82.10 | 38.35 | 21.84 | 41.52 | 60.43 | 124.35 |
| N |  | S/A Ratio | . 05 | . 31 | 4.17 | . 66 | . 31 | . 18 | . 33 | . 49 |  |
| D |  |  |  |  |  |  |  |  |  |  |  |
| A | 255 | Cyclopoids | 1.44 | 217.53 | 38.93 | 37.52 | 105.51 | 91.56 | 1.73 | 230.61 |  |
| N |  | Calanoids | - | 8.83 | 75.02 | 49.63 | 29.95 | 26.99 | . 06 | . 77 |  |
| C |  | Cladocerans | - | 13.49 | 20.47 | 52.42 | 59.86 | 8.09 | - | 1.35 |  |
| E |  | Total | 1.44 | 239.85 | 134.42 | 139.57 | 195.32 | 126.64 | 1.79 | 232.73 | 149.55 |
|  |  | S/A Ratio | . 01 | 1.60 | . 88 | . 93 | 1.31 | . 85 | . 01 | 1.56 |  |
| N | 885 | Cyclopoids | 42.30 | 826.03 | 438.36 | 104.46 | 180.59 | 17.79 | 1.81 | 132.82 |  |
| D |  | Calanoids | - | . 79 | 2.16 | 1.34 | . 56 | . 22 | - | . 66 |  |
| L |  | Cladocerans | . 02 | . 11 | 69.27 | 63.24 | 29.06 | 6.34 | - | 1.46 |  |
|  |  | Total | $42.32$ | $826.93$ | $509.79$ |  |  |  |  |  | 289.74 |
|  |  | S/A Ratio | $.15$ | $2.85$ | $1.76$ | $.58$ | $.73$ | $.08$ | $.01$ | $.47$ |  |
|  | 019 | Cyclopoids | . 121 | . 192 | . 516 | . 086 | . 230 | . 471 | . 630 | . 462 |  |
|  |  | Calanoids | . 067 | . 051 | 3.938 | 1.445 | . 526 | . 427 | . 467 | . 331 |  |
| B |  | Cladocerans | . 014 | . 220 | 2.158 | . 068 | . 069 | . 031 | . 015 | . 004 |  |
| 1 |  | Total | . 202 | . 463 | 6.612 | 1.599 | . 825 | . 929 | 1.112 | . 797 | 1.920 |
| 0 |  | S/A Ratio | . 22 | . 24 | 3.44 | . 83 | . 43 | . 48 | . 58 | . 42 |  |
| M | 255 |  |  |  |  |  |  |  |  |  |  |
| A |  | Cyclopoids | . 051 | 1.659 | . 707 | . 502 | 1.290 | 1.939 | . 075 | 1.795 |  |
| 5 |  | Calanoids | - | . 170 | 1.654 | 1.640 | 1.626 | 2.003 | . 007 | . 001 |  |
| 5 |  | Cladocerans | - | 3.415 | 2.746 | 5.956 | 3.005 | . 090 |  | . 024 |  |
|  |  | Total | . 051 | 5.244 | 5.107 | 8.098 | 5.921 | 4.032 | . 082 | 1.820 | 4.638 |
| 1 |  | S/A Ratio | . 01 | 1.13 | 1.10 | 1.75 | 1.28 | . 87 | . 02 | . 39 |  |
| N | 885 |  |  |  |  |  |  |  |  |  |  |
| D |  | Cyclopoids | . 990 | 5.578 | 4.983 | 1.042 | 1.042 | . 147 | . 050 | . 841 |  |
| 1 |  | Calanoids | - | . 004 | . 141 | . 217 | . 115 | . 090 | - | . 006 |  |
| $L$ |  | Cladocerans | . 008 | . 010 | 19.249 | 18.259 | 11.171 | 4.580 | - | . 131 |  |
|  |  | Total | . 998 | 5.592 | 24.373 | 19.518 | 12.328 | 4.817 | . 050 | . 978 | 10.330 |
|  |  | S/A Ratio | . 10 | . 54 | 2.36 | 1.89 | 1.19 | . 47 | . 01 | . 10 |  |

Appendix V. Seasonal changes in the relative importance of major food organisms (wet weight) identified in trout stomachs. The number of stomachs examined and the number of empty stomachs in parenthesis is indicated on the top of each bar (after Tavarutmaneegul 1978).



[^0]:    * Based on seined area $=500 \mathrm{~m}^{2}$

