

INTERNAL REPORT 139

GRAZING AND PRODUCTION BY ZOOPLANKTON IN LAKES OF THE CEDAR RIVER WATERSHED

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ABSTRACT

Zooplankton grazing rates and life history stage densities for secondary production estimates were determined in three lakes in the Cedar River watershed, Washington. Eight copepod species, seven cladoceran and nine rotifer species were identified in the three lakes. No one species of cladoceran or copepod occurred in all the lakes, but the rotifers are common throughout. Copepods in the lakes showed no clear diel migration, while two cladocerans did migrate. Copepods were most important numerically in the lakes. Some principal members were *Diaptomus ashlandi* which reached a seasonal maximum adult density of 11/l (mean of water column) in Lake Sammamish and *Limmocalanus* in Chester Morse which reached a maximum of 0.7/l. Two *Diaptomus* species are important in Findley Lake. Densities averaged about 10 times greater in Sammamish than in the two oligotrophic lakes. Data on population dynamics from the egg ratio technique are given for the common cladocerans in the three lakes.

Grazing of phytoplankton by zooplankton stimulated photosynthetic carbon uptake in the light in excess of 200 percent over ungrazed populations. Phytoplankton loss rates from grazing ranged from 0.002 to 0.268 $\mu\text{g chl } a/$ animal day. Feeding was found to be maximum at low concentrations of algae. These rates account for from 2-247 percent of the average growing season productivity in the lakes. Net plankton ($>50\mu$) were seldom grazed and since that size fraction and algal mass in general increased with mean productivity and nutrient content in the lakes such decreasing efficiency in food transfer is seen as a major effect of eutrophication.

INTRODUCTION

Zooplankton play an important role in the dynamics of lake systems from at least three standpoints. Their herbivorous grazing activity can represent a significant loss rate to the phytoplankton and a control of their biomass, particularly in oligotrophic lakes. They perform, through consumption and metabolic processes, much of the nutrient regeneration so important to maintaining primary production in the lighted zone of stratified lakes (Johannes 1968). Finally, the energy converted by the zooplankton sustains the production of planktivorous fish.

The objectives of this project are to quantitatively define these roles for the crustacean zooplankton in three lakes of Cedar River drainage, Washington. These lakes are Sammamish, Chester Morse and Findley and have been physically described elsewhere (Taub et al. 1972). Grazing rates are to be determined *in situ* in each lake at least frequently enough to represent seasonal changes. Regeneration rates of nutrients (N and P) in the water column could be estimated from grazing rate measurements with help from experimental data in other Biomes. Production of crustacean plankton are to be estimated in the three lakes by examining the biomass

changes in the life history stages of the dominant species. Work is progressing and although not complete, some of the findings thus far will be presented.

MATERIALS AND METHODS

Population Dynamics and Production

Net hauls for zooplankton were collected in the three lakes at frequencies varying from weekly to less than once per month with the least frequency occurring during the winter months at Findley Lake. Hauls were collected with three sizes of nets - a 0.12-m Wisconsin, a 0.30-m closing net, or a 0.50-m closing net. Concentration of plankton was determined by dividing the total number in the haul by the volume in the cylinder of lake water filtered. To eliminate the variable of net size, studies were made comparing the sampling efficiency of the two smaller nets versus the 0.50-m net. Thus, when a haul was made with the 0.12-m or 0.30-m net, the calculated concentration of the haul was multiplied by the appropriate factor for the specific net (e.g., 1.44 times calculated concentration of 0.12-m net) to adjust the results to equal that with the 0.50-m net.

As a prelude to calculating production, the complete life cycle, population changes, and life history of the specific organism must be known. This is largely what the present study has concentrated upon for the last year. Now that this information is available, productivity can be calculated from biomass increments for life history stages of each species using development times from the literature, laboratory data, or field results. Biomass can be calculated from average lengths using length-weight relationships. Unfortunately, most species occurring in the three lakes have not been previously studied, in detail, and the length-weight relation must be determined in the laboratory. This work has just begun and upon completion, secondary productivity values can be calculated for 1972.

Grazing Rates

Consumption of plankton algae by zooplankton was determined in 4l dark and clear bottles held for about 4 hours at 1 percent of surface light intensity in the three lakes, except in Findley Lake where the incubation time was 24 hours. Two experiments were conducted in Lake Sammamish, three in Chester Morse, and one in Findley Lake during 1972. Three were conducted in Lake Sammamish, two in Chester Morse, and one in Findley in 1973. The amount of phytoplankton consumed was determined by measuring the change in radio-carbon activity of the phytoplankton during the four-hour exposure to natural concentrations of grazing zooplankton. The phytoplankton were "tagged" by a preliminary exposure (2 hours) of the water samples and contained plankton to 6-30 $\mu\text{C}/\ell$ of $\text{Na}_2^{14}\text{CO}_3$. Initial concentrations of chlorophyll α were determined as a measure of food concentration. Experimental controls were set up by removing zooplankton by filtering or inactivating them with a neuro-anesthetic (physostigmine salicylate) that is neutral to phytoplankton.

Partitioning of the grazing activity into three phytoplankton size groups (ultra, nano, and net plankton) was accomplished by filtering

subsamples from the four-liter bottles through a series of three pore-size filters - 50 μ , 5 μ , and 0.45 μ . The grazing results could then be tied to phytoplankton productivity and growth rate kinetics where similar partitioning was done. Nucleopore filters replaced millipore in 1973, which improved the accuracy of the size partitioning. See Stoll (1973) for more detailed explanation of methods.

Feeding rates were determined by first estimating filtering rates or "the volume of ambient medium containing the number of cells eaten by one animal in a given time" (Rigler 1971) according to the following equation:

$$F = V \frac{\log C_0 - \log C_t}{0.4343 t}$$

where V is the volume of water per animal, C₀ is the final ¹⁴C activity of cells in the control bottle, and C_t the final ¹⁴C activity of cells in the test bottle at time t. Use of this equation assumes that the feeding rate of zooplankton is proportional to the concentration of phytoplankton and that cell concentration decreases exponentially with time.

Feeding rate was evaluated in several ways. By multiplying the feeding rate by the concentration of zooplankton the total removal rate of phytoplankton (chl *a*) was determined and compared to biomass (chl *a*) to indicate fractional removal rates. Further multiplication of the chl *a* removal rate by 50, as an average C:chl *a* ratio, allowed comparison of net productivity and grazing loss. Finally, feeding rate was related to biomass of food (chl *a*) to determine if such a relationship exists in the lakes and the seasonal changes.

RESULTS AND DISCUSSION

Species

Table 1 lists the zooplankton species which have been found in the three lakes.

Additional species are undoubtedly present as minor constituents. It will be noted from Table 1 that no crustacean zooplankton occurs in all three lakes, while almost all the rotifer species are found in all the lakes. Standing stock, population cycle, and life history of the most abundant species will be discussed in later sections.

Vertical Distribution and Movement

Vertical distribution studies over a 24-hour period have been completed for the three lakes. In the earliest study (Chester Morse) samples were taken at the mid-point of a 5-m strata with a 9l Van-Dorn sampler. For the last two studies a 0.3-m closing net became available and was used to make a separate vertical haul through each 5-m strata.

Lake Sammamish

Figure 1 shows the vertical distribution of the most abundant organisms for the five sampling times on 22-23 August, 1973. There appears to be no prominent diel vertical movements. Most of the organisms exhibit some small upward movement at sunset, followed by downward movement till mid-day. The graphs show clear distinctions in the strata occupied by the different organisms. Almost the entire population of *Diaphanosoma*, a cladoceran, is found within the photic zone throughout the 24-hour period. In contrast, *Cyclops* nauplii and copepods are largely distributed below the photic zone while the *D. ashlandi* copepods are fairly well distributed through the water column.

Chester Morse Lake

Again, the results for Chester Morse show no conspicuous diel movement (Figure 2). *Limnocalanus* adults and immatures show some movement downward during mid-day with their highest position in the water column attained at dawn and dusk. *Limnocalanus* nauplii show a complex diel movement with their highest position occurring at mid-day and their lowest at sunset with a subsequent noticeable movement upward at midnight. It is interesting to note the different niches inhabited by the two nauplii so that they avoid direct competition. The *Limnocalanus* nauplii are found in the lower two-thirds of the water column, while the *Epischura* nauplii are largely confined to the upper one-third of the lake.

Findley Lake

The two cladocerans, *Daphnia* and *Holopedium*, present during the diel sampling, show a noticeable upward migration at night (Figure 3). No clearcut migration is evident for the *D. kenai* adults. It should be remembered that in Findley Lake the photic zone often extends to the maximum lake depth, and therefore, the cladocerans are distributed throughout the water column rather than being restricted to the upper portions as in the other two lakes.

Seasonal Abundance

Figure 4 is a comparison of the yearly percent composition of the three categories of zooplankton for the three lakes of interest. It must be remembered that while this graph shows rotifers to be very important in the standing stock of the lakes; their importance in productivity values will probably be considerably less due to their small biomass. It is apparent that copepods dominated the standing stock in Lake Sammamish and Findley Lake. Cladocerans were never dominant in any lake, although most important in the standing stock of Chester Morse. Standing stock concentrations, population cycles, and life history of the most important species will be discussed in detail for each lake.

Lake Sammamish

Crustaceans dominate the zooplankton fauna of Lake Sammamish. Of these, *Diaptomus ashlandi* is the most abundant. Figure 5 shows the seasonal

cycle for this species. Adults were present most of the year, July being the only month they were not collected. Maximum numbers of adults (11/l) occurred in November and December followed by peak egg concentration (13/l) in February and March. Nauplii development was rapid, reaching a peak of 29/l in March; most were gone by early summer. Copepodid development stretched from spring to fall with maximum numbers (14/l) occurring in mid-summer. This seasonal development cycle is very similar to the one reported for *D. ashlandi* in Lake Washington by Comita and Anderson, 1959.

Figure 6 shows the developmental cycle for *Cyclops bicuspidatus* in Lake Sammamish. Due to the difficulty in separating later stage (IV and V) copepodids from adults, copepodids and adults are plotted in one category. Reproduction peaks a bit later than for *D. ashlandi* and extends over a longer period; in fact, nauplii were present throughout the year. In general, *Cyclops* is about one-third as numerous as *Diaptomus*.

The yearly population trends for cladocerans are illustrated in Figures 7 and 8. The concentration scale on these figures reveals that the cladocerans are much less abundant than copepods in Lake Sammamish. The two *Daphnia* species in Sammamish are characterized by dicyclic population cycles. *D. scholderi* had two closely spaced population peaks in the summer, while *D. thorata* peaked in late summer and early winter. The remaining cladocerans, *Diaphanosoma* and *Bosmina*, were also characterized by dicyclic populations. *Bosmina* had a major peak (1/l) in early summer and a smaller peak (0.5/l) in early winter. The first peak (0.7/l), and major one, of *Diaphanosoma* occurred in mid-summer while its smaller second peak (0.3/l) was simultaneous with that of *Bosmina*. Maximum concentration of any one species of cladoceran rarely reached 1/l, while *D. ashlandi* reached over 28/l and *Cyclops* reached over 11/l.

Because of their anticipated minor role in the total secondary production of the lakes, the life history, population cycling, and standing stock data for the rotifers will not be presented for any of the lakes in this progress report. It is planned to include these data in the final production analysis.

Chester Morse Lake

In contrast to Lake Sammamish which is dominated by copepods, the Chester Morse zooplankton is composed of fairly equal populations of copepods and cladocerans. The yearly population cycle for *Limnocalanus*, the most abundant copepod, is graphed in Figure 9. Reproduction occurs during the winter with maximum nauplii numbers (1.2/l) found during December and January. The majority of the copepodids have become adults by June and the population largely consists of adults until reproduction begins in October. Both copepodids and adults achieved peak numbers of about 0.7/l. This life cycle is almost identical to that reported by Roff and Carter (1972) in a high arctic lake. While Roff and Carter list populations of *L. macrurus* that initiate reproduction activity at a different time of the year, all known populations, including this one from Chester Morse, are univoltine.

Epischura nevadensis (Figure 10) is the other important copepod species in Chester Morse. Interestingly, both of these species are large, adults reaching lengths of over 1.5mm-2mm. *Epischura*'s life cycle is centered more during the warmer months. Reproduction occurred in two distinct pulses with the second one resulting in a higher number of young (0.8/l) and occurring over a longer time span. Adults never achieved populations of 0.1/l indicating a high mortality rate in the population.

Figure 11 details the seasonal cycle of the common cladocerans in Chester Morse. The three species "bloom" in a sequential fashion. *Holopedium* develops first, reaching a population of about 3/l in June. *Daphnia* soon follows, peaking at 0.7/l, but extending from late July to early September. The last species to "bloom", *Bosmina*, peaked in October at just over 3/l and still retained fairly high numbers through December.

Findley Lake

Zooplankton of Findley Lake are characterized by two abundant copepods and two abundant cladocerans. Two *Diaptomus* species comprise the copepods; one an unidentified species the size of *D. ashlandi* at maturity (about 1 mm); the other is *D. kenai* a very large (about 2.5 mm) organism at maturity. The cladocerans are two species common in Chester Morse, *Daphnia rosea* and *Holopedium*. Graphs of the *Diaptomus* species are not presented since the nauplii and immature stages are easily confused when counting. Preliminary analysis suggests that separation of these stages can be affected through length measurements, which at this time are incomplete for all 1972 Findley Lake samples.

Daphnia (Figure 12) shows one major peak in September when it reached its maximum population of 1.5/l and then smaller peaks in November. *Holopedium* (Figure 12) shows two peaks of similar magnitude (around 0.2/l) and close together. With the difficulty of sample collection after Findley Lake freezes over and the consequent long interval between samples, the life history of organisms at Findley Lake can be only approximately known.

Population Dynamics

Use of the egg-ratio technique developed by Edmondson (1960) provides a detailed picture of the cladoceran population dynamics. In addition, this information has been used in modeling efforts (McNaught 1972) and can be used to calculate production (Wright 1965).

This type of analysis will be extended to egg bearing copepods and rotifers during the next year. Unfortunately, two of the most common copepods, *Limnocalanus* and *Epischura*, lay their eggs directly into the water, which means that the egg-ratio technique will not apply.

Tables 2, 3, and 4 give the birth (b) and death (d) rates, population change rate (r), and mean eggs/female (E) for the common cladocerans in the three lakes.

Grazing effect on phytoplankton productivity

The first three experiments were conducted in Chester Morse Lake in 1972. Light bottles were used for both the experimental and control volumes. In most cases the results show a definite stimulation of primary production in the heavily cropped complements of algal communities, even over the short experimental periods.

Figure 13 illustrates this stimulation of production rates in grazed versus ungrazed volumes in the different size classes measured on June 7. The major effect of grazing was in the nano plankton range where a 78 percent increase occurred in the grazed over the ungrazed volumes. The effect on the whole community is shown as a total. Grazing caused nearly a doubling in $^{14}\text{CO}_2$ uptake in the grazed volumes over the ungrazed volumes. The primary size range of phytoplankton fell in the nano plankton group, 5μ to 50μ in diameter (although ultra plankton less than 5μ are included since millipore filters were used). The major zooplankter was the copepod *Limnocalanus* (Table 5). Two subsequent studies showed greater stimulation (over 200 percent increase) in one and essentially no effect in the other (for details see Stoll 1973).

The causes for this stimulation may be two. Grazing by zooplankton has been suggested as a primary mode of recycling nutrients, particularly phosphorus (Johannes 1968). Cooper (1973) suggested that recycling of nutrients from grazing could result in substantial stimulation of primary production. Stimulation of primary production could be due to factors other than nutrient recycling. De Amezaga, et al. (1972) in their work on Castle Lake, California, suggest that increases in primary production are strongly related only to reduction in standing crop due to grazing at certain times, which was also suggested by Cooper. Because differences in P and N between grazed and ungrazed samples could not be detected the results in these experiments may primarily be an effect due to cropping. However, it is also felt that the rapid uptake by phytoplankton of regenerated nutrients would have made detection of the released quantities difficult.

Phytoplankton loss rates

The grazing effect on phytoplankton was determined in dark bottles at natural concentration of both the herbivores and the producers. Relative decreases in grazed versus ungrazed samples ranged from 13 to 36 percent. These differences were adequate to provide reasonable estimates of feeding rates which are shown in Table 6. Nano plankton and ultra plankton were the principal groups of the phytoplankton grazed and usually in that order, although in two instances the net plankton was the principal group (Table 6). When net plankton was the only group grazed, rates were relatively low.

The 1972 rates were determined in mid or late summer, some time after the maximum phytoplankton productivity and biomass occurred in the lake and also after the net plankton peak in the spring. At the time of these studies the phytoplankton was composed of 90 percent plankton as indicated by chlorophyll α and productivity (Hendrey 1973).

Millipore filters have been found to underestimate the contribution of ultra plankton by a sizable percentage. Work in 1973 has not only improved the accuracy of the separation by using nucleopore filters, but also provide grazing rate measurements from the spring when net plankton were abundant as well as later when they have disappeared.

Comparisons have shown that nucleopore filters increased the importance of ultra plankton from a small fraction of the nano plankton to levels equal to nano plankton.

Only the spring experimental (April) results are available at this time. It is clear that during the spring diatom outburst in Lake Sammamish when, for example, *Fragilaria* and *Stephanodiscus* ($>50\mu$) comprise most of the phytoplankton biomass very little grazing occurs (see 4/10/73, Table 6). The rate during this time was an order of magnitude lower than later when net plankton were less important and nano plankton were grazed. However, it is surprising that the relatively high concentration of nano plankton on 4/10/73 was not grazed even though zooplankton were as abundant as on 4/20/73.

The net plankton in the oligotrophic lakes Chester Morse and Findley are relatively scarce compared to mesotrophic Sammamish. Thus, even during the spring diatom outburst in Chester Morse, the size of the phytoplankton are smaller than Sammamish and hence are readily grazed (Table 5). Although grazing results are not available for Lake Washington, Hendrey (1973) has shown that the fraction of productivity and biomass contributed by net plankton progressively increases with productivity in the Cedar River Lakes and, thus, is much greater in Washington than Sammamish.

Grazing by zooplankton usually accounted for sizeable losses of phytoplankton productivity, except when dominance and hence productivity by net plankton was great. Table 7 shows again that in oligotrophic lakes Findley and Chester Morse net plankton never dominated the plankton groups. As a result most of the phytoplankton mass was thus available to be grazed. The one measurement during spring in Chester Morse indicates that large loss rates are possible, greatly in excess of primary productivity, even during a diatom outburst if cell size is small enough. In Sammamish, the spring loss rates were less, because of the large contribution of productivity from larger cells which were not utilized. As a result, on the average, three times more of the primary productivity was consumed in mesotrophic Lake Sammamish than in the oligotrophic lakes (Table 7).

There are two mechanisms operating in the eutrophication process that result in a greater accumulation of phytoplankton biomass with an increase in nutrient supply rate. As just described for the Cedar River lakes, the fraction of net phytoplankton increases as productivity increases. This is probably a result of changed nutrient supply with net plankton more able to compete with smaller forms. With more net plankton produced with eutrophication a smaller and smaller fraction then is available to grazing. Even though secondary productivity may increase with eutrophication larger amounts of unavailable algal mass will accumulate. This in fact is what occurs in these lakes as winter phosphorus is correlated with summer algal biomass (Welch, et al. 1973).

The other mechanism involves the saturation of the filtering mechanism with increases in food concentrations. For the 1972 data Stoll (1973) found that the half-saturation concentration (as indicated by a Michaelis-Menten formulation) in these lakes was about $0.2 \mu\text{g chl } a/l$. If such a relationship persists once all the 1973 data are analyzed then even if net plankton are not present, the feeding rate per animal would be saturated at relatively low concentrations of algae. Certainly total grazing loss would increase as the density of zooplankton increased, but such parameters do suggest a tendency to saturate the grazing loss mechanism as algal biomass increases.

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Table 1. Zooplankton species by lake.

Organism	LS	CM	FL
Copepods			
* <i>Diaptomus ashlandi</i>	X		
<i>D. franciscanus</i>		X	
* <i>D. kenai</i>			X
* <i>D. sp.</i>			X
* <i>Limnocalanus macrurus</i>		X	
* <i>Epischura nevadensis</i>	X	X	
* <i>Cyclops bicuspidatus</i>	X	X	
<i>Cyclops sp.</i>			X
Cladocerans			
* <i>Daphnia thorata</i>	X		
* <i>D. scholderi</i>	X	X	
* <i>D. rosea</i>		X	X
* <i>Bosmina longirostris</i>	X	X	
* <i>Diaphanasoma leuchtenbergianum</i>	X		
* <i>Holopedium gibberum</i>		X	X
<i>Leptodora kindtii</i>	X	X	
Rotifers			
* <i>Kellicottia longispina</i>	X	X	X
<i>K. bostoniensis</i>	X	X	
* <i>Polyarthra sp.</i>	X	X	X
<i>Keratella cochlearis</i>	X	X	X
<i>K. quadrata</i>	X	X	X
* <i>Conochilus unicornis</i>	X	X	X
<i>Collotheca mufabilis</i>	X	X	X
<i>C. pelagica</i>	X	X	X
<i>Notholca squamula</i>	X	X	X

*indicates most common species

Table 2. Birth and death rates, population change rate, and mean number of eggs/ $\frac{1}{l}$ for cladocerans in Findley Lake, 1972.

Sampling interval	<u>Holopedium</u>				<u>D. rosea</u>			
	b	r	d	E	b	r	d	E
11 Jul						0.147		0
25 Jul		-0.124		0	0.104	0.125	-0.021	1.500
1 Aug		0.441		0	0.223	0.187	0.036	1.529
8 Aug	0.095	-0.192	0.287	0.644	0.140	-0.056	0.196	0.812
15 Aug	0.542	0.011	0.531	3.750	0.086	0.017	0.069	0.667
29 Aug	0.191	0.086	0.105	0.800	0.239	0.078	0.161	1.373
14 Sep	0.058	-0.120	0.178	0.353	0.095	-0.038	-0.133	0.620
6 Oct	0.095	-0.026	0.121	1.187	0.020	-0.147	0.167	0.273
21 Oct	0.182	-0.025	0.207	2.889	0.004	0.080	-0.076	0.083
4 Nov	0.300	0.040	0.260	5.571		0.117		
12 Nov	0.166			3.636				
	avg 0.204				avg 0.114			

Table 3. Birth and death rates, population change rates, and mean number eggs/♂ for cladocerans in Chester Morese, 1972

Sampling interval	<u>Holopedium</u>				<u>Bosmina</u>				<u>D. rosea</u>				
	b	r	d	E	b	r	d	E	b	r	d	E	
22 April	0.100	0.065	-0.055	0.315									
20 May	0.270	0.013	0.257	3.837					0.270	-0.090	0.360	3.750	
3 June	0.070	-0.170	0.190	0.169						-0.190		0	
7 June	0.157	0.475	-0.318	1.749					0.230	0.770	-0.540	0.043	
11 June	0.122	-0.100	0.222	1.367					0.050	-0.100	0.150	0.600	
22 June	0.165	-0.059	0.224	1.910					0.040	0.030	0.010	0.500	
30 June	0.104	-0.167	0.271	1.027					0.090	0.150	-0.060	0.750	
6 July	0.020			0.136					0.080	0.070	0.010	0.667	
21 July	0.120								0.110	0.010	0.100	0.938	
14 Aug									0.060	-0.010	0.070	0.355	
4 Sept					0.058	0.017	0.041	0.167		0.060	-0.090	0.150	0.363
29 Sep					0.049	0.104	-0.055	0.450		0.050	0.090	-0.040	0.423
13 Oct					0.039	0.065	-0.026	0.471		0.090	-0.050	0.140	0.927*
27 Oct					0.059	0.016	0.075	0.634		0.103			
22 Dec					0.010	0.053	-0.043	0.233					
27 Dec					0.010	-0.064	0.074	0.290					
					0.037								

*Resting eggs present, not included in eggs/♂.

Table 4. Birth and death rates, population change rates, and mean number eggs/♀ for cladocerans in Lake Sammamish, 1972

Sampling interval	<u>Diaphanasoma</u>				<u>Bosmina</u>				<u>D. scholderi</u>			
	b	r	d	E	b	r	d	E	b	r	d	E
21 Feb					0.077	-0.101	0.178	0.083	0.020	-0.031	0.051	0.374
11 Mar					0.077			0.500	0.077	-0.017	0.094	1.000
4 April									0.140	0.020	0.120	1.850
18 April					0.068	0.039	0.029	0.833	0.039	0.032	0.007	0.425
12 May	0.365	0.086	0.279	1.750	0.131	0.024	0.107	1.125	0.140	0.086	0.054	1.250
2 June	0.113	0.050	0.063	0.857	0.068	0.262	-0.194	0.500	0.113	-0.044	0.157	0.320
13 June	0.157	0.057	0.100	1.067	0.604	-0.043	0.647	0.523	0.255	0.034	0.221	1.833
24 June	0.166	-0.075	0.241	1.281	0.525	-0.097	0.622	0.356	0.086	-0.074	0.160	0.595
17 July	0.215	0.380	-0.165	2.583	0.239	0.075	0.164	1.666	0.077	0.255	-0.178	0.285*
24 July	0.255	0.001	0.254	1.374	0.293	-0.034	0.327	1.211	0.030	-0.037	0.067	0.176
7 Aug	0.049	-0.111	0.160	0.250	1.120	-0.085	1.204	1.111	0.030	-0.091	0.121	0.176
14 Aug	0.030	-0.033	0.063	0.182	0.030	0.013	0.107	0.200	0.010	-0.011	0.021	0.074
11 Sept	0.182	-0.058	0.240	2.888	0.077	-0.076	0.153			0.003		0
8 Oct	0.300	0.028	0.272	2.500					0.020			0.133
22 Oct	0.199	0	0.199	2.250								
2 Nov	0.039	0.056	-0.017	0.333								
11 Nov	0.166	0.207	-0.041	0.657	0.104	0.147	-0.043	1.031	0.040	0.124	0.084	0.333
18 Nov	0.020	-0.015	0.035	0.125*	0.086	0.058	0.028	0.750	0.040	-0.028	0.068	0.500
2 Dec	0.049	-0.076	0.125	0.363*	0.086	-0.016	0.102	0.778				
18 Dec	0.122			1.500*	0.020			0.258				
	0.152				0.222				0.074			

*Resting eggs present, not included in eggs/♀.

Table 5. Dominant grazers in all experiments. Same rotifers were also observed but not in significant enough numbers to include for grazing purposes. Very few nauplii were observed.

Date	Lake	Significant genera	Animals/liter
6-7-72	Chester Morse	<u>Limnocalanus</u>	6
6-19-72	Chester Morse	<u>Holopedium</u>	3.5
		<u>Limnocalanus</u>	1
		<u>Diaptomus</u>	0.2
7-9-72	Chester Morse	<u>Daphnia</u>	2.7
		<u>Limnocalanus</u>	2.1
		<u>Holopedium</u>	1.2
7-24-72	Sammamish	<u>Daphnia</u>	11
		<u>Diaphanasoma</u>	3
		<u>Diaptomus</u>	3
8-27-72	Sammamish	<u>Diaptomus</u>	121
		<u>Daphnia</u>	17
9-22-72	Findley	<u>Diaptomus</u>	27
		<u>Daphnia</u>	11

Table 6. Filtering and feeding rate determined in the three Cedar River Lakes during 1972-73. () measure of unfiltered samples.

Lake	Date	Size	$\mu\text{g chl } a$ ℓ	# zoopl. ℓ	Filtering rate ml/anim/day	Feeding rate $\mu\text{g chl } a$ /anim/day
Findley	9/22/72	Net	0		0	0
		Nano	0.5		27.6	0.014
		Ultra	0.07		71.52	0.005
		Total	0.58	37	99.1	0.019(0.06)
	8/26/73	Net			0	
		Nano			49.2	
Ultra				25.0		
Total			48	74.2		
Chester Morse	7/9/72	Net	0.007		0	0
		Nano	0.710		240.24	0.17
		Ultra	0.061		0	0
		Total	0.77	6		0.17
	5/1/73	Net	0		0	0
		Nano	1.64		32.4	0.053
Ultra		3.82		56.4	0.215	
Total		5.46	46		0.268	
Sammamish	7/24/72	Net	0.18		0	0
		Nano	5.90		50.4	0.297
		Ultra	0.25		65.04	0.016
		Total	6.3	17	115.44	0.313(0.727)
	8/27/72	Net	0.09		18.0	0.002
		Nano	2.80		0	0
		Ultra	0.12		0	0
		Total	3.0	138	18.0	0.002(0.05)
4/10/73	Net	6.98		1.6	0.011	
	Nano	4.07		0	0	
	Ultra	0.23		0	0	
	Total	11.28	227		0.011	
4/20/73	Net	1.92		0	0	
	Nano	1.37		12.0	0.016	
	Ultra	0.34		26.4	0.009	
	Total	3.63	241	38.4	0.025(0.139)	

Table 7. Phytoplankton loss rates through zooplankton grazing and the relative size of producers present and percent of growing season productivity in the Cedar Drainage Lakes in 1972-73.

Lake	Spring					Summer				
	Date	Loss rate	Algal size present	Algal size grazed	Percent productivity	Date	Loss rate	Algal size present	Algal size grazed	Percent productivity
Findley						9/22/72	35	nano	nano ultra	16
						8/26/73			nano ultra	
Chester Morse	5/1/73	617	nano	ultra nano	235	7/9/72	51	nano	nano	20
Sammamish	4/10/73	125	net	net	21	7/24/72	266	nano	nano	44
	4/20/73	302	net	ultra nano	50	8/27/72	14	nano	net	2

loss rate - $\text{mg cm}^{-3} \text{ day}^{-1}$ assuming $C/\text{chl } a = 50$

net > 50μ ; nano 50- 5μ ; ultra > 5μ

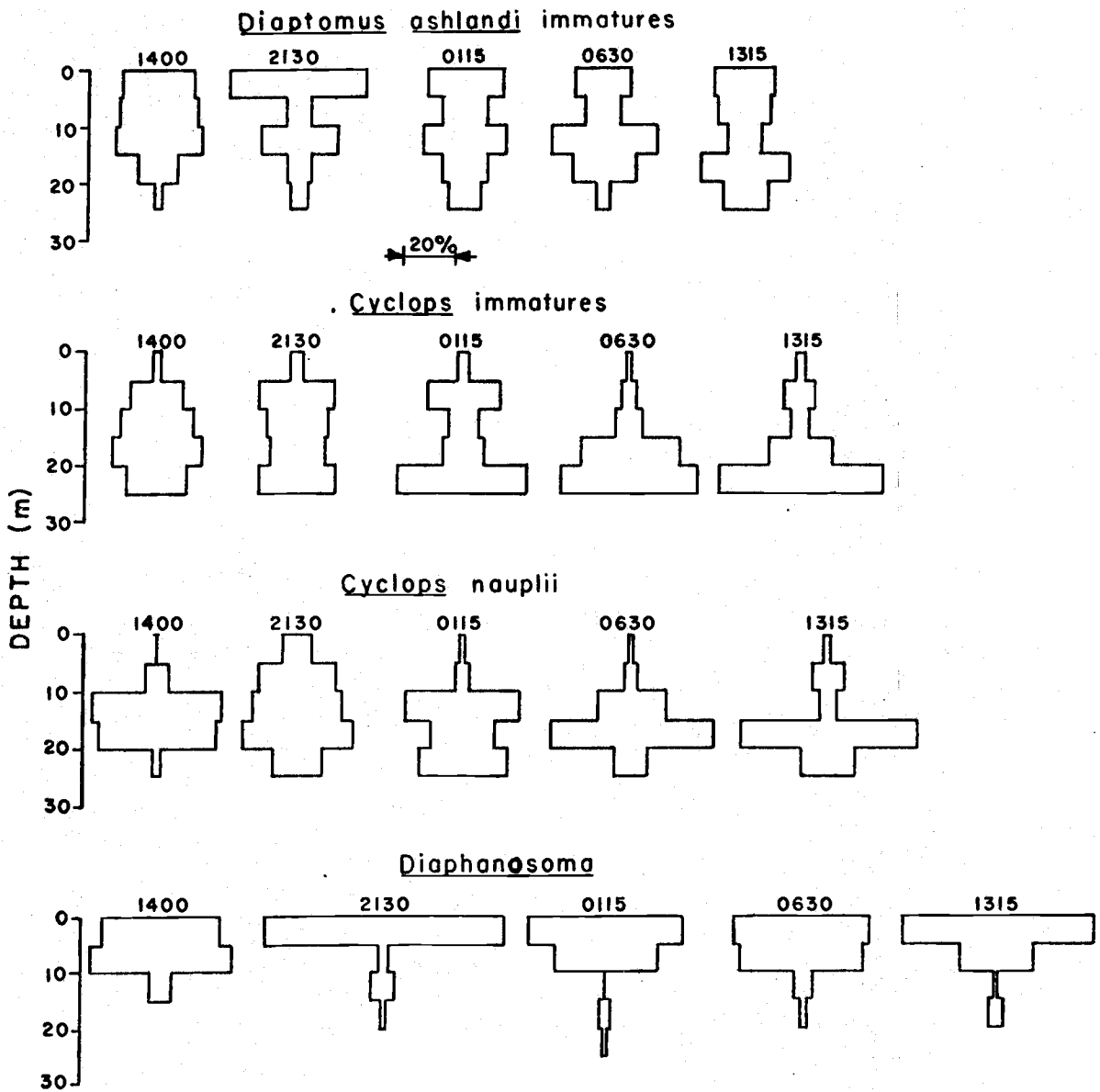


Figure 1. Percent composition of *Diaptomus ashlandi* immatures, *Cyclops* immatures and nauplii, and *Diaphanosoma*, as a function of depth during a diel study in Lake Sammamish on 22 and 23 August 1973. Photic zone - 7.8 m. Thermocline - 8-10 m.

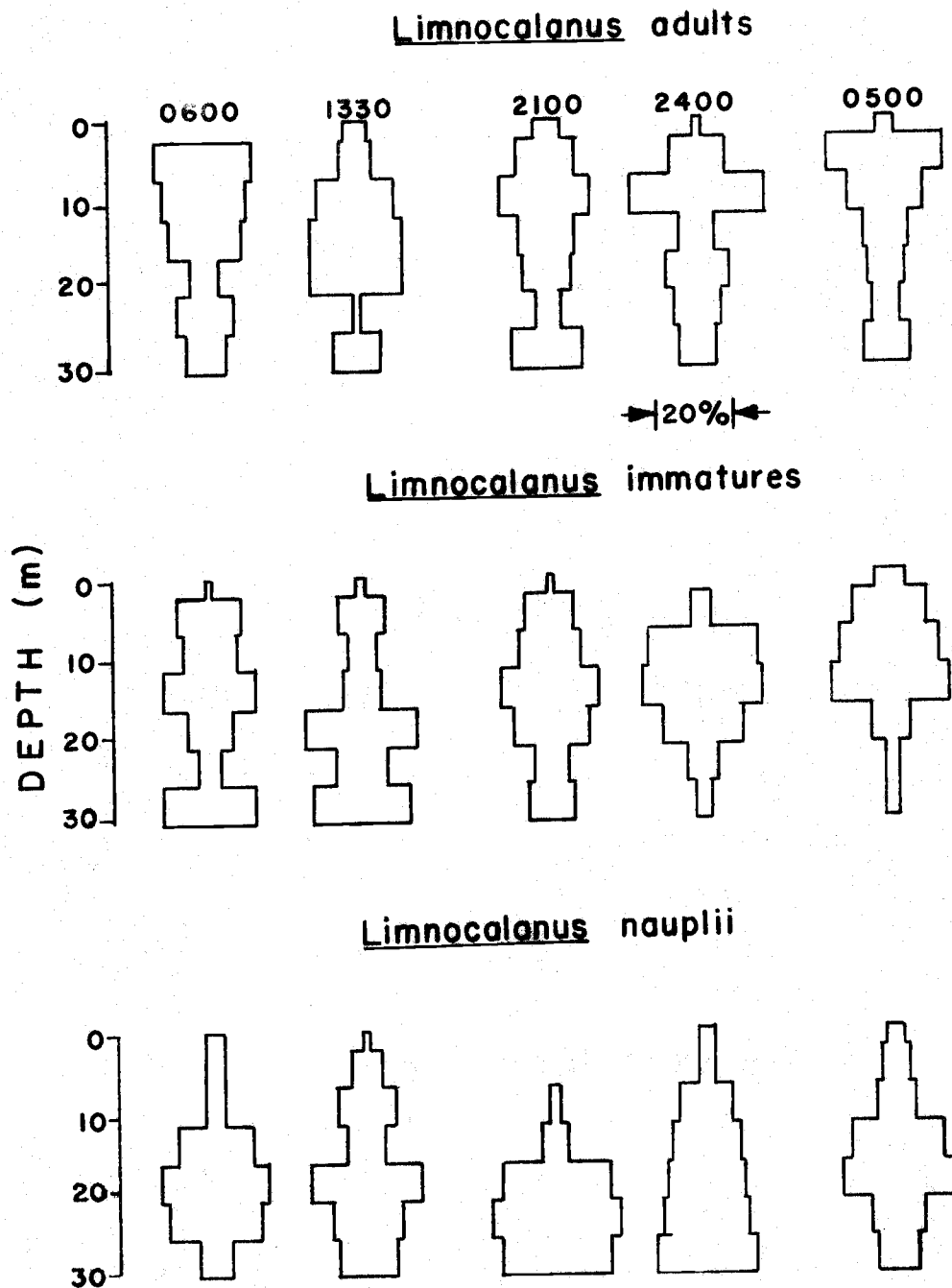


Figure 2. Percent composition of *Limnocalanus* adults, immatures, and nauplii, *Epischura* nauplii, *Kellicottia*, and *Chl.*^a, as a function of depth during a diel study in Chester Morse Lake on 1 and 2 May 1973.

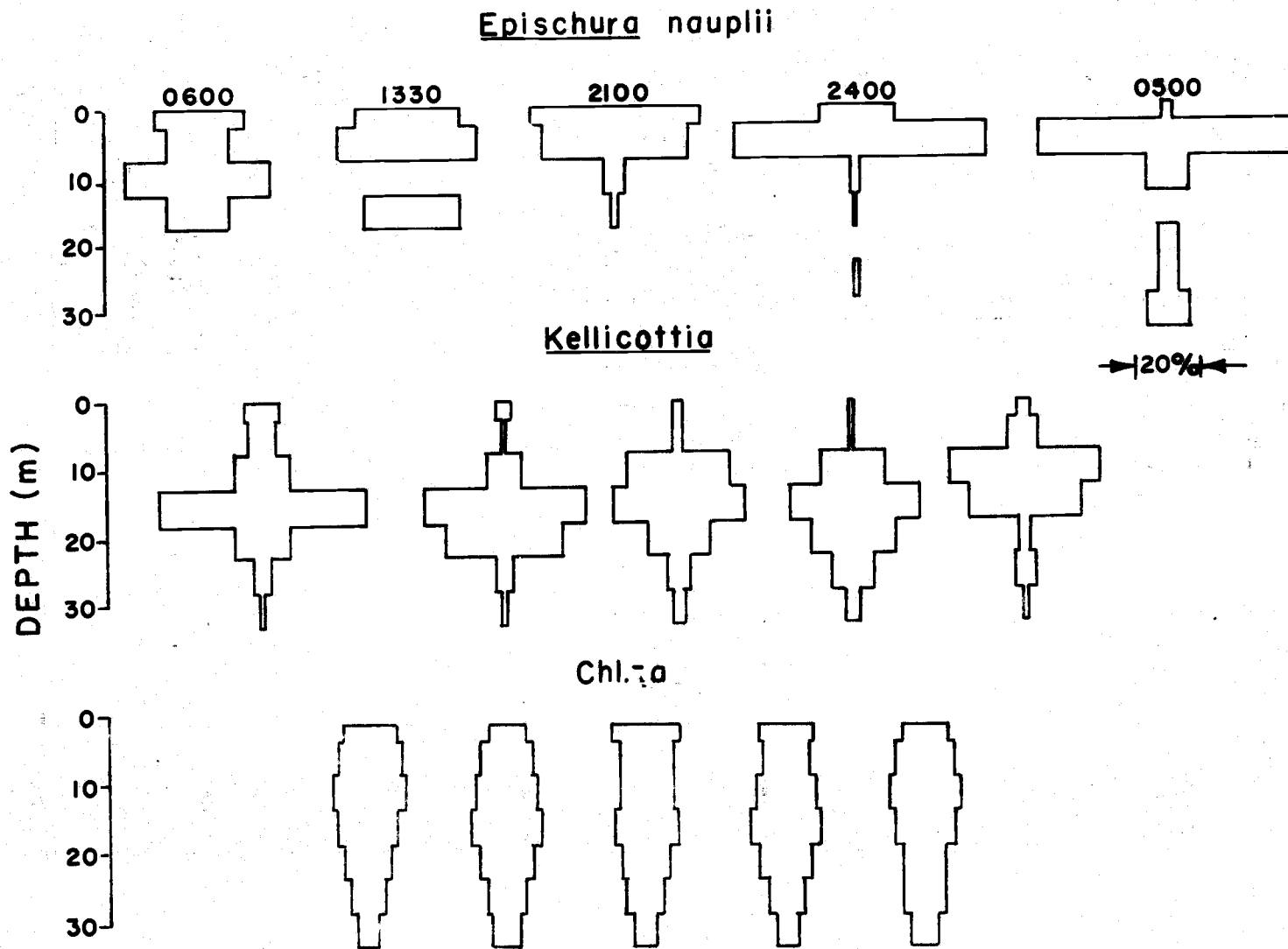


Figure 2. Cont.

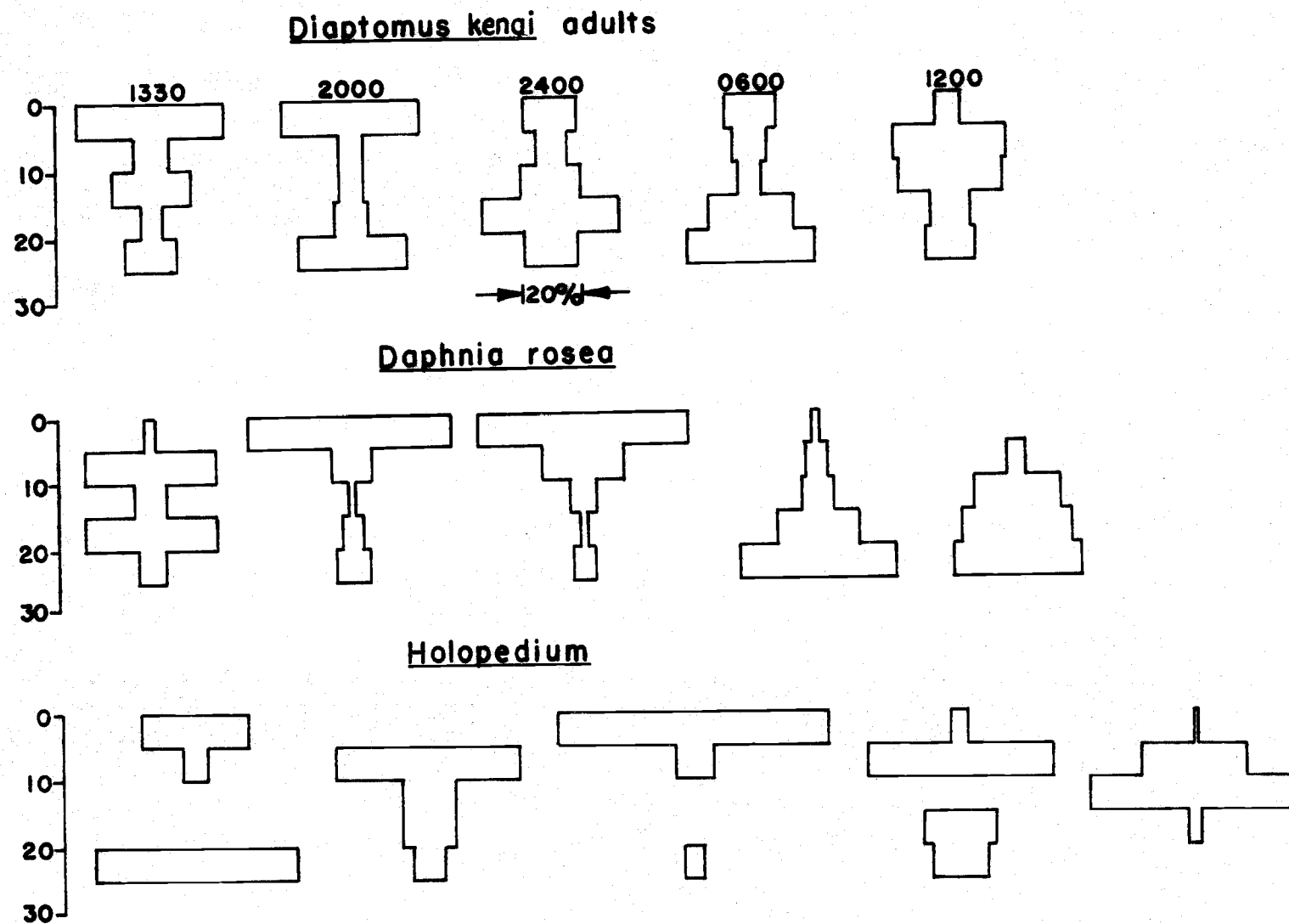


Figure 3. Percent composition of *Diaptomus kenai* adults, *Daphnia rosea* and *Holopedium*, as a function of depth during a diel study in Findley Lake on 8 and 9 August 1973.

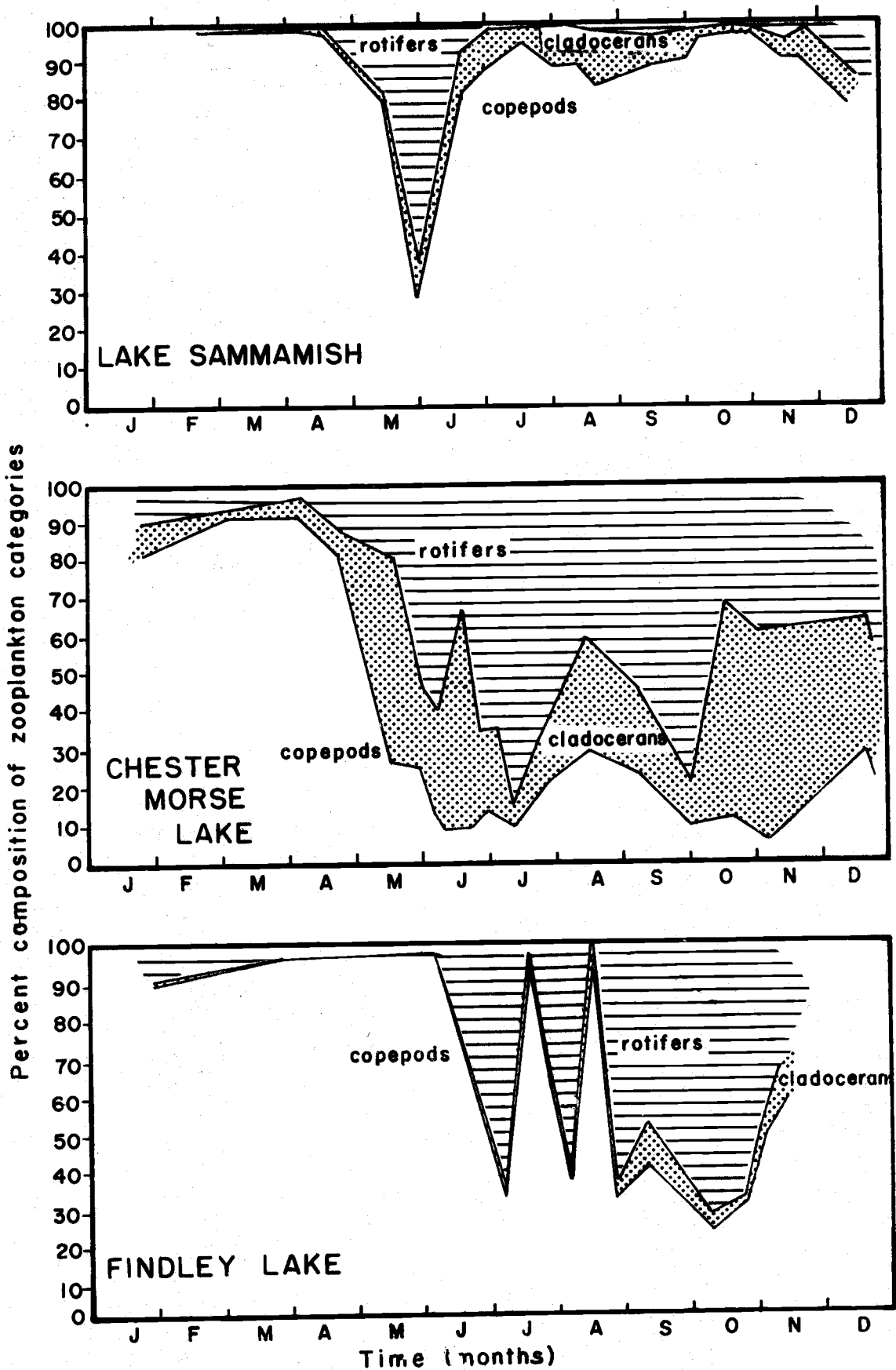


Figure 4. Composition of zooplankton categories in Lakes Sammamish, Chester Morse, and Findley, as a function of time in 1972.

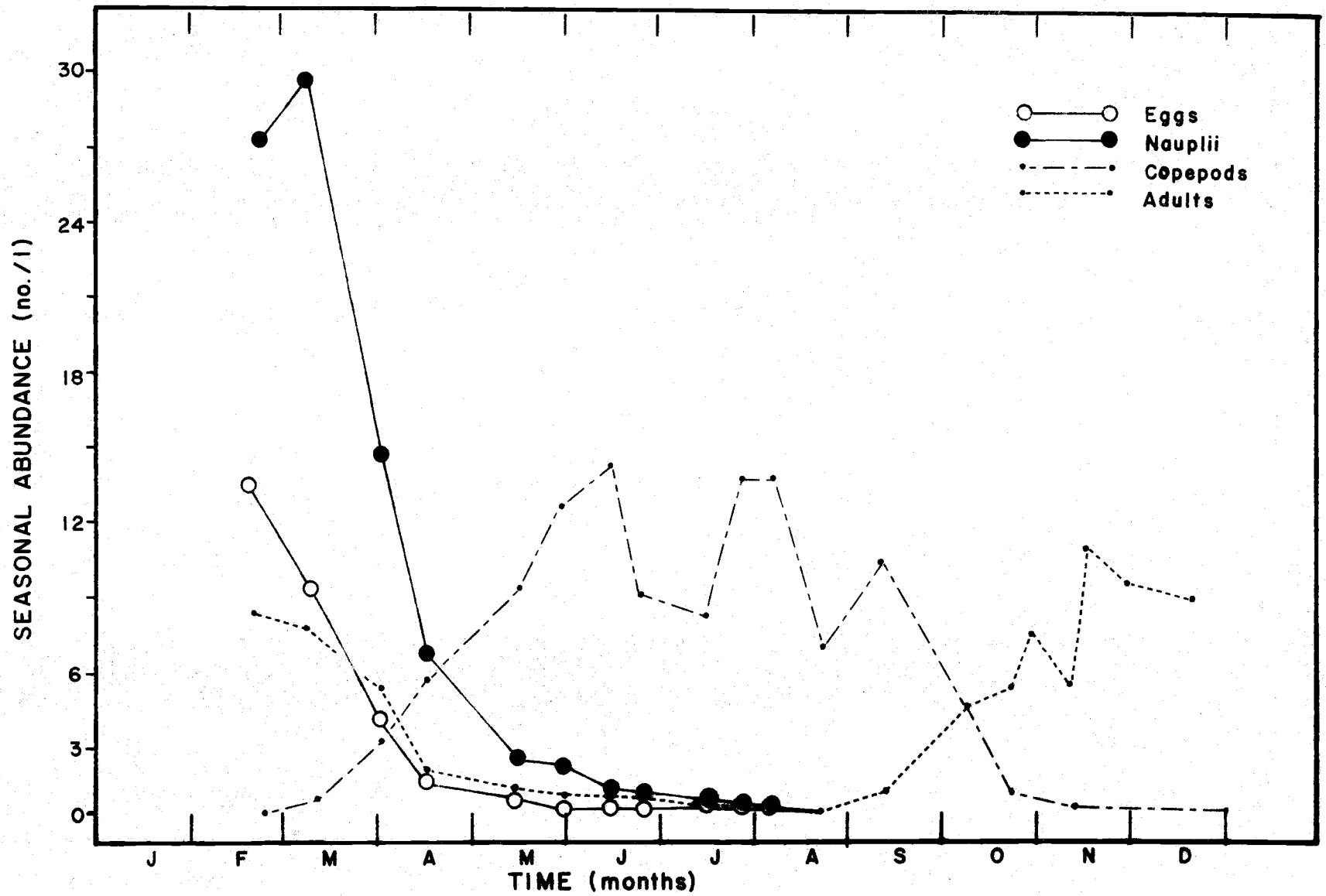


Figure 5. Seasonal abundance of *Diaptomus ashlandi* in Lake Sammamish, 1972.

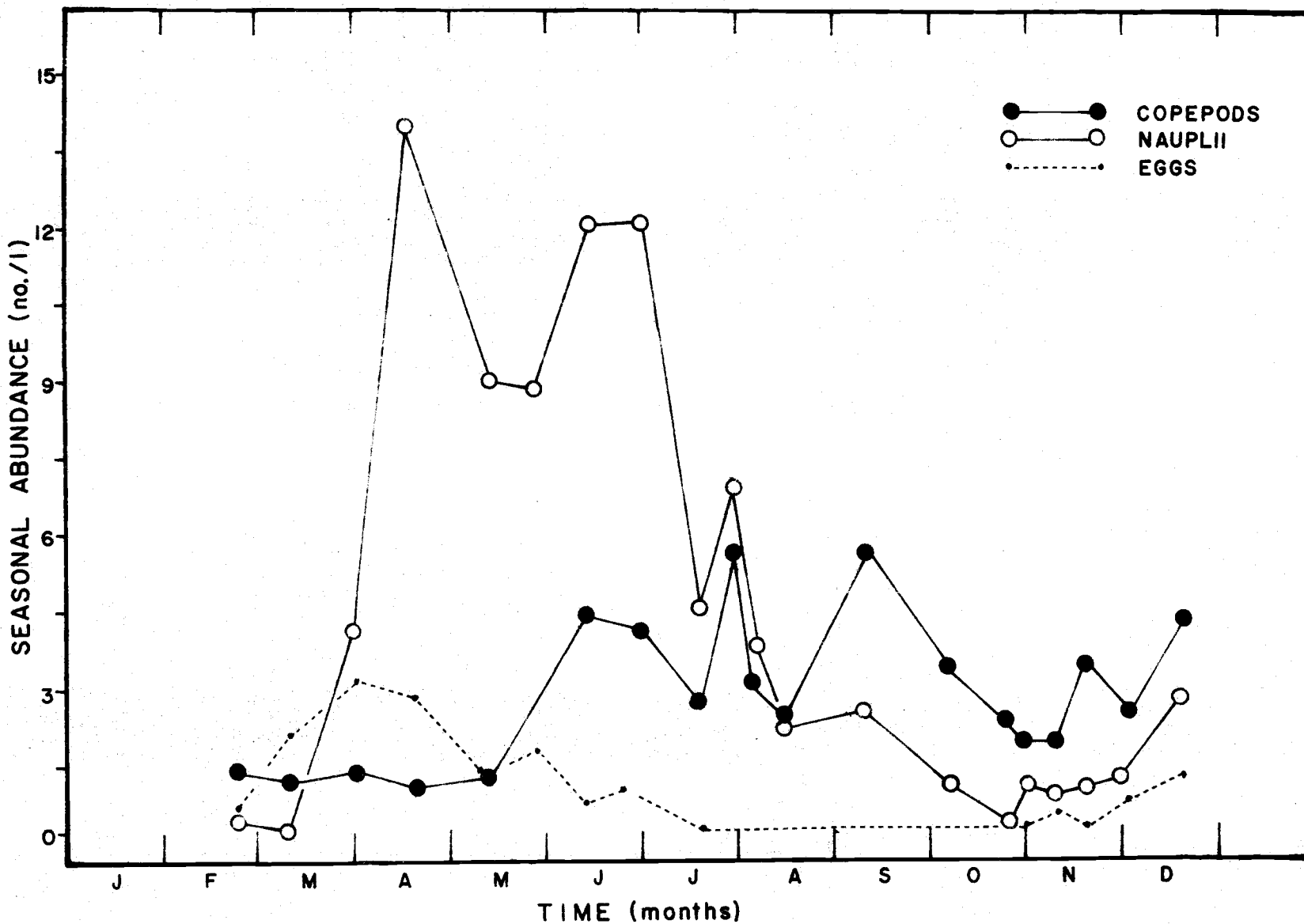


Figure 6. Seasonal abundance of *Cyclops bicuspidatus* in Lake Sammamish, 1972.

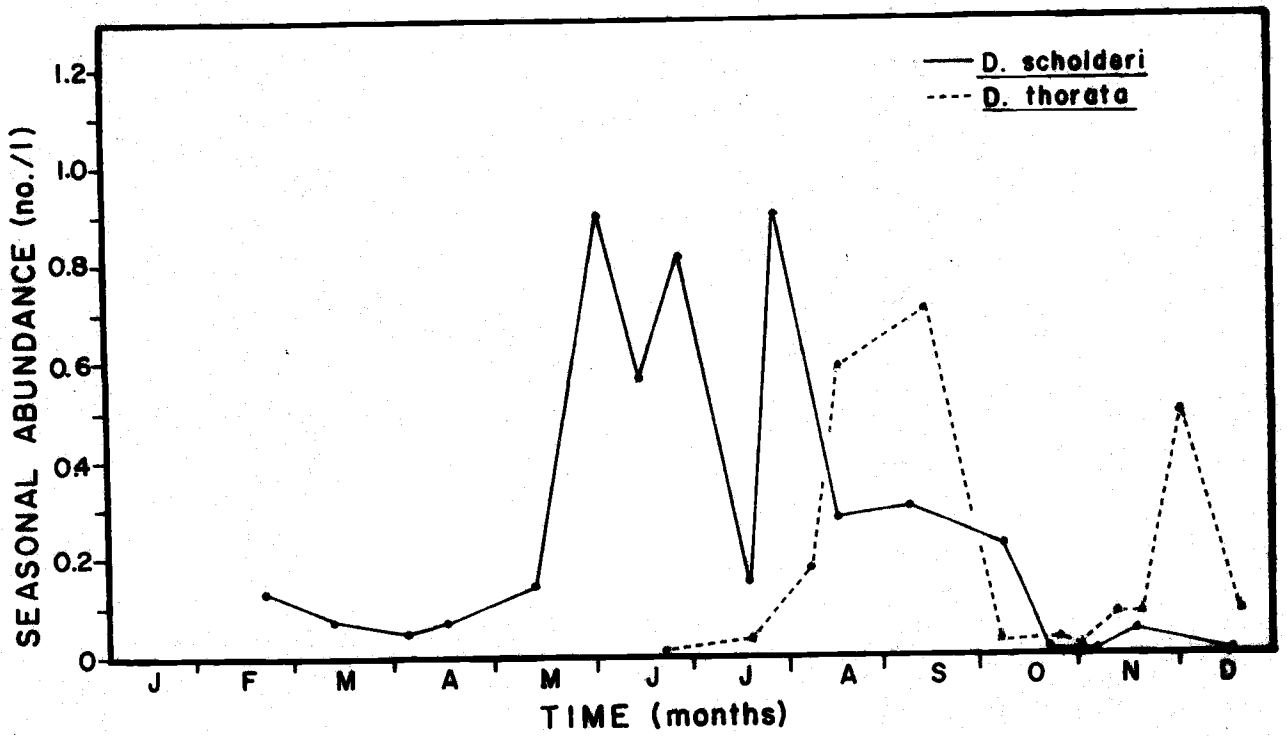


Figure 7. Seasonal abundance of *Daphnia* in Lake Sammamish, 1972.

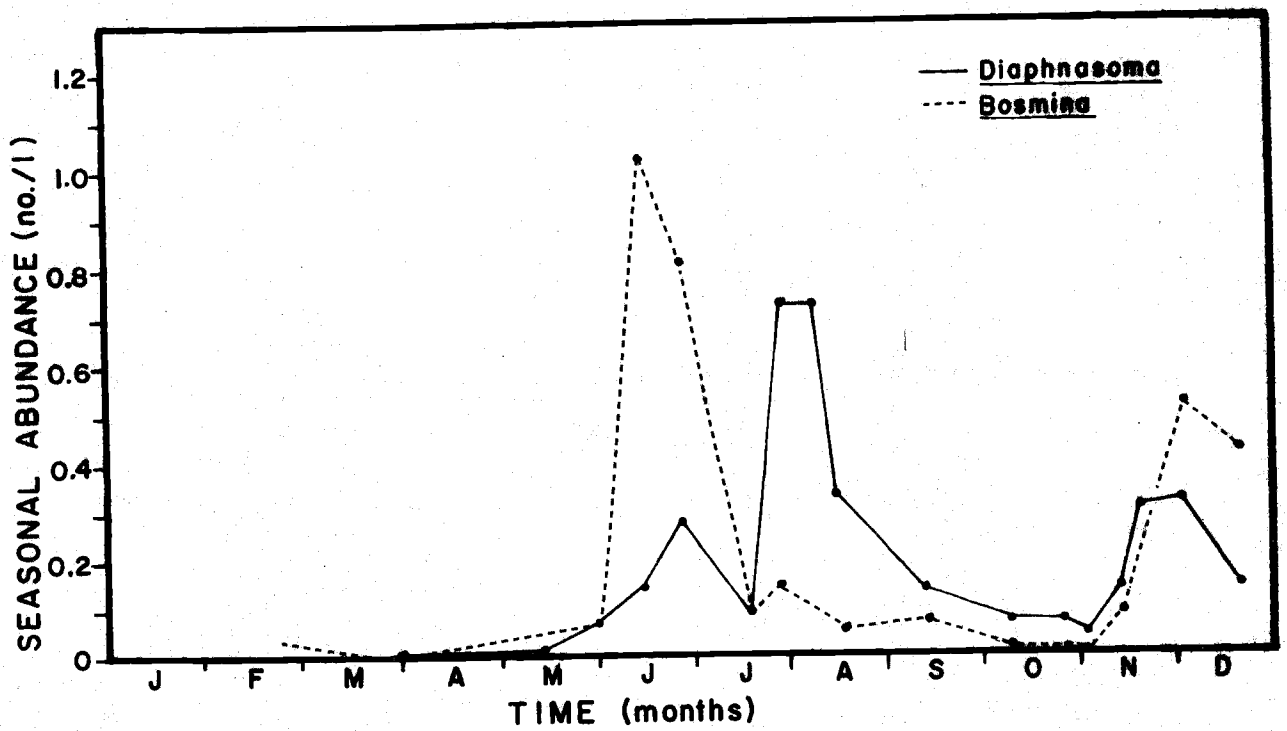


Figure 8. Seasonal abundance Cladocerans in Lake Sammamish, 1972.

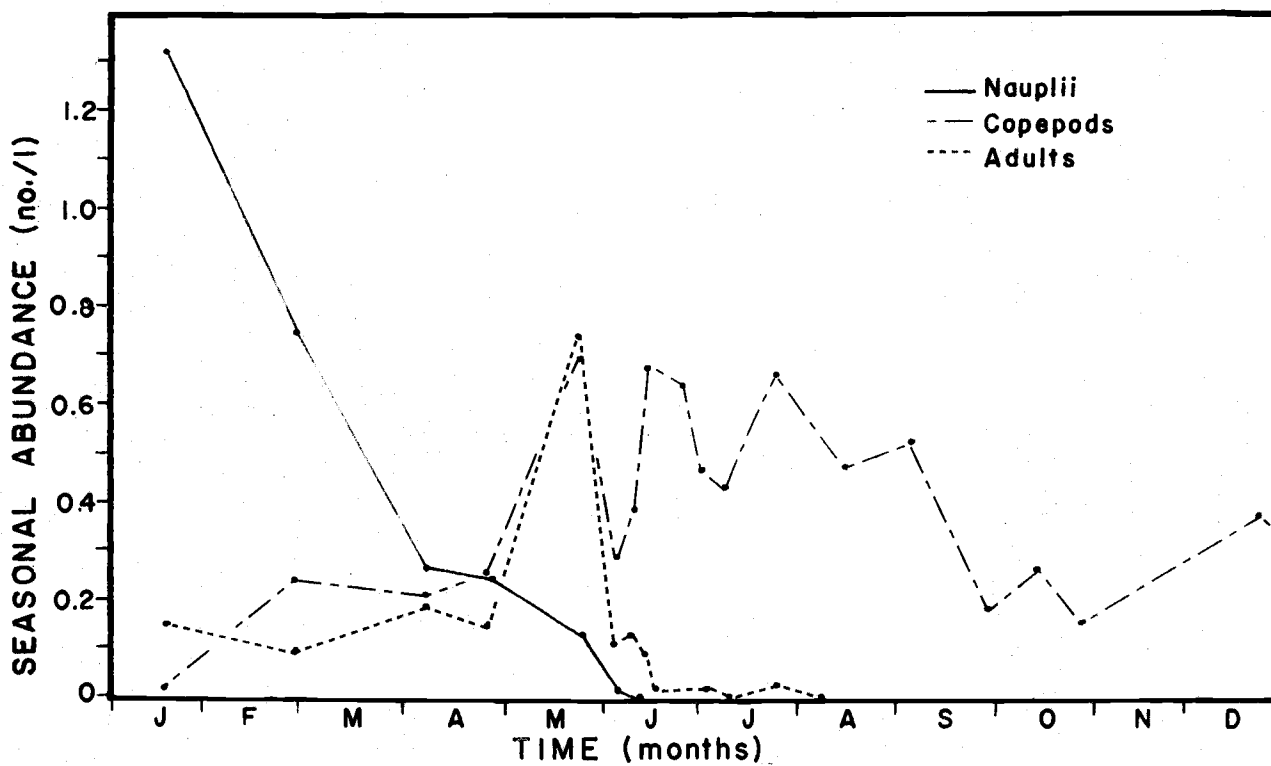


Figure 9. Seasonal abundance of *Limnocalanus macrurus* in Chester Morse Lake.

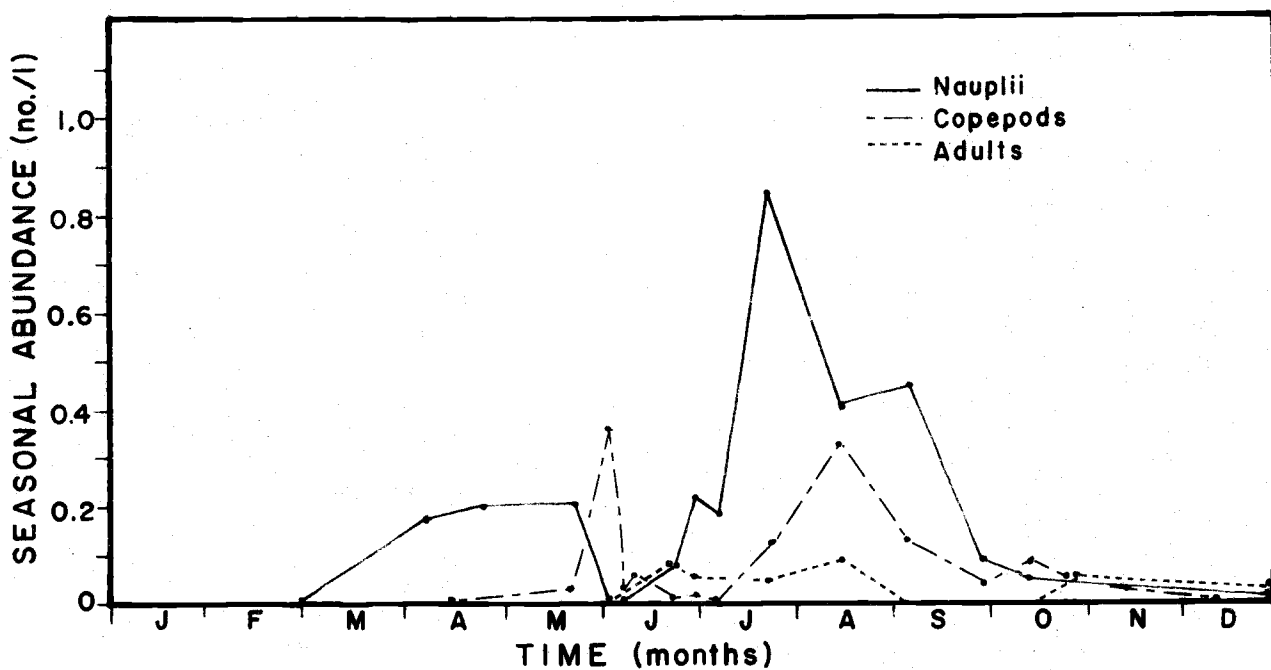


Figure 10. Seasonal abundance of *Epischura nevadensis* in Chester Morse Lake, 1972.

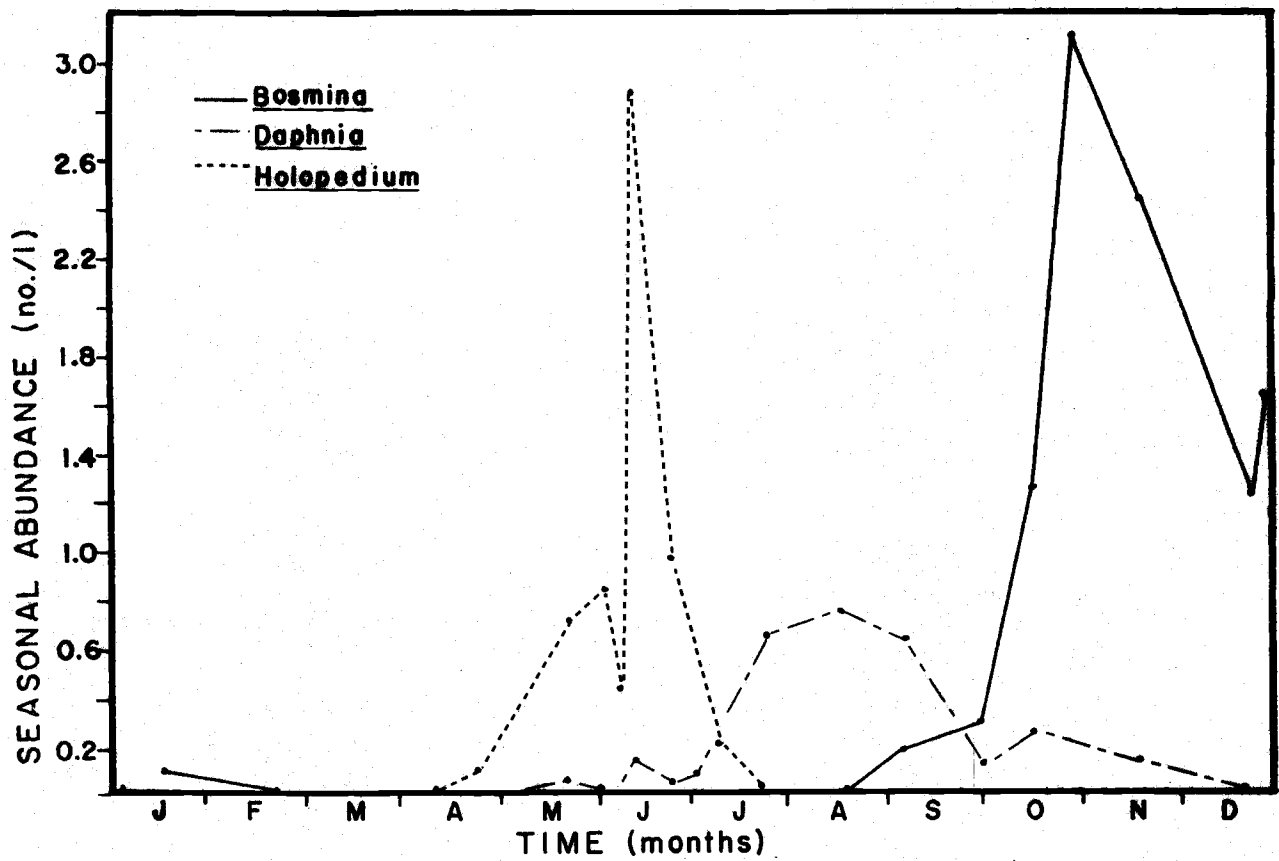


Figure 11. Seasonal abundance of Cladocerans in Chester Morse Lake, 1972.

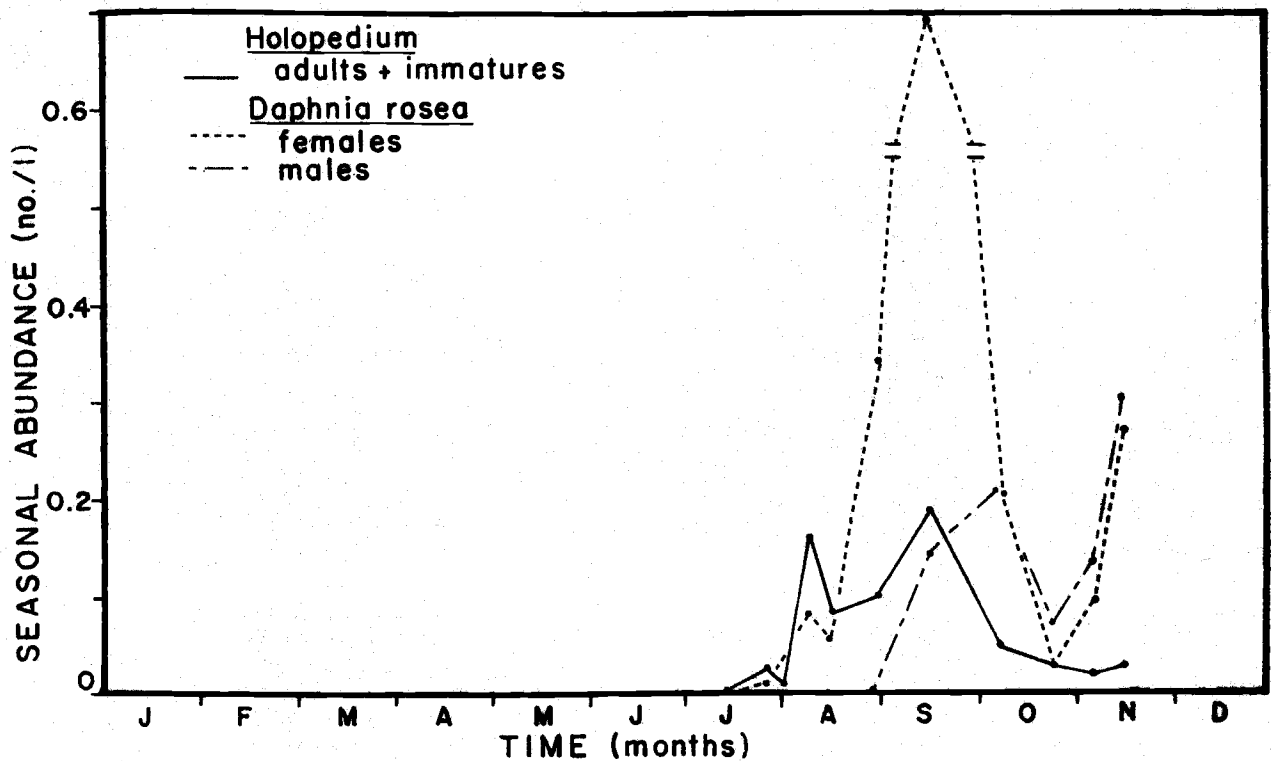


Figure 12. Seasonal abundance of Cladocerans in Findley Lake, 1972.

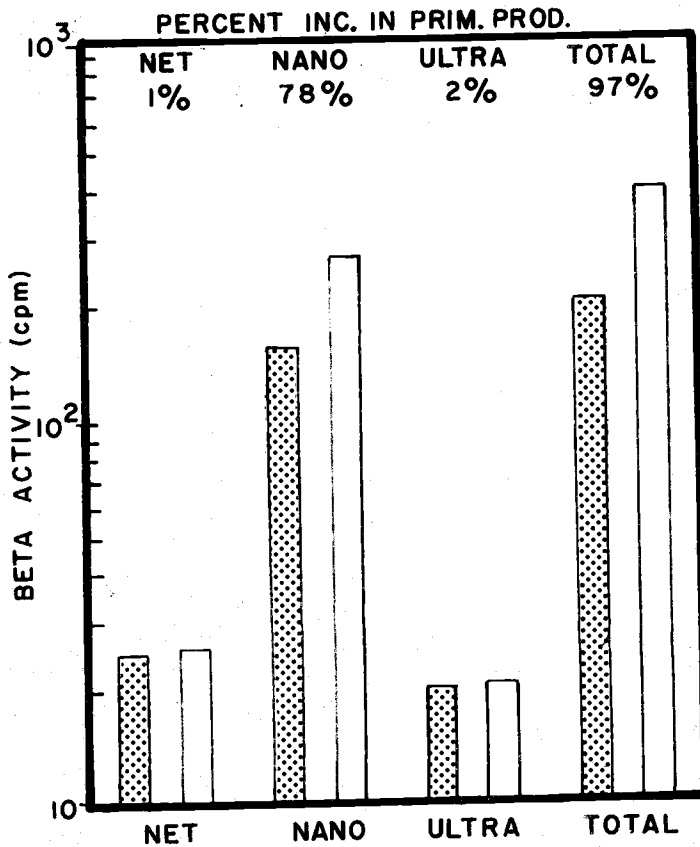


Figure 13. Differences between grazed, , and ungrazed, , samples from light bottle experiments conducted in Chester Morse Lake on June 7, 1972. The bars are on a logarithmic scale and represent differences in beta activity in different algal size classes as well as a total. Total uptake of $^{14}\text{CO}_2$ was measured during the whole experimental period. Significant differences between grazed and ungrazed samples occur only in the nano plankton range where a greater production rate is seen in the grazed sample.