THE FERTILIZATION OF GREAT CENTRAL LAKE
II. ZOOPLANKTON STANDING STOCK

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ABSTRACT

The regional, vertical, and seasonal abundance of the dominant zooplankton species were studied in conjunction with a series of nutrient additions to Great Central Lake. Two rotifer species, *Kellicottia* spp., *Conochilus unicornis*, three cladocera species, *Bosmina coregoni*, *Holopedium gibberum*, and *Daphnia longiremis*, and three copepod species, *Cyclops bicuspidatus thomasi*, *Epischura nevadensis*, and *Diaptomus oregonensis* were the most numerically abundant zooplankton species. The introduction of the fertilizer and the consequent higher rate of primary production produced no changes in the species composition. The zooplankton exhibited a relatively uniform horizontal distribution within the upper 20 m along the lake, a factor which was attributed to the lake circulation. All eight species were concentrated in the euphotic zone (upper 40 m), and five were most abundant in the upper 10 m. The center of abundance for the remaining three species was between 20 and 30 m depth. The respective depths of maximum abundance for the various species showed little variation between daylight and darkness. Seasonally, there were two periods, June to July and September to October, of maximum abundance for most species. The cause for somewhat lower levels of abundance in August is not known. The average zooplankton biomass showed a similar seasonal pattern with a maximum weight in July which exceeded 8 g/m^2. The average biomass over a 6-month period, May through October, exceeded 5 g/m^2 (more than 10 times greater than for the comparable period prior to fertilization in 1969). In contrast to the high standing stock of zooplankton, the estimated growth rate for underyearling sockeye salmon, the principal predator species in the lake, was only slightly improved over 1969 (1.2 vs. 0.9%/day). In comparison with other lakes producing young salmon the growth rates appear low with respect to the zooplankton stock. It was suggested that the temperature structure of the lake, 14° to 23°C above the thermocline and 4° to 6°C below the thermocline, may reduce availability and prevent the efficient utilization of the zooplankton by the underyearling sockeye salmon.

The following account is the second in a series of papers which report on the effects of sustained nutrient additions to an oligotrophic lake. In the first report, Parsons et al. (1972) showed that an increased primary productivity resulted from nutrient additions made to Great Central Lake, B.C.; the objective of this report is to determine if nutrient additions affected the standing stock and diversity of secondary producers.

The overall purpose of these studies has been to determine if nutrient additions will increase sockeye salmon (*Oncorhynchus nerka*) production; zooplankton, as the principal food of underyearling sockeye salmon, occupy a central position in the food chain of young sockeye during lake residence. Previous studies (Ivlev, 1961; Johnson, 1965; Brocksen et al., 1970) have suggested that prey density and availability may limit the predator biomass. The latter authors compiled data for several sockeye nursery lakes with which they were able to demonstrate a direct relationship between mean zooplankton biomass (prey) and the mean growth rate and biomass of underyearling sockeye salmon (predator). Other studies (Ricker, 1962) have indicated that the ocean survival, i.e. the return to coastal waters of adult sockeye salmon, can be directly correlated in many instances with the size at which the sockeye as year-old migrants leave the nursery lakes to enter the ocean for 2 or more years. While the above studies rely heavily upon circumstantial data, as well as data which were collected for other purposes, they serve as a rational basis for attempting to increase the available zooplankton biomass for the enhancement of salmon growth.

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Manuscript accepted September 1971.
FISHERY BULLETIN: VOL. 70, NO. 1, 1972.

METHODS

Sampling of zooplankton was initiated in mid-1969, using a 0.25 m^2 mouth area cylinder-cone net with 100 micron mesh aperture, hauled vertically from 20 m or 50 m. The samples were collected at infrequent intervals during 1969 and the first 14 weeks in 1970; thereafter vertical net hauls were made at two locations at least once every 4 days until the first week of November. Additional vertical net hauls were made once or twice each month from the lake bottom, 200 m, to the surface. Miller nets (Miller, 1961) with 0.01 m^2 mouth area and 100 micron mesh aperture were used at weekly intervals during the period June through August and thereafter at monthly intervals to determine the areal and vertical distribution of zooplankton. The areal sampling at 18 locations along the lake consisted of 5 min oblique tows from 20 m to the surface while underway at 2 m/sec. The daylight vertical distribution of zooplankton was monitored at 18 depths between the surface and 65 m by making three consecutive tows each with six Miller nets at 2 m/sec at one location. Additional tows were made to sample other depths and also at other periods of the day. Details of the sampling and sampling locations are reported elsewhere (Kennedy et al., 1971[2]).

[2] Kennedy, O. D., K. Stephens, R. J. LeBrasseur, T. R. Parsons, and M. Takahashi. 1971. Primary and secondary productivity data for Great Central Lake, B.C., 1970. Fish. Res. Board Can., Manuscr. Rep. No. 1127, 379 p.

In the analyses of samples special effort was made to maintain up to date species counts and measurements for comparison with other events as they were occurring in the lake. The common zooplankton constituents were identified, measured into size categories, and counted from an aliquot of the total sample; fractions of 1/50 or 1/100 using a Stempel pipette were used depending upon the sample size. The size categories (length in microns) reported in Table 1 were based upon individual measurements for different stages of development of the respective species. It is to be noted that the lengths refer to mean sizes of organisms during the spring and summer growing period. Individual length measurements for the different species and for different times of the year may be found in the MS data report (see footnote 2).

Species counts in vertical net hauls are reported as number per m^2, in oblique and horizontal tows as number per m^3. In this report, unless otherwise indicated, counts all refer to numbers of individuals which fall within the size range occupied by mature (Stage VI) copepods and egg-bearing cladocera; these were usually the two largest size groups for the species reported in Table 1.

RESULTS

SPECIES

Table 2 lists the species of zooplankton which have been found in Great Central Lake. Additional species may be present as minor constitu-

TABLE 1.—Zooplankton size ranges for species sorting in Great Central Lake.

Species	Group						
	I	II	III	IV	V	VI	VII
	Size range μ						
Cyclops bicuspidatus	Egg	125-275	375-550	550- 750	750- 850	850- 950	950-1,100
C. vernalis	Egg	275-375			750- 900	900-1,100	1,100-1,350
Epischura nevadensis	Egg	275-450	450-650	650- 900	900-1,100	1,100-1,350	1,350-2,250
Diaptomus oregonensis	Egg	125-275	450-750	750- 900	900-1,100	1,100-1,350	
D. kenai	Egg			650-1,100	1,100-1,750		1,750-2,500
Bosmina	Egg	125-225	225-325	325- 450	450- 650	650- 800	
Holopedium	Egg	375-450	450-750	750-1,100	1,100-1,750		
Daphnia longiremis	Egg	450-750	450-750	750-1,100	1,100-1,750		
D. pulex	Egg	450-650	450-750	750-1,100	1,100-1,750	1,750-2,500	
Kellicottia	Egg	ca. 80					
Conochilus	Egg	ca. 80					
Keratella	Egg	ca. 80					

TABLE 2.—Zooplankton species found in Great Central Lake, 1970.

Rotifera	Copepoda
**Kellicottia* spp.	**Cyclops bicuspidatus thomasi*
Keratella cochlearis	*C. vernalis*
K. quadrata	**Epischura nevadensis*
**Conochilus unicornis*	**Diaptomus oregonensis*
	D. kenai
Cladocera	Unknown
**Bosmina coregoni*	Actinopoda
**Holopedium gibberum*	Pollen
**Daphnia longiremis*	Egg clusters
D. pulex	Arachnoidea (mites—2 spp.)
Scapholeberis kingi	Chironomid larvae
Polyphemus pediculus	Fish larvae (cottid)
Alona affinis	

* Indicates the most common species.

ents of the zooplankton and it is also possible that new species are being introduced into the lake through a hydroelectric installation which discharges water from an adjacent watershed into the lake. It will be noted from Table 2 that the common zooplankton constituents consisted of two rotifer species, three species of cladocera, and three species of copepods; these species are identified throughout the text by their generic names. There has been no change in the species composition during the course of the experiment, i.e. the common species have remained numerically abundant while the rare species have continued to occupy a minor role.

PATCHINESS

It was anticipated that the zooplankton would exhibit contagious distributions reflecting local circulation patterns, species preferences, and predation. Accordingly, oblique samples from 20 m were collected at weekly intervals at 18 positions along the lake, both near the shore and in midlake. In general, with the exception of the area near the inlet and outlet of the lake where the abundance of organisms was sometimes low, there was greater variability found with respect to the date of sampling than the location of sampling. Weekly means and standard deviations computed for each species showed that *Cyclops* was the only species in which the standard deviation exceeded the weekly count for more than half the surveys (11 out of 17). The apparent variability in *Cyclops* abundance might be due contagion or, more likely, to the fact that sampling was limited to depths (20 m) where *Cyclops* were seldom abundant (see section on vertical distribution). The major source of variability in weekly mean counts appears to be associated with the number of organisms counted, i.e. the number of organisms in a sample and the size of the aliquot counted. The weekly mean number of organisms for each species were grouped together with their respective standard deviations as follows: 1-50, 51-250, 251-500, 501-1,000, 1,001-2,000, 2,001-5,000. The mean coefficient of variation (C.V.), the range, the number of means present in each group, and the number of times a standard deviation exceeded its respective mean are shown in Figure 1 (e.g. for 50 or fewer organisms counted, the standard deviation in 17 out of 23 samples exceeded the mean). The magnitude of C.V., or the relative variation about a mean, is closely associated with the number of organisms counted. The high degree of variability about a mean of 50 or fewer organisms reflects counting errors due to the subsampling technique used in the initial analyses of the samples. However, counts of organisms of 250 or more per m³ tend

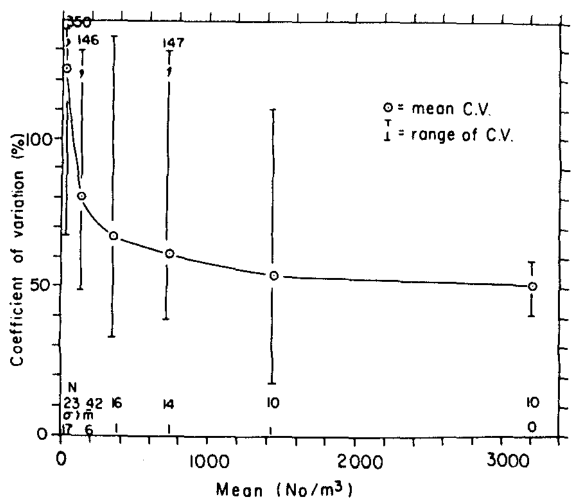


FIGURE 1.—Coefficient of variation computed for mean counts of species sampled in oblique (20 m to surface) tows, where N is the number of weekly means, $\bar{m}$ and σ is the standard deviation.

to be relatively uniform, suggesting that horizontal patchiness or local contagion is not a typical feature of Great Central Lake zooplankton. The observations of lake circulation (McAllister, personal communication) (Parsons et al., in press), and the chlorophyll *a* distribution (Parsons et al., 1972) confirm that the epilimnion is well mixed, thus assuring a nearly uniform dispersal of planktonic organisms along the lake.

The 50-m vertical hauls made at Stations 1 and 2 provide further opportunity for examining the variability with respect to different sampling locations. Here, the comparisons of *mean* counts indicated a high degree of similarity between the two locations with respect to species composition, stage of development, and abundance. However, examination of samples collected on the *same day* indicated a high degree of variability. Forty-nine samples were collected from Stations 1 and 2 during May through December; species counts for Station 1 were plotted against the respective count for Station 2. Values which fell outside of a mean ± half the expected mean (where the expected mean equals half the counts for Stations 1 and 2 combined) are tabulated in Table 3. On half the sampling dates the counts for a particular species tended to be similar at both locations (e.g. in the first column of Table 3, the number of samples with a mean $\pm\ m/2$ is generally greater than half the total number of samples, $N/2$). Greater numbers of four species were found at Station 2 than at Station 1. It is noteworthy that three of the four species, *Kellicottia, Cyclops*, and *Daphnia*, have their greatest abundance below the epilimnion at depths greater than that sampled on the areal surveys. However, there was no apparent correlation in the relative abundance of any of these three species with respect to each other or to other species at either station.

TABLE 3.—Comparison of counts of zooplankton from 50-m vertical hauls at Stations 1 and 2, $N = 49$.

Species	Counts $= (m \pm \frac{m}{2})$	Station 1 $>(m + \frac{m}{2})$	Station 2 $<(m - \frac{m}{2})$
Cyclops	33	5	11
Epischura	31	10	8
Diaptomus	24	10	15
Bosmina	26	17	6
Holopedium	25	15	9
Daphnia	22	6	21
Kellicottia	24	9	16
Conochilus	29	14	6

There were, however, periods when three or more species would be more abundant at one position than at the other. For example, from July 3 to July 21 (six sets of samples) three to six species were most abundant at Station 1 while during the period August 21 to September 8 (six sets of samples) three to seven species were most numerous at Station 2. Similarly, for other periods of 4 to 12 days, one or another species was in greater abundance at one station than the other.

These data have not been examined further to show if variation in species abundance between sampling positions can be correlated with variations in the lake circulation or other environmental factors such as fertilization or predation by underyearling sockeye. However, it is apparent that all seasonal changes in species composition and abundance were reflected throughout the near-surface waters of the lake and that no local area of high or low zooplankton concentration could be clearly defined within the main body of the lake.

VERTICAL DISTRIBUTION

Horizontal tows made within the upper 60 m revealed marked differences in species composition and abundance with depth during the period of thermal stratification. As an example the weekly tows made during July were combined and the average concentration of each species at each of 17 depths sampled during daylight is shown in Figure 2. The inset associated with each species distribution shows the relative distribution (25% quartile intervals) of the respective populations sampled during a 24-hr period in August.

Five of the eight species shown in Figure 2 have their maximum concentration within the upper 10 m, while the maximum concentration of the other three species was below 20 m. Thus the species maxima fall either above or below the thermocline. However, it should be noted that the number of organisms per m^3 decreased from a maximum of greater than $7{,}000/m^3$ be-

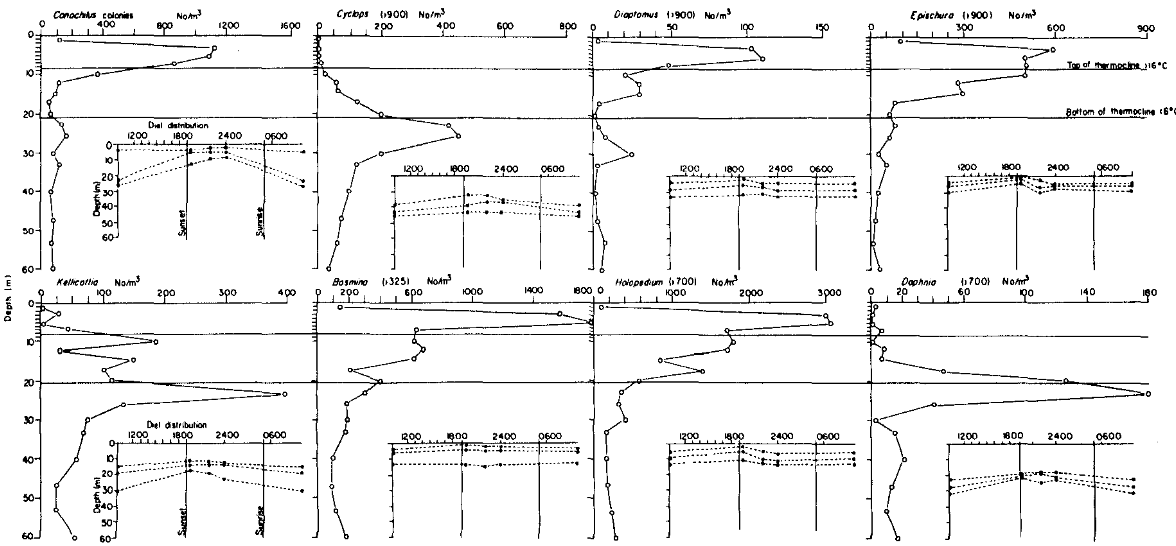


FIGURE 2.—Vertical distribution of common zooplankton species in Great Central Lake mean no./m³ for July 1970. (Horizontal lines indicates the top and bottom of the thermocline, McAllister (personal communication). Inset shows the vertical distribution at 25% quartile intervals over a 24-hr period. Note: the scale indicating the quantity of organisms varies for each species.)

tween 3 m and 5 m to a minimum of approximately 500/m³ at depths below 40 m. The maximum concentration of individual species ranged from 180/m³ for *Daphnia* to greater than 3,000/m³ for *Holopedium*. The tendency for some species to show an increase in abundance in deep samples was likely due to contamination from shallower depths since in the process of setting and hauling with nonclosing nets the deeper nets actually sample for a slightly longer time than the shallower nets. Variations in abundance with respect to time of sampling was noted for all species (Figure 2 inset). The effect was generally most pronounced just after sunset when the maximum concentration per m³ of a species might be increased by 30%. Rotifers, which were presumably the least motile of the zooplankton, exhibited the largest shift in abundance towards the surface with the onset of darkness. Some species, notably *Holopedium* and *Epischura*, returned to their daylight depth of maximum abundance within 2.5 hr after sunset. Other species, such as rotifers, *Bosmina*, and *Daphina* exhibited relatively little movement during darkness. It is apparent from Figure 2 that the shift in species abundance were all within the daylight range occupied by the bulk of the respective populations. Furthermore, more than 75% of the zooplankton populations were at all times within the euphotic zone (i.e. surface to 30-40 m).

SEASONAL ABUNDANCE

In Figure 3 the mean monthly numbers of zooplankton are shown for the 50-m vertical haul samples. Three species, *Cyclops, Bosmina,* and *Kellicottia,* were relatively abundant throughout the year, whereas the other species were present in numbers which exceeded 1,000/m² for periods of 4 to 5 months. *Conochilus* were the only species present during 1970 to appear subsequent to the initiation of nutrient addition. (They were present in 1969 samples.) *Cyclops* ranged from a winter minimum of 2,000/m² to a maximum in September and October of 30,000/m². *Epischura* were never numerically dominant but ranged in numbers from 2,000 to 4,000/m² from May through September. Counts of *Diaptomus* did not exceed 1,000/m² until August, but by September there was a

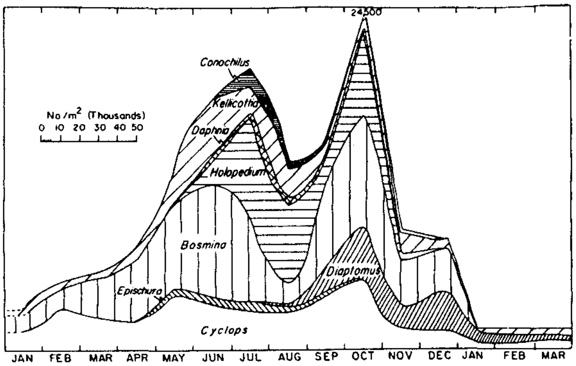


FIGURE 3.–Monthly mean zooplankton abundance (no./m^2 in the upper 50 m data from Stations 1 and 2 combined).

7-fold increase which in turn doubled to ca. 26,000/m^2 by October. The November-December catches of *Diaptomus* exceeded 10,000/m^2, which was approximately two orders of magnitude greater than their standing stock 12 months earlier. Substantial numbers of *Diaptomus*, 3,000 to 4,000/m^2, were carried through into 1971. *Bosmina* were the most abundant species collected throughout the year. Their numbers ranged from ca. 8,000/m^2 in January to ca. 60,000/m^2 in June and again in October. The December concentrations of *Bosmina* were twice that of the preceding January. However, by January of 1971 *Bosmina* had virtually disappeared from the water column, 0 to 50 m. *Holopedium* attained their maximum abundance in July, approximately 3 months after they began appearing in the samples in significant quantities, i.e. greater than 1,000/m^2. Following a secondary maximum in October, *Holopedium* were virtually absent from samples collected from December through March. *Daphnia* were the least numerous of the zooplankton species routinely sampled. They occurred in numbers of 1,000 to 3,000/m^2 from June through September. *Kellicottia* exceeded 10,000/m^2 from May through August and again in October and November. Nearly twice as many *Kellicottia* were present in December as were present at the beginning of 1970. The maximum abundance of *Conochilus* colonies (2,000/m^2) was during July; no colonies were found prior to June and by December the number of colonies had declined to approximately 500/m^2.

In toto there were two to three times more zooplankton present in December of 1970 than there were the preceding January. It is of interest to note that the greater abundance of zooplankton at the end of 1970 was not maintained through the first 3 months of 1971 and further, that *Bosmina* had been apparently supplanted by *Diaptomus* in 1971. On a monthly basis there were fewer than 22,000 organisms/m^2 in January while in October, where the maximum concentration was observed, there were nearly 10 times as many organisms present. Zooplankton counts exceeded 100,000/m^2 in June, July, September, and October. The decrease in zooplankton abundance in August was approximately 15% lower than that in either July or September; this decline was attributable mainly to fewer numbers of *Bosmina.*

Individual species counts (4-day running mean number/m^2) in vertical hauls have been presented in Figure 4 in order to show the seasonal variations in abundance in greater detail than is shown in Figure 3. The general features of both figures are the same but in Figure 4 the rapid increase and decrease in numbers of some species are shown more clearly, e.g. *Holopedium* and *Epischura*. From Figure 4 it is possible to infer some relationship between the addition of nutrients and the appearance of *Conochilus* or the sustained increase in the abundance of *Diaptomus*. It is noteworthy that all species, with the exception of *Epischura* and possibly *Daphnia*, went through a secondary maximum in October which was nearly as great as or greater than their level of abundance earlier in the summer.

SEX RATIO

Adult stages of *Cyclops* and *Epischura* showed marked imbalances from an expected 50:50 ratio of females to males through the year (Table 4). Males of these two species were clearly predominant during the late winter and early spring months. *Cyclops* females were predominant among the adults taken in June through August whereas *Epischura* females were never numerically dominant for more than two or three sampling periods, i.e. July 21 to 31, August 28 to

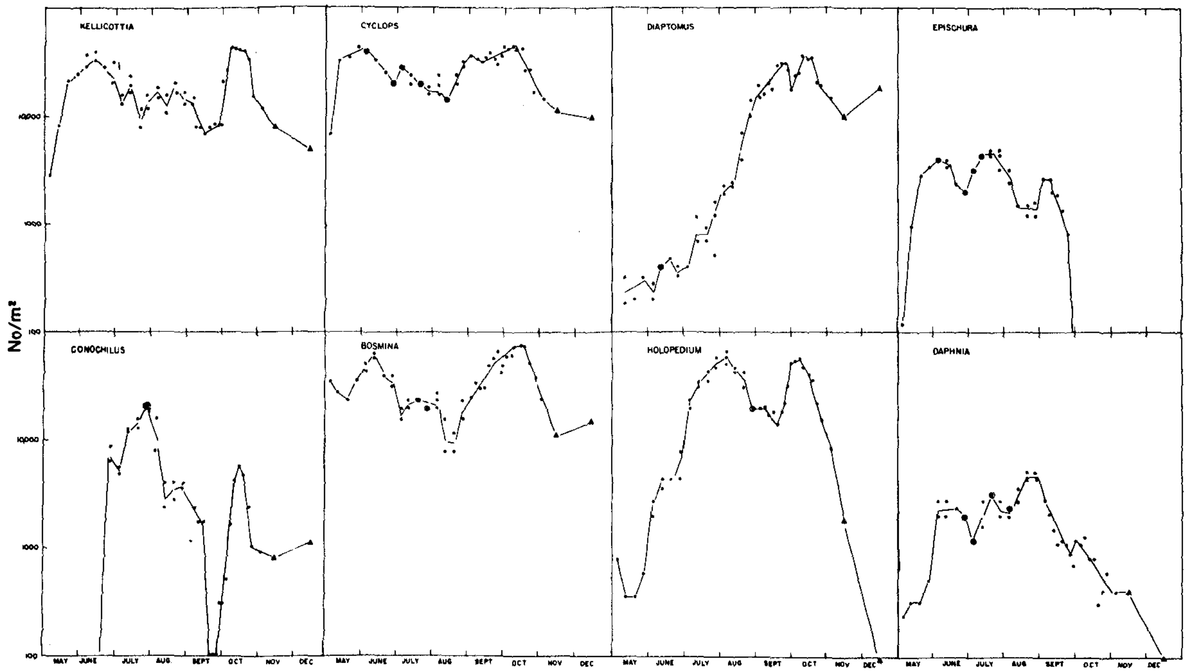


FIGURE 4.—Species counts (no./m^2 in 50-m vertical hauls at Stations 1 and 2. (Points represent a 4-day running mean, solid triangle indicates monthly mean, circle with dot indicates more than one sample with the same count. Note: the numbers of organisms are shown on a logarithmic scale.)

TABLE 4.—Copepod sex ratios.

Month	Species					
	Cyclops		*Diaptomus*		*Epischura*	
	F/M	F_2/F_1	F/M	F_2/F_1	F/M	F_2/F_1
Jan.-April	0.6		1.2		0.5	
May	0.6	2.8	1.5	0.7	0.7	1.3
June	2.6	1.1	1.1	1.9	0.7	1.4
July	1.9	1.0	1.5	1.1	1.0	1.1
Aug.	1.9	1.6	1.3	1.0	1.1	0.8
Sept.	0.8	2.2	1.2	0.9	1.4	0.9
Oct.-Dec.	1.0	2.0	1.3	0.9	1.0	0.5

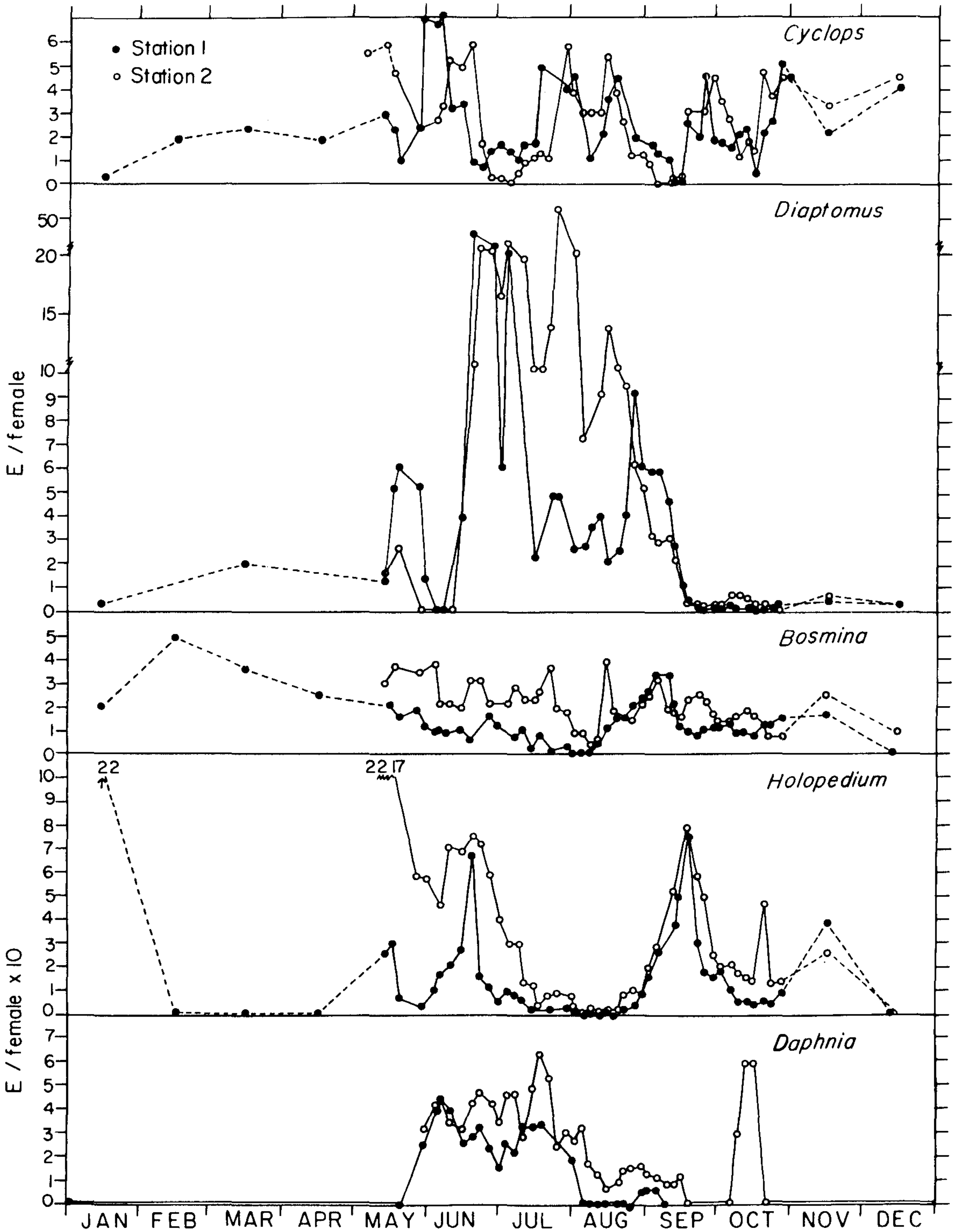
F/M Number of adult females/number adult males.
F_2/F_1 Number of adult females at Station 2/number of adult females at Station 1.

September 14. In contrast there was a tendency for *Diaptomus* females to be slightly more abundant than males throughout the year. The only period for which *Diaptomus* males were consistently more numerous than females was from June 22 to July 10. Included in Table 4 is the ratio of the number of female copepods at Station 2 to the corresponding number at Station 1. *Cyclops* was the only species in which the females were as numerous or more numerous at Station 2 than at Station 1.

EGG PRODUCTION

Counts were made of all readily identifiable eggs; these consisted of eggs in the brood pouch of cladocera and the egg sacks of *Cyclops* and *Diaptomus*. Rotifer species were not examined for eggs, while *Epischura* eggs were positively identified on only one occasion from a horizontal tow made at 1 m depth in August. It is possible that *Epischura* eggs develop close to the surface at depths of less than 1 m since they were not found at other standard depths sampled between 1 m and 65 m. Also other data, not presented here, indicate that the smaller size groups of *Epischura* were found closer to the surface than the adult stages.

The data presented in Figure 5 show the ratio of eggs per female for vertical samples collected at Station 1 and Station 2. It was noted in Table 4 that maximum numbers of copepod females occurred during the summer, June through September; *Cyclops* females were more numerous at Station 2 than Station 1 and *Diaptomus*


Station 1
Station 2
Cyclops
Diaptomus
Bosmina
Holopedium
Daphnia
E / female
E / female x 10
22
22 17
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

females were in about equal numbers at both stations. In Figure 5 the eggs per *Cyclops* were about equally numerous at both stations. There were three and possibly four periods of maximum egg production for *Cyclops* females, i.e. June, mid-July through to the third week in August, and the last week of September through to the first week of November; the latter time interval could possibly be interpreted as consisting of two separate periods of egg production (late September and late October). *Diaptomus* females at Station 1 had two major periods of egg production, mid-June through mid-July and mid-August through the first week of September, with a period of relatively low egg production from mid-July to the end of August. At Station 2 there was no clear cessation of *Diaptomus* egg production from mid-June through to the first week of September. For a major part of this period there were more than 10 eggs per female being produced. There was also a brief period of *Diaptomus* egg production in mid-May.

The production of *Bosmina* eggs ranged between 0 and 0.5 per individual. From May through mid-August more eggs were produced at Station 2 than at Station 1 and thereafter the egg production was nearly equal at both stations. The summer minimum which occurred in the first 2 weeks of August was followed by a rise in the number of eggs in the first week of September continuing until the end of the third week of September. The summer maximum of adult *Bosmina* shown in Figure 4 occurred approximately 1 week after that of the eggs while the maximum standing stock of *Bosmina* (which occurred in mid-October) was preceded by the production of eggs 3 to 5 weeks earlier. *Holopedium* exhibited two clearly defined peaks in the production of eggs, from the first to the third week of June and again from the first to the third week of September. The corresponding maximum in the standing stock of *Holopedium* shown in Figure 4 occurred

FIGURE 5.—Ratio of the number of eggs to the number of adult females. The data from 50-m vertical samples at Stations 1 and 2 have been averaged to give a 4-day running mean ratio. Note: scale changes for different species.

from the second week of July through to August 25 and from September 27 to about October 20; the summer minimum occurred between the two peaks. The production of *Daphnia* eggs took place from June to mid-September with a second brief rise in egg production during mid-October at Station 2. The numbers of eggs produced per female at Station 2 by all species of cladocera was generally greater or equal to that at Station 1. It should be noted that the latter was found for both the prefertilization period in May as well as during the period of nutrient additions.

ZOOPLANKTON BIOMASS

The wet weights for 1970 50-m vertical hauls at Stations 1 and 2 were combined and expressed as a monthly mean wet weight (g/m^2) together with the range about the mean weight (Figure 6). Included in Figure 6 (below) are individual weights for the 1969 sampling. The maximum wet weight in 1969 never exceeded 1 g/m^2 whereas in 1970 the weights ranged as high as 15 g/m^2. The average wet weight of zooplankton during the period May through October was approximately 0.5 g during 1969; for the same period in 1970 the average weight was 10 times larger, i.e. 5.3 g. The sample weights increased at a rate of 3% per day May through July to a maximum average wet weight of 8.6 g/m^2; there-

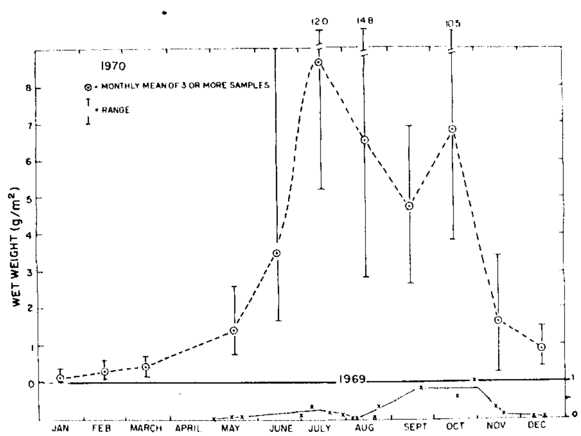


FIGURE 6.—Zooplankton wet weight (g/m^2) for 50-m vertical hauls. In the lower part of the figure, the points marked "x" indicate individual weights (g/m^2) for 1969 samples.

after the weights declined at an average rate of 1.5% per day to the December biomass of 0.9 g/m². The actual rate at which the mean weight of zooplankton declined in any one month following July was greater than the average computed above due to the increase in biomass in October. Inspection of Figures 3 and 4 indicates that the decline in biomass seen in August was a result of fewer numbers of *Epischura, Bosmina,* and *Holopedium. Epischura* never reached its earlier level of abundance after August and was virtually absent from the samples by October whereas most other species, *Daphnia* excepted, showed an increase in abundance in October which gave rise to the October increase in biomass.

Dry weights of Great Central Lake zooplankton (determined by the freeze-dry method) ranged from 14% to 26% of the wet weight with a mean of 19%. The variation in the percentage dry weight was directly attributable to the species composition of a sample. For example, the dry weight of *Holopedium* was 14% of their wet weight, whereas the dry weight of *Cyclops* was approximately 26% of the wet weight. The average dry weights of the summer zooplankton (May through October) integrated over a 25-m column, i.e. the depth range in which most zooplankton were concentrated, for 1969 and 1970 was 4 mg and 40 mg/m³ respectively (from Figures 2 and 6).

TABLE 5.—Length-weight measurements of adult crustaceans.

Species	Mean length (*Microns*)	Wet weight (*Micrograms*)
Cyclops	960	6
Diaptomus	1,100	11
Epischura	1,500	66
Bosmina	300	4
Holopedium	900	17
Daphnia	900	10

Length-wet weight determinations were made for different sizes and stages of the common crustacean species and the data are summarized in Table 5. The data in Table 6 were obtained by multiplying the maximum concentration (no./m³) of a species within particular depth intervals (Figure 2) by their respective weight from Table 5, thereby providing a measure of biomass with depth. Included in Table 6 are the mean July temperatures within the respective depth intervals. Nearly 60% of the total biomass occurs in the upper 10 m where the mean temperature was about 18°C. In the thermocline, from 10 to 20 m, with a temperature range from 12° to 6°C (mean temperature, 9°C) the biomass was about 50 mg/m³ or approximately 30% of the total. From 20 to 30 m depth the biomass was about 8% of the total. The remaining 3 to 4% of the total biomass occurred below 30 m (30 to 60 m). While these data were derived from July sampling it should be noted that the general distribution of the biomass with depth was similar throughout the period of thermal stratification, i.e. June to October.

DISCUSSION

The zooplankton standing stock in 1970 shows a phenomenal increase over 1969. This can be largely attributed to the affect of the nutrient additions upon the rate of primary production. The results of Parsons et al. (1972) demonstrate a marked increase in the rate of primary production within the upper 5 m; at the same time there was little or no change in the standing stock of primary producers. While experiments and observations of a direct relationship between particular species of primary and secondary producers have not been attempted, the obvious inference is that the zooplankton through increas-

TABLE 6.—Relative biomass of July crustacean zooplankton in various depth intervals (from Figure 2).

Depth range (m)	mT °C	Mean maximum biomass (mg/m³)						
		Cyclops	*Diaptomus*	*Epischura*	*Bosmina*	*Holopedium*	*Daphnia*	Total
0-10	18	--	1.3	39.6	7.2	51.0	.1	99.2
10-20	9	1.2	.3	19.8	2.8	28.9	.5	53.5
20-30	6	3.1	.3	4.9	1.2	3.4	1.8	14.7
>30	<5	.6	--	2.3	.7	1.7	.2	5.6

ing stock size were able to utilize the higher rates of primary production.

It is also apparent that the higher biomass in 1970 cannot be entirely attributed to fertilization since the biomass in May (prefertilization) was also higher than any of the 1969 values. However, the nearly continuous production of eggs by most species and the maintenance of an increased standing stock over a 6-month period are indicative of a direct relation between zooplankton and nutrients. It is also noteworthy that there was no change in species diversity.

The techniques employed for wet weight determinations in this study have produced weights which are apparently lighter than would be obtained by other investigators. Wet to dry ratios in the literature suggest that the dry weight is 5% to 10% of the wet weight. Schindler and Noven (1971) employed a ratio of 6%, although their reason for using this particular value is not given; the present results indicate that the dry weight is 19% of the wet weight. Consequently, the present weights could be increased approximately three times for comparison with other studies. Thus in the lakes which range from oligotrophic to eutrophic, listed by the above authors, Great Central Lake has, in terms of its mean summer zooplankton biomass, changed from oligotrophic to oligotrophic-mesotrophic, i.e. 12 mg in 1969 to 120 mg dry weight/m^3 in 1970. In lakes producing sockeye salmon the mean abundance of zooplankton ranges from values which are less than 5 mg dry weight/m^3 to greater than 1 g dry weight/m^3 (Johnson, 1965). The mean concentrations in Great Central Lake have increased from the very low end of the range to values which are commonly reported for some of the larger sockeye producing lakes, e.g., Babine Lake.

Johnson (1965) concluded that there was a general relationship between the rate of growth of underyearling sockeye and zooplankton abundance. However, he also suggested that with increasing fish density food abundance was supplanted by a space effect as a limiting factor. In Great Central Lake the underyearling sockeye in October of 1970 were ca. 30% heavier than fish caught in October of 1969 (Parsons et al., in press; Barraclough and Robinson, 1972). In addition to the increase in weight these authors report (on the basis of the number of adult salmon spawning) that the number of sockeye fry in the lake were from two to five times more numerous than in the previous year. Assuming an initial weight of 120 mg for individual fry of each year the respective rate of growth over their first 200 days of lake residence was 0.9% and 1.2% per day for 1969 and 1970 respectively. The increased growth rate of sockeye in 1970 is less than might be anticipated from the 10-fold increase in zooplankton abundance. Johnson's data (1965) indicated that a population density of 1 fish per m^2 might be the point at which space becomes a factor limiting growth. The maximum estimate of 1×10^7 sockeye in Great Central Lake during 1970 is approximately 1 fish in every 5 m^2. Consequently it appears unlikely that the density of the fish population in Great Central Lake limited their growth.

Among other factors which limit growth of sockeye, Foerster (1968, Figure 45) indicates that temperature has a major affect upon growth and the efficiency with which food is utilized. The optimum temperature for food conversion for sockeye lies between 10° and 15°C. At higher or lower temperatures the efficiency of food conversion decreases, especially at temperatures in excess of 20°C or less than 6°C. The laboratory studies of Brett et al. (1969) with fingerling sockeye support the findings reported above. In their experiments 15°C was found to be the optimum temperature for growth at high rations; however, maximum efficiencies with which a ration was utilized occurred at lower temperatures, e.g. the maximum food conversion efficiency of 40% with a 0.2% increase in fish weight per day occurred at a temperature range of 8° to 10°C and a ration of 1.5% of the fish weight/day. Temperatures between 5° and 17°C were found to provide the laboratory fish the optimum conditions for conversion efficiencies and growth. In Great Central Lake, during their first 200 days of lake residence, the underyearling sockeye concentrate at depths of 50 m or greater during daylight; with the approach of sunset the fish move to shallower depths and by nightfall the major portion of the population is at depths between 10 and 20 m while some fraction of the population occur in the upper 10 m. This pattern of vertical migrations appears to be repeated daily (Barraclough and Robinson, 1972). Narver (1970) has reported similar vertical movements for sockeye populations in Babine Lake. For the greater part of the day the salmon in Great Central Lake are at temperatures of 4° to 5°C, a somewhat shorter period (ca. 6 hr) is spent at temperatures of 6° to 12°C (10 to 20 m depth) while a relatively brief period (ca. 1 hr) may be spent at temperatures ranging from 14° to 23°C (0-10 m depth). Details of the time actually spent at different depths by the sockeye are reported by Barraclough and Robinson (1972). It is apparent that the fish are utilizing the maximum concentrations of prey which occur at above optimum temperatures in the upper 10 m for very short intervals. Consequently in assessing the relationship between the increased abundance of prey brought about through fertilization and the sockeye it should be noted that possibly 60% of the total biomass, i.e. the portion in the upper 10 m, may be only partially available to the fish (Table 6). Furthermore, some prey species because of their size (rotifers) or structure (*Holopedium*) may not be a particularly useful food source for the salmon. *Holopedium,* for example, was among the largest and most numerous species of crustaceans in the lake; however, a large fraction of their biomass is comprised of a gelatinous material of dubious food value. The difference in the wet to dry weight ratio between *Holopedium* and other zooplankton (14% to ca. 26% respectively) attests to the water composition of *Holopedium.* The quality of prey together with the observations of Foerster (1968) and Brett et al. (1969) emphasize the need for caution in interpreting predator-prey relations. In the present instance, the benefits of the fertilization appear to have been only partially transferred to the sockeye salmon. Since the thermal structure of the lake is a factor beyond immediate control, it would be interesting to consider possible benefits from the addition or deletion of some prey species and to attempt to shift the level of primary and secondary production to depths and temperatures favoring sockeye salmon growth.

LITERATURE CITED

BARRACLOUGH, W. E., AND D. G. ROBINSON.
1972. The fertilization of Great Central Lake. III. Effect on sockeye salmon. Fish. Bull., U.S. 70: 37-48.

BRETT, J. R., J. E. SHELBOURN, AND C. T. SHOOP.
1969. Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka,* in relation to temperature and ration size. J. Fish. Res. Board Can., 26: 2363-2394.

BROCKSEN, R. W., G. E. DAVIS, AND C. E. WARREN.
1970. Analysis of trophic processes on the basis of density-dependent functions. *In* J. A. Steele (editor), Marine food chains, p. 468-498. Oliver and Boyd, Edinburgh.

FOERSTER, R. E.
1968. The sockeye salmon, *Oncorhynchus nerka.* Fish. Res. Board Can. Bull. 162, 422 p.

IVLEV, V. S.
1961. Experimental ecology of feeding of fishes (Transl. by D. Scott). Yale Univ. Press, New Haven, 302 p.

JOHNSON, W. E.
1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka.* Mitt. Int. Ver. Limnol. 13: 66-87.

MILLER, D.
1961. A modification of the small Hardy Plankton Indicator for simultaneous high speed plankton hauls. Bull. Mar. Ecol. 5: 165-172.

NARVER, D.
1970. Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. J. Fish. Res. Board Can. 27: 281-316.

PARSONS, T. R., C. D. MCALLISTER, R. J.LEBRASSEUR, AND W. E. BARRACLOUGH.
In press. The use of nutrients in the enrichment of sockeye salmon nursery lakes—a preliminary report. FAO Technical Conference on Marine Pollution, Rome, 9-18 December 1970.

PARSONS, T. R., K. STEPHENS, AND M. TAKAHASHI.
1972. The fertilization of Great Central Lake. I. Effect on primary production. Fish. Bull., U.S. 70: 13-23.

RICKER, W. E.
1962. Comparison of ocean growth and mortality of sockeye salmon during their last two years. J. Fish. Res. Board Can. 19: 531-560.

SCHINDLER, D. W., AND B. NOVEN.
1971. Vertical distribution and seasonal abundance of zooplankton in two shallow lakes of the experimental lakes area, northwestern Ontario. J. Fish. Res. Board Can. 28: 245-256.