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A Limnological Survey of Lake Mainit, Philippines[1]

Abstract

Morphology, bathymetry and climate are described for Lake Mainit, one of the principal lakes of Southeast Asia. Thermal and water chemistry data show that the lake is not meromictic, despite its great depth, and that the water is dilute. Primary production is high but standing crop and diversity of phytoplankton and zooplankton range from moderate to low. The species composition of plankton and other biota is discussed.

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1. Introduction

Lake Mainit on Mindanao ranks with Laguna de Bay, Lake Taal, and Lake Lanao as a major lake of the Philippines. Due to its inaccessibility and the scientific diversion provided by nearby Lake Lanao, Lake Mainit has nevertheless remained virtually unknown. The first biological work on Lake Mainit is probably that of MANACOP (1937), who concentrated his attention on the fishes. TRESSLER subsequently visited Lake Mainit to collect samples for the Wallacea Expedition (WOLTERECK 1941). The lake has apparently remained unstudied since that time.

The present survey is based on trips to Lake Mainit during August and November 1971. I was greatly aided on both occasions by Mr. RODRIGO CALVA, who did most of the echosounding. I wish to thank Dr. D. G. FREY, who accompanied me on the first excursion, and Mr. E. C. PIDDUCK, who provided transportation. Certain of the analyses were carried out with the help of laboratory facilities provided by Mindanao State University through its president, Dr. MAUYAG TAMANAO. I am indebted to the Manila office of the Ford Foundation for its logistic support of my overall research efforts in the Philippines. I am especially grateful to Dr. B. BERZINS for his

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prompt and thorough taxonomic work on the rotifers, to Dr. S. Holmgren, whose help with the taxonomy of the Lake Lanao phytoplankton has served as a basis for the phytoplankton identifications made in this paper, and to Dr. D. G. Frey for his identification of the *Chydorus* species.

2. Morphology and Bathymetry

Lake Mainit is situated on a small peninsula extending north from the eastern side of Mindanao. The lake lies only 27 m above sea level and is separated on the west from the Mindanao Sea by a narrow strip of land (Fig. 1). The relief of this strip is uniformly sharp and includes numerous peaks forming a ridge between 500 and 600 m above sea level. The ridge continues past the north end of the lake into the watershed of the Mayag River, which is flanked on the west by several peaks exceeding 1000 m. North of the lake where the relief is not so sharp, there is a small lake of uncertain origin, Lake Mahokdum. Several hot springs are reputedly located

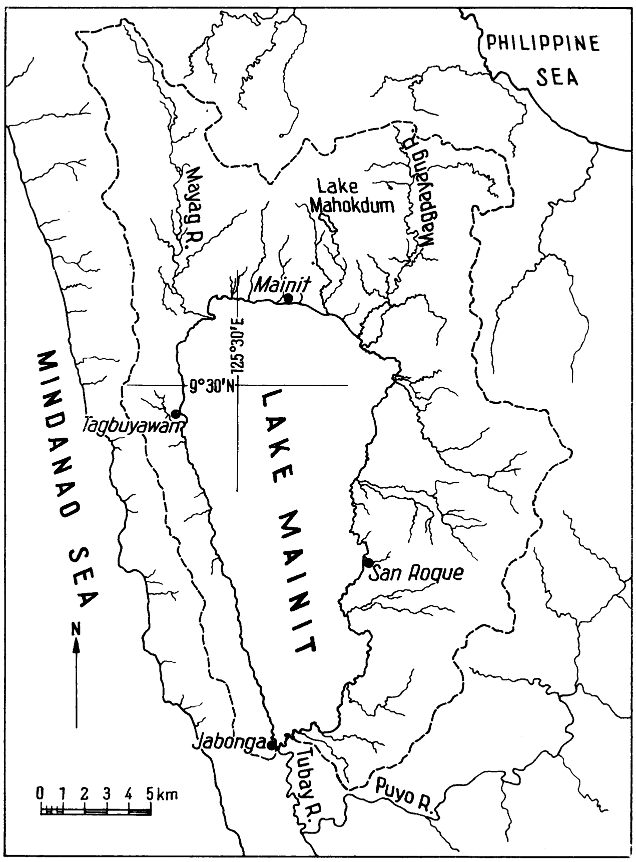

Fig. 1. Lake Mainit and its watershed. The watershed boundary (dashed line) on the west side of the lake is about 500 m above the lake surface. Relief is steep but much more irregular in the northwest portion of the watershed and is gentle in the northeast portion. The east side of the lake is flanked by peaks as high as 1000 m. A wide corridor of very low elevation parallels the course of the Tubay River. Source maps were obtained from the Philippine Board of Technical Surveys and Maps.

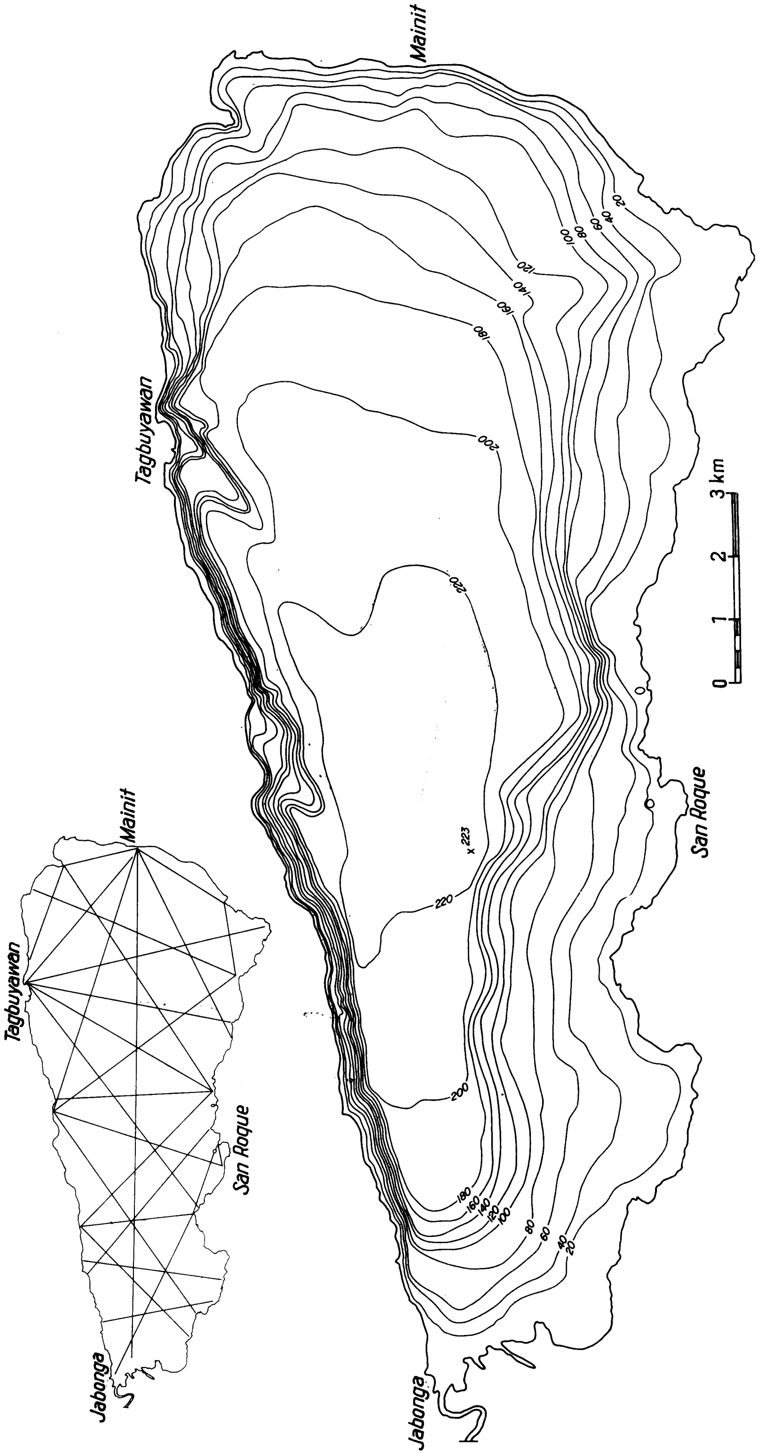

Fig. 2. Bathymetric map of Lake Mainit. The lake surface is 27 m above sea level. Contours at 20-m intervals show the steep relief on the west shore and flat central plateau. The insert indicates the orientation of echosounding traces that were used in the construction of the bathymetric map.

on the north and east sides of the watershed. The springs were not visited in the course of this survey, but they may account for the name of the lake. "Mainit" is the common Visayan word meaning "hot," but residents of the village of Mainit seem uncertain about the derivation of the name. An extensive mountainous region with peaks over 1000 m bounds Lake Mainit on the east, but only a small portion of this territory is included in the watershed. To the south, Lake Mainit empties via the Tubay River, which flows parallel to the western mountain ridge some 25 km before emptying into the Mindanao Sea.

The origin and age of Lake Mainit are matters of speculation, but topographic maps provide a few significant facts. The lake basin is adjoined on the south by a relatively broad (3 km) corridor of very low ground (< 40 m) bounded on the west by the Tubay River. The Puyo and Asig Rivers, which together drain a large region to the southwest of Lake Mainit, flow into the Tubay through this plain. It would thus seem that the lake once extended southward at least 15 km from its present boundary and included a much larger watershed. The formation of deltas by these rivers evidently led to the filling the south end of the lake basin. If this interpretation is correct, the Tubay now flows over a portion of the former lakebed and the plain adjoining the river consists of rather deep alluvial deposits.

The watershed of Lake Mainit is currently very small (313.1 km^2) relative to the lake, which implies very low sedimentation rates for the lake basin. Each of the small rivers draining into the lake, notably the Mayag and Magpayang, has nevertheless built up a substantial delta area at its confluence with the lake. The size of the deltas and the very low gradient in the river valleys suggest that the lake is quite old. The watershed has recently been completely deforested, but agriculture is still limited to small areas on the alluvial plains. The population density of the watershed is low and probably does not significantly affect the nutrient budget of the lake.

The lake basin appears to be of tectonic rather than volcanic origin. The very steep gradient of the west shore (Fig. 2) is probably a fault scarp, which would account for the contrast in slope between shores. Bare sedimentary rock on the east slope seems to rule out any important role of lava dams.

The bathymetric data previously available for Lake Mainit consist of a single sounding of 165 m reported by Woltereck (1941). The bathymetric map (Fig. 2) shows that the lake in fact has greater maximum and mean depths than any other Philippine lake. Morphometric statistics derived from Fig. 2 include: area, 140.6 km^2; maximum depth, 223 m; volume, 18.0 km^3; mean depth, 128 m. The minimum possible replacement time for the lake, assuming no loss of moisture to the air, is 12.5 years. A realistic correction for evaporative losses on the basis of hydrologic data for Lake Lanao (Frey 1969) suggests an actual replacement time of about 15 years.

Lake Mainit occupies an even deeper cryptodepression than Lake Taal on Luzon. Since the lake extends 198 m below sea level and is close to the Mindanao Sea, incursions of salt water might easily have occurred during the history of the lake. An examination of the sediments would be interesting from this standpoint, but no cores have been taken to date.

3. Climate

Climatic data for the Lake Mainit region are characteristic of the southeastern coasts of the Philippines. No weather records are available from near the lake, but regular records are kept at Surigao, 44 km north of Mainit. Although there is considerable variation between years, the 30-year record of rainfall and temperature for Surigao (Fig. 3) clearly illustrates the trend toward heavy rainfall and low tempera-

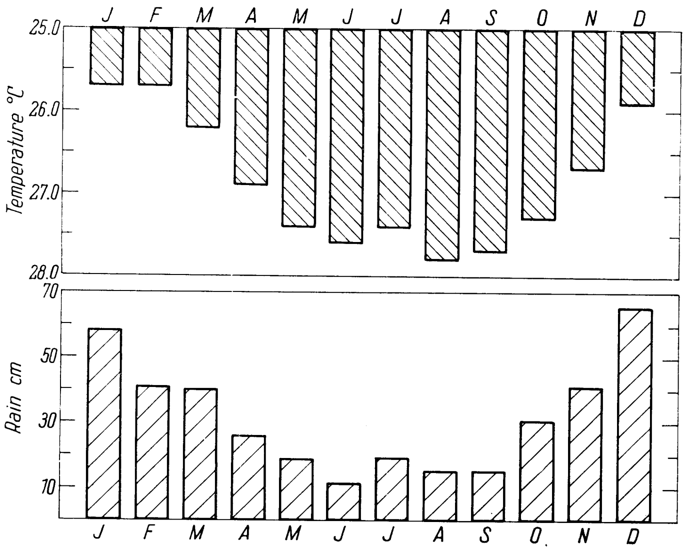

Fig. 3. A 30-year mean of temperature and rainfall for Surigao, 47 km north of Lake Mainit and 22 m above sea level. Data are as reported by the U. S. Weather Bureau (1970).

tures from November through March and a combination of dryer weather and higher mean temperatures during other months, especially June through September. Mean annual rainfall is 318 cm/year and mean air temperature (average of daily maximum and minimum temperatures) is 26.8 °C (U. S. Weather Bureau 1970).

Much of the variation in mean temperature is probably due to seasonal changes in cloud cover rather than changes in daylength or mean angle of incidence of sunlight. Prevailing winds are southeasterly in this part of the Philippines during November and December and pick up moisture from the South Pacific. During January and February, a monsoon originating in North Asia brings moisture and cool air from the Japan Sea. These overlapping periods of high moisture undoubtedly reduce the total daily insolation and hence the maximum temperatures during the winter months of the northern hemisphere.

Typhoons generally pass north of Mindanao, but the peripheral weather disturbances associated with many typhoons must cause important fluctuations in wind strength, insolation, and rainfall during the warm season, as they do on Lake Lanao (Lewis, 1973).

4. Temperature and Water Chemistry

The temperature profile for 1 August (Fig. 4) was made with a Kahl bathythermograph and extended only to 160 m. The profile for 7 November is based on continuous readings to 50 m with a thermister and subsequent thermister readings for Van Dorn samples at 60, 90, 150, and 200 m. The thermister was calibrated against a thermometer reading to 0.02 °C. The deep-water portions of the August and November thermal profiles are essentially identical, which would imply that the bottom 160 m of the water column was undisturbed between the two sampling dates.

Below 60 m, the water column had a uniform thermal gradient of 1.4×10^{-3} °C/m. The minimum temperature measured was 26.02 °C at 200 m, just above the bottom at the sampling station. This nearly isothermal bottom portion of the water column is primarily influenced by the extent of seasonal cooling, whose effects were not directly observed on Lake Mainit.

The contrasting thermal structure of the upper water column on the two sampling dates reflects changes in weather (Fig. 4). As would be expected during the hottest month of the year, the August temperature profile shows a marked heat accumulation in the upper 20 m. The complex distribution of heat in this profile is evidence of a pronounced non-seasonal variation in the depth of mixing similar to that documented for Lake Lanao (LEWIS 1973). The depth of mixing was near 12 m at the time the profile was made, as indicated by the selective heat accumulation above this depth. Oxygen depletion below 12 m (Fig. 5) indicates that the 12-m partition in the epilimnion was at least several days old at the time of sampling. The November profile was taken during cooler weather, which accounts for the substantial loss of heat from the upper water column and disappearance of the thermocline at 12 m.

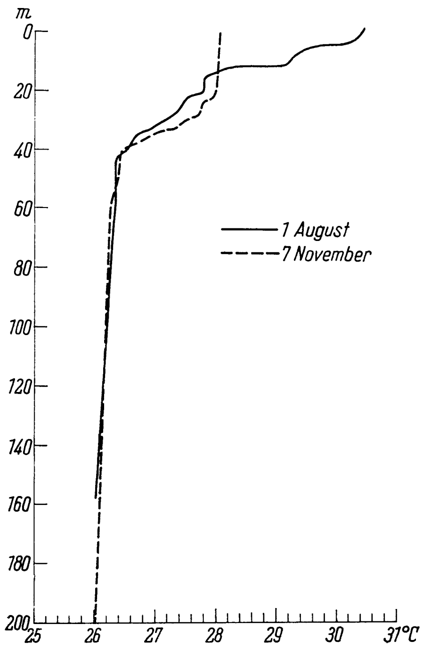

Fig. 4. Temperature profiles for 1 August and 7 November on Lake Mainit. The slight differences in the deep water temperatures between dates are probably due to measurement errors.

Oxygen was present in measureable amounts to at least 75 m during August (Fig. 5), but no samples were taken in the deepest water on this occasion. Oxygen below 55 m was almost certainly residual from deep mixing that accompanied the temperature minimum in January or February. By November there was no trace of oxygen at 50 m. Samples from 75, 100, 125, 140, 175, and 200 m in November contained no oxygen and smelled of hydrogen sulfide.

Methyl orange alkalinity at 10 depths between the surface and 70 m averaged 56.1 ppm in August and did not vary with depth outside the limits of the standard titrimetric determination ($\pm$ 1 ppm). In November, titration of sealed samples for the entire water column was delayed for three days, but alkalinities for the 0–70 m stratum were not significantly different from the August data. Samples from 100, 125, 140, and 200 m averaged 57.6 ppm, indicating a small but probably significant biogenic enrichment of CO_2 in the deep water.

Depth profiles for potassium, calcium, and sodium during November are shown in Fig. 6. Concentrations were determined by atomic absorption on sealed, acidified (1% 1 N HCl) samples that had been stored three months. There is a slight but significant increase in the concentration of each cation in deep water. Deep-water enrichment on a volume basis amounted to about 10% of the epilimnetic concentrations of sodium and potassium, and about half as much for calcium. Calcium was slightly more concentrated at 50 m than at greater depths. Since 50 m was the approximate lower boundary of dissolved oxygen, the 50-m peak of calcium may have arisen from some rapid anaerobic regeneration mechanism for calcium, perhaps including the solution of a small amount of precipitated calcium carbonate. Rapid regeneration may also account for the less pronounced enrichment of calcium in the deepest water.

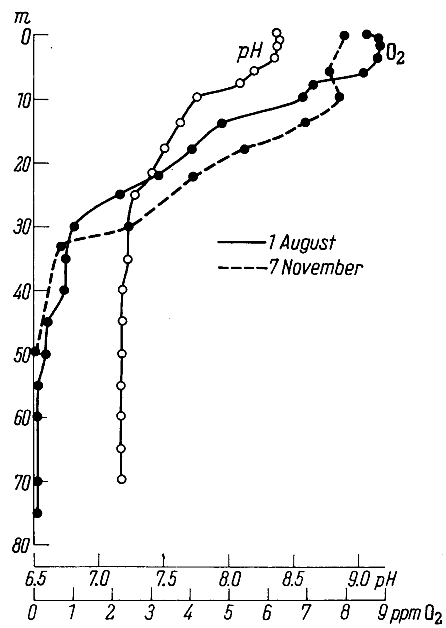

Fig. 5. Oxygen and pH profiles for Lake Mainit. The uppermost segment of the August oxygen profile represents supersaturations as high as 120% from a bloom of bluegreen algae. Significant amounts of oxygen extended to 70 m in August but were depleted at 50 m and below by November.

The proportions of cations are somewhat unusual due to the predominance of sodium. In Lake Lanao, which has nearly identical ionic concentrations, there is considerable evidence that sodium is transferred to the lake during typhoons (Lewis 1973). The same is probably true of Lake Mainit, in which case the ionic composition reflects the selective enrichment of monovalent ions by addition of marine salts to a highly dilute runoff.

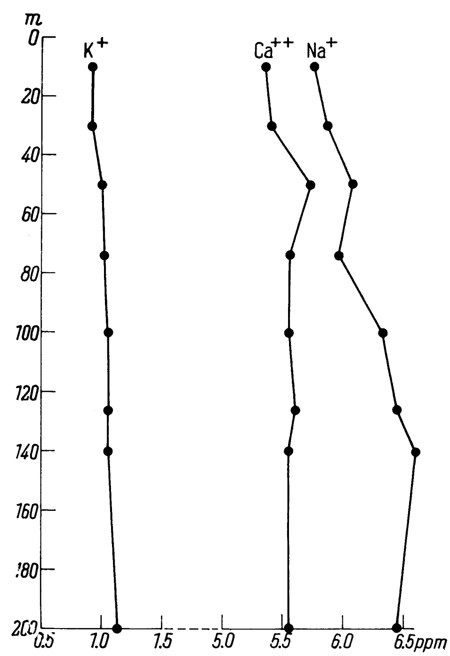

Fig. 6. Concentrations of cations in Lake Mainit during November. Proportionate increases in sodium and potassium with depth are comparable (10%). The calcium peak at 50 m suggests rapid regeneration of ionic calcium under anaerobic conditions, possibly by solution of the precipitated carbonate.

Cation analysis included copper and zinc on all samples. No detectable concentration of either ion could be found by atomic absorption, indicating that both ions were present at concentrations considerably below 5 ppb. Livingstone's (1963) review suggests that both ions are present at approximately 10 ppb in unpolluted freshwaters. The very low values for Lake Mainit must be near the regional baseline concentrations, because the lake is remote from any industrial sources of heavy metals.

The temperature and water chemistry data collectively provide a means of judging the amount of deep mixing in the lake during recent years. Lake Mainit is clearly not meromictic, although biogenic meromixis would be expected in the absence of substantial and frequent deep-water turbulence. The profiles of dissolved substances in fact suggest annual dilution of the deep water during the seasonal temperature minimum. The lake would of course resist complete circulation due to its great depth, but loss of thermal structure during the cool season probably permits a vertical turbulent transfer of dissolved substances that is sufficient to offset most of the vertical differential that develops during the stratification period. A large oxygen debt is undoubtedly carried over from one year to the next due to the rapid rate of oxidation at high temperatures and the great mean depth of the lake.

5. Transparency, Primary Production, Standing Crop

Net primary production of the plankton community was estimated on two dates by the *in situ* carbon-14 uptake method. Duplicate 125-cc "light" bottles and a single "dark" bottle were filled with water from various depths, inoculated with $Na_2{}^{14}CO_3$, and suspended for 3 hours at midday at the depth from which they had been taken. Aliquots of 50 cc from each bottle were subsequently filtered onto Millipore HA filters at less than 0.5 atm vacuum. Filters were counted by liquid scintillation using the cocktail described by Schindler and Holmgren (1971). The data on spectral composition of light at various depths were obtained with a Whitney Photometer and Jena filters at the time of the August incubation.

The transparency and productivity profiles are given in Fig. 7. On 2 August, net (dark-corrected) production amounted to 1120 mgC/m^2 for the incubation period, or a daily net production of about 2 gC/m^2. The immediate explanation for this very high fixation rate is a high efficiency in the use of sunlight. On the basis of extensive measurements of solar energy under comparable light conditions at Lake Lanao (Lewis 1973), the solar input for the incubation period can be estimated as 210 cal/cm^2, or about 105 cal/cm^2 of the wavelengths useful for photosynthesis. Assuming an approximate biomass-energy equivalence of 10 cal/mgC, the efficiency of energy fixation on 2 August was slightly greater than 1%. On 8 November, production was 560 mgC/m^2 for the incubation period or about 1 gC/m^2 day. Although there was less sunlight available for the November incubation (estimated 180 gcal/cm^2), a lower efficiency of sunlight use (0.6%) partially accounts for the somewhat lower fixation rate.

Fixation rates comparable to those observed in Lake Mainit are characteristic of only the most productive temperate lakes. Eutrophic temperate lakes are generally shallow and frequently receive significant artificial nutrient supplies. Lake Mainit is eutrophic from the productivity standpoint, but has the morphometry of an oligotrophic lake and optical properties that are typical of much less productive temperate lakes. Despite the high rate of photosynthesis on 2 August, 1% of the incident sunlight penetrated to a depth of 13 m. The lake was even more transparent on 8 November (Secchi disc, 4.2 m). Such high transparency in a productive lake can be explained either by a high rate of production per unit standing crop or by an extensive vertical distribution of photosynthesis. Although both factors seem to apply to Lake Mainit, vertical distribution of carbon fixation provides the most striking contrast with productive temperate lakes.

The vertical distribution of photosynthesis can be assessed by the use of curve-shape statistics. The simplest of these is RODHE's (1958) V/O (Volumen/Oberfläche) ratio, which is lowest for lakes in which photosynthesis is most markedly dispersed through the water column. The ratios for Mainit on 2 August and 8 November are 0.17 and 0.15. Such low values indicate extensive vertical distribution of carbon fixation that is characteristic of temperate oligotrophic lakes. Among the V/O ratios that RODHE reports, the ratios for Lake Mainit rank with ratios of the unproductive lakes of Lappland rather than the higher values that typify more productive temperate lakes such as Lake Erken.

Phytoplankton standing crop as determined by census data and cell volumes (Table 1) averaged 2021mg/m^3 in the 0–15m stratum on 2 August and 982mg/m^3 on 8 November. These figures are somewhat higher than would be expected from the transparency data (Fig. 7). TALLING (1965) observed a similar anomaly in Lake Victoria and speculated that it may be explained by the low amounts of non-living seston. Microscopic examination of samples from Lake Mainit would seem to bear this out.

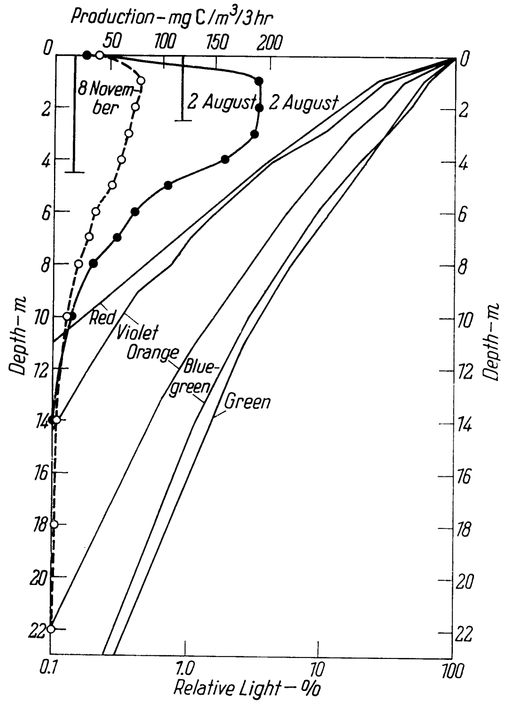

Fig. 7. Production profiles and transparency for Lake Mainit. Both production profiles are based on C-14 uptake during 3-hour in situ incubations at midday. Spectral separation of light for August was accomplished with Jena filters having transmission maxima of 420, 480, 530, 600 and 660 nm.

Areal standing crop for the euphotic zone was 28 g/m^2 (0–14 m) on 2 August and 18 g/m^2 on 8 November (0–18 m). The corresponding biomass turnover times, assuming 10% C content, are 1.4 and 1.8 days. Higher turnover rates have been reported for temperate lakes with low standing crops (FINDENEGG 1965), but the turnover reported here probably exceeds that of most first-class temperate lakes with a comparable standing crop (vide RODHE *et al.* 1958, NAUWERCK 1963).

6. Phytoplankton

The diatoms of Lake Mainit were identified by HUSTEDT subsequent to the Wallacea expedition but were not included in his taxonomic treatment of the Wallacea samples (HUSTEDT 1942). Fortunately, WOLTERECK (1941) gives a résumé of HUSTEDT's findings, including a list of 25 genera. All of these genera except *Synedra* and *Melosira* are probably littoral. WOLTERECK lists two unspecified species of *Melosira* and two species of *Synedra*.

Table 1 shows that in 1971 species of *Melosira* and *Synedra* were the only important planktonic diatoms, as might be expected from HUSTEDT's earlier findings. At least two species of *Synedra*, tentatively identified here as *S. radians* (= *S. acus* v. *radians*) and *S. rumpens*, are among those described by HUSTEDT for other parts of Southeast Asia (HUSTEDT 1938). Great numbers of frustules from another *Synedra* species, probably *S. delicatissima* (= *S. acus* v. *delicatissima*), were found in the sediments but not in the plankton. *Melosira*, which is as ubiquitous an element of the plankton in tropical Asia as it is in tropical Africa (RICHARDSON 1968), was present in two forms. One moderately heavy *Melosira* species, probably *M. granulata*, which might have been expected to require high turbulence to offset sedimentation, was present in significant numbers on both sampling dates despite calm weather. The second form, which appears to be *M. granulata* v. *angustissima*, was not more abundant, although its very delicate frustules and small size would seem to adapt it better for planktonic existence. Frustules of *M. granulata* v. *angustissima* did predominate in the superficial sediments, however, which indicates that its overall importance is greater than the two samples suggest.

BEHRE's (1956) treatment of algae other than diatoms and dinoflagellates in the Wallacea samples lists only seven species for Lake Mainit. These belong to the genera *Calothrix*, *Gloeococcus*, *Staurastrum*, *Micrasterias*, *Cladophora*, *Merismopedia*, and *Anabaena*. Of these, only *Anabaena* appeared in the 1971 samples. One concentrated net sample obtained in 1971 did not contain either *Staurastrum* or *Micrasterias*, but these desmids could well be present in very low numbers. The remaining four species that BEHRE lists would probably not be dominant planktonic elements in Lake Mainit at any time, considering what is known of their ecology.

The organization of the phytoplankton community is very similar to that of Lake Lanao (LEWIS 1973), and to a considerable extent of the Indonesian lakes studied by RUTTNER (1952) as well. Planktonic diatoms and bluegreens are of limited diversity but contribute sizable portions of the standing crop through the success of one or two species--in this case *Anabaena* and *Lyngbya* among the bluegreens and *Synedra rumpens* among the diatoms. Chlorophyta on the other hand are much more diverse, but individual species do not stand out as dominants (Table 1). Motile forms are highly successful but not obviously diverse.

In August the standing crop of both *Anabaena* and *Lyngbya* had reached bloom proportions. Depth-series samples for zooplankton showed that most of the *Anabaena* biomass was distributed within the top 5 m. *Anabaena* filaments were exceptionally long at this time, frequently more than 1.0 mm per unit. Such large biomass units suggest the absence of effective cropping, perhaps due to the lack of calanoid copepods in the lake. The filament length of *Anabaena* had declined to a mean of 75 μ by November and the total bluegreen biomass had receded. All other groups except diatoms had increased modestly or remained stable, thus creating a rather even distribution of standing crop among the higher taxa. The expansion of the *Synedra rumpens* population by November shows that this and perhaps other diatom species periodically can become dominant elements of the phytoplankton.

Table 1. Results of the phytoplankton census for Lake Mainit on 2 August and 8 November 1971. Counts are means of duplicate samples of the 0–15 m stratum. Samples were taken with an integrating tube sampler, preserved with Lugol's solution, and counted with an inverted microscope. Maximum volume of water counted for the rarer species was 0.18 cc. Cell columes for individual species were estimated from geometric models scaled to mean dimensions for the species.

	2 August cells per cc	μ^3 per cc	μ^3 %	8 November cells per cc	μ^3 per cc	μ^3 %
Cyanophyta						
Chroococcus turgidus	530	37,100		662	46,340	
Aphanothece sp.	89,730	89,730		24,495	24,495	
Anabaena (*Anabaenopsis?*) sp.	40,964	860,244		8,512	178,752	
A. spiroides	1,242	40,986		324	10,692	
Lyngbya limnetica	167,300	334,600		2,650	5,300	
Romeria gracilis	2,962	2,962		*	*	
Dactylococcopsis fascicularis	4,514	9,028		3,466	6,932	
– sp.	295	4,425		103	1,545	
Total	307,537	1,379,075	68.2	40,212	274,056	27.9
Chlorophyta						
Gloeocystis planctonica	220	13,860		528	33,264	
Coccomyxa sp.	3,742	11,226		*	*	
Dimorphococcus sp.	416	14,560		780	27,300	
Dictyosphaerium pulchellum	96	4,800		0	0	
Coelastrum cambricum	329	23,359		462	32,802	
Chlorella spp.	623	6,230		*	*	
Lagerheimia subsalsa	12	1,500		0	0	
Oocystis submarina	398	19,900		522	26,100	
– sp.	44	11,000		0	0	
Ankistrodesmus setigerus	8	280		44	1,540	
Tetrahaedron minimum	199	4,975		717	17,925	
T. regulare	55	1,375		301	7,525	
Selenastrum sp.	530	530		*	*	
Kirchneriella lunaris	69	1,725		0	0	
Kirchneriella sp.	39	975		110	2,750	
Scenedesmus arcuatus	11	825		0	0	
Scenedesmus spp.	44	1,100		22	550	
Total	6,835	118,220	5.8	3,486	149,756	15.2
Bacillariophyceae						
Synedra radians	2	380		7	1,330	
S. rumpens	94	10,340		1,181	129,910	
Melosira granulata	25	7,500		88	26,400	
M. granulata v. *angustissima*	30	3,000		52	5,200	
Total	151	21,220	1.0	1,328	162,840	16.6
Dinophyceae						
Gymnodinium sp.	146	175,200		52	62,400	
Peridinium sp.	113	124,300		52	57,200	
Total	259	299,500	14.8	104	119,600	12.2
Cryptophyceae						
Cryptomonas marssonii	149	178,800		177	212,400	
Rhodomonas minuta	157	10,990		740	51,800	
Total	306	189,790	9.4	917	264,200	26.9
Unclassified fragments	552	13,800	0.7	464	11,600	1.2
Grand total	315,640	2,021,605	99.9	46,511	982,052	100.0

* Census on 8 November did not include these minute species.

All bacteria that could be distinguished under oil immersion were counted by the same method as phytoplankton, except that individual fields were vertically scanned to compensate for lost depth of field at higher magnification. Total cocci and bacilli numbered 37 × 10^6/l on 2 August. Sulfur bacteria (*Beggiatoa?*) were distinguishable by their internal sulfur granules, but were not numerous in the top 15 m (46 × 10^3/l). *Planctomyces* was the only other morphologically distinguishable form. This stellate organism of uncertain taxonomic status was rather common (935 × 10^3/l) and exactly matched RUTTNER's (1952, p. 92) illustration of a specimen from an Indonesian lake.

7. Zooplankton

From the Wallacea samples of Lake Mainit, WOLTERECK (1941) lists *Keratella valga, Conochiloides dossuarius*, two *Brachionus* species, *Bosmina longirostris, Diaphanosoma*, and an unspecified cyclopoid. BREHM (1938) identified the *Diaphanosoma* species as *D. sarsi*. Table 2 includes all the zooplankton species that turned up in the 1971 samples, except for some unidentified ostracods that were present in very small numbers in the uppermost 70 m. The 1971 samples contained a single cyclopoid

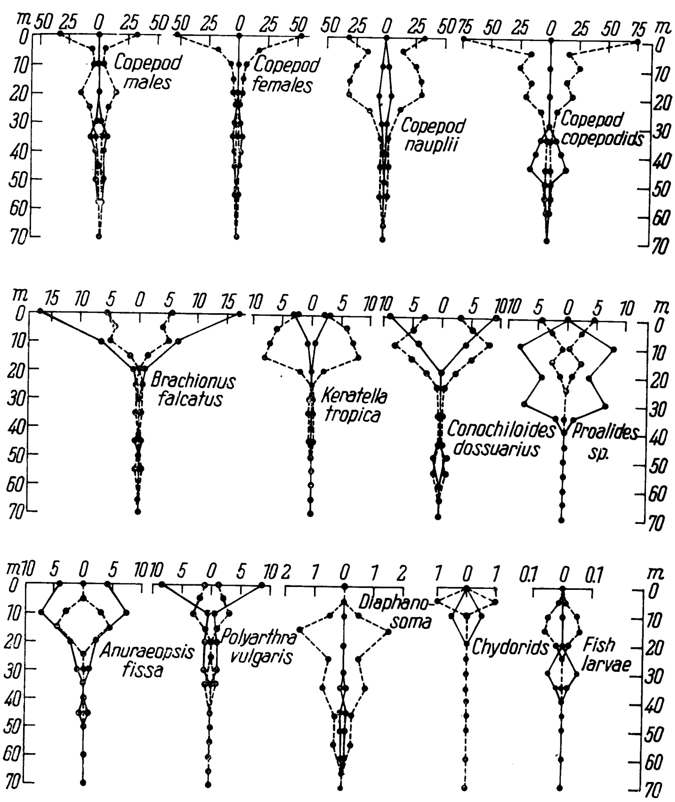

Fig. 8. Vertical distribution of zooplankton in Lake Mainit. The abscissa for each graph measures individuals per liter, half of which are plotted on each of the two sides of the zero mark. The solid line represents a vertical series taken at midday (1130) on 2 August, and the dashed line is for an evening series (2030) on 7 November. Four different scales have been used for the abscissa.

Table 2. Composition and abundance of zooplankton in Lake Mainit. Numbers of individuals per unit surface area were calculated from the weighted sum of the vertical series data of Fig. 8. Numbers of individuals per liter were converted to biomass by use of the mean volume per individual as estimated from measurements of organisms from each category. Protozoa were censused by phytoplankton techniques from sedimented core samples

	2 August Thousands of indiv./m^2	mm^3/m^2	mm^3/m^2 %	7 November Thousands of indiv./m^2	mm^3/m^2	mm^3/m^2 %
Zooplankton > 100 μ						
Copepods						
Nauplius 1	175	44		833	208	
2	30	9		211	63	
3	< 1	< 1		87	30	
4	5	2		63	28	
5	6	6		232	182	
Total	215	60		1,428	512	
Copepodid I	5	5		423	423	
II	5	8		206	309	
III	43	113		182	486	
IV	133	557		173	727	
V	183	1,186		318	2,067	
Total	368	1,869		1,304	4,011	
Male	176	1,127		651	4,173	
Female	127	1,651		616	7,977	
Total Copepods	886	4,706	38.5	4,000	16,674	80.3
Eggs	512	179	1.5	1,449	509	2.4
Rotifers						
Brachionus falcatus	325	65		146	29	
Keratella tropica	40	1		251	5	
Conochiloides dossuarius	165	41		254	63	
Proalides sp.	360	360		88	88	
Anuraeopsis fissa	255	8		95	3	
Polyarthra vulgaris	130	14		81	9	
Total rotifers	1,275	489	4.0	915	197	1.0
Eggs	193	26	0.2	182	24	0.1
Cladocera						
Chydorus barroisi	10	21		5	10	
Diaphanosoma sarsi	1	4		51	256	
Total Cladocera	11	25	0.2	56	266	1.3
Eggs (*Chydorus*)	10	5	0.0	< 1	< 1	0.0
Eggs (*Diaphanosoma*)	< 1	< 1	0.0	< 1	< 1	0.0
Total zooplankton > 100 μ	2,172	5,220	42.7	4,971	17,137	82.5
Total eggs	715	210	1.7	1,632	532	2.5
Total zooplankton + eggs	2,887	5,430	44.4	6,603	17,669	85.0
Zooplankton < 100 μ						
Protozoa						
Ciliates	585,000	1,170	9.6	225,000	450	2.2
Flagellates > 10 μ	3,195,000	4,793	39.3	1,545,000	2,317	11.2
Flagellates < 10 μ	16,365,000	818	6.7	6,808,000	340	1.6
Total Protozoa	20,145,000	6,781	55.6	8,578,000	3,107	15.0
Grand total – all zooplankton	20,147,887	12,211	100.0	8,584,603	20,776	100.0

species that is similar in size and gross morphology (♀, 650 μ) to *Thermocyclops* of Lake Lanao. This species unfortunately was not mentioned in KIEFER's (1938) taxonomic treatment of the Wallacea copepods, so its identity remains uncertain.

The data of Fig. 8 and Table 2 derive from a vertical series of samples taken on each of the two sample dates. The sampling gear consisted of a 45-l transparent zooplankton trap of the type described by SCHINDLER (1969). The trap was fitted with a number 20 net and bucket. For each depth in the series, subsamples representing 1–5 liters of the water column were counted for all species. The entire 45-l sample was subsequently examined for larger forms. Copepod nauplii were divided into instars on the basis of size and morphology by a technique developed for *Thermocyclops hyalinus* in Lake Lanao (LEWIS, unpublished). Although the division is not perfect, culture experiments verify the fundamental validity of the separation. Copepodids were separated on the basis of leg development, which gives an unambiguous separation in all but the last copepodid stage. Adult and stage V copepodids were distinguished in males by secondary sexual changes in the antennae and in females by segmentation of the urosome. Since transitions to the adult stage may become evident at somewhat different times in the two sexes, some variation in the sex ratio is expected.

Due to its transparency and large size, the trap captured fish fry and small shrimp as well as zooplankton. On 2 August, the apparent standing crop of fish fry (1.0–15.0 mm) amounted to 950 individuals/m^2 or about 950 mm^3/m^2. On 7 November, there were 1400 individuals/m^2 or about 1400 mm^3/m^2. No shrimp were captured on 2 August, but on 8 November the sampling indicated a population of about 250 individuals/m^2 (1–5 mm), or 120 mm^3/m^2, belonging to an endemic species referred to by WOLTERECK (1941) as *Para-lio-telphusa mainitensis* (currently *Mainitia mainitensis* BALSS–Dr. F. CHACE personal communication). Because of the high mobility of small fish and shrimp, these estimates should be considered minimal.

The standing crop of larger zooplankton was dominated by cyclopoids in both August and November (Table 2). The total number of copepods apparently increased considerably between the two sampling dates, although some variation can be attributed to spatial heterogeneity in the distribution of the population. In August the high proportion of late copepodid stages is probably residual from a past reproductive peak, and the rarity of late naupliar and early copepodid stages indicates that several weeks of negligible reproduction had preceded the sampling period. The relatively high egg ratio (4.0 eggs per female) and high proportion of early naupliar stages indicates a resumption of reproduction just prior to sampling. The apportionment of individuals among stages in the November sample shows that reproduction had been steady but not spectacular during the August-November interval. The lower egg ratio in November (2.4 eggs per female) is evidence of an oncoming decline in the population growth rates during November.

Causes for change in density and age structure of copepod populations cannot be determined from the information at hand. It does appear that the copepod species of Lake Mainit has more than one reproductive period per year. The observed increase in population size during August and September may be an annual phenomenon, since primary production is likely to be greatest during the hot season.

The absence of any wholly herbivorous (diaptomid) copepods is remarkable, since other types of large grazers are not abundant. The cyclopoid nauplii are thus likely to be relatively important herbivores and probably constitute a major route of energy flow to the primary carnivore level, which is principally composed of older individuals of the same species.

The rotifer fauna is neither rich nor abundant. This is consistent with the findings of RUTTNER (1952) for the lakes of Indonesia. Numbers of individuals in August and

November were divided among the six species with rather surprising equitability, and the census did not reveal any truly rare species. All genera except *Proalides* are common elements of the Indonesian plankton. The *Proalides* species of Lake Mainit is similar to *P. tentaculata*, but may be a distinct species (BERZINS, personal communication).

Cladocera were not quantitatively important during August or November, but both species were present in sufficiently large numbers to suggest that both are persistent elements of the euplankton and not displaced littoral forms. Both species have been found previously at other locations in Southeast Asia (BREHM 1933, JOHNSON 1954).

Protozoa constitute a major portion of total zooplankton biomass of Lake Mainit. It is difficult to judge whether this is unusual since there is a general paucity of ecological information on the protozoan component of the zooplankton. Colorless flagellates and ciliates were not a major part of the standing crop in any of the Sunda Lakes studied by RUTTNER (1952). However, some preservation and census techniques may lead to the consistent underestimation of protozoan standing crop. At least one intensive study of a temperate lake (NAUWERCK 1963) has shown that the protozoa dominate the zooplankton biomass during much of the year. The protozoa may consequently prove to be of more general importance in plankton than they presently appear to be. Alternatively, the larger non-protozoan components of the Lake Mainit zooplankton may be under abnormally heavy cropping pressure from the large populations of small, euryhaline fishes that inhabit the lake. If this is true, size selection may favor the protozoa instead of crustaceans and rotifers.

The zooplankton and phytoplankton biomass can conveniently be compared as standing crop per unit surface area. The ratio of phytoplankton to zooplankton (g/m^2) is 28 : 12 or 2.3 for 2 August and 18 : 21 or 0.86 for 8 November. Such high ratios suggest that the zooplankton cannot efficiently use the phytoplankton food source and that cropping was not a significant deterrent to phytoplankton growth at the time of sampling.

The November zooplankton samples were intentionally taken in the evening, because the August samples had been taken at midday. A comparison of vertical distributions for individual species on the two dates (Fig. 8) thus provides some information about diurnal migration. Interpretation of the distribution data must be conservative, considering the long interval between sampling periods, but the similar chemical conditions of the upper water column during August and November make it likely that gross differences in distribution are diurnal in nature.

In three Indonesian lakes RUTTNER (1943) demonstrated some tendency toward an evening or nocturnal upward migration among all copepods, Cladocera, and rotifers, except for *Pedalia intermedia* in Lake Toba, which showed the opposite tendency, and a few indeterminate cases that showed no obvious pattern. Migration was generally less marked for rotifers than for Cladocera or copepods.

The differences between midday and evening distributions of copepods and Cladocera were the same in Lake Mainit as in RUTTNER's lakes. Nocturnal concentration at the surface was marked in adult copepods and copepodids. The interesting dichotomous noctural distribution of male copepods (Fig. 8) was verified by replicate counts but has no obvious explanation. Copepod nauplii show the same pattern as the older stages, but with less clarity, perhaps because of their lower motility.

RUTTNER distinguished between species that are present at the surface during the day, even in small numbers, and those that are not. In Lake Mainit large proportions of all rotifer populations except *Proalides* were present at the surface at midday. This was not expected on the basis of RUTTNER's data, since those of RUTTNER's populations that could be found at the surface during the day were not found there in large numbers. All rotifer species in Lake Mainit except *Anuraeopsis* were also present at the surface in the evening. Proportions of the population at the surface were lower in the evening than at midday for *Brachionus*, *Keratella*, *Conochiloides*, and *Polyarthra*. The rotifers of Lake Mainit thus appear to belong to three groups: 1) *Proalides*, which was present at the surface in the evening but not at midday; 2) *Anuraeopsis*, which was distributed just the opposite of *Proalides;* 3) *Brachionus*, *Keratella*, *Conochiloides*, and *Polyarthra*, which were present at the surface at midday and in the evening but were deeper on the average in the evening than at midday.

8. Fish and Other Biota

Small fish of several species were being harvested in great quantities with fine-mesh seines during both August and November. The largest portion of the catch was made up of a small (1—10 cm) eleotrid, presumably identical with the one found by the Wallacea expedition (*Ophieleotris agilis*) and considered by WOLTERECK (1941) to be an endemic species. Another large portion of the catch was made up of *Glossogobius giurus*. Other species included an anabantid (*Trichogaster trichopterus*) a channid (*Ophiocephalus striatus*), a syngnathid, and a hemiramphid. Small numbers of a phallostethid, probably the endemic *Solenophallus thessa* mentioned by WOLTERECK (1941), were present in the catch.

A few cyprinids were also present. WOLTERECK reports finding *Rasbora philippina* in Lake Mainit, but the specimens collected in 1971 unquestionably belong to the genus *Puntius* (= *Barbus* or *Barbodes*) rather than *Rasbora*. Use of HERRE's (1924) key leads to the conclusion that all the specimens are *P. binotatus*, which has a wide distribution in Southeast Asia. The presence of *P. binotatus* in Lake Mainit is of some interest in connection with the swarm of endemic species in nearby Lake Lanao (HERRE 1933, MEYERS 1960, KOSSWIG and VILLWOCK 1965). There are several presently indistinguishable reasons why *P. binotatus* should not have diversified at all in Lake Mainit as it apparently did in Lake Lanao. Lake Mainit may not be nearly so old as Lake Lanao, or, perhaps more likely, Lake Mainit has periodically reached salinities that cannot be tolerated by *Puntius*. The most interesting possibilities are that Lake Mainit offers less potential for effective allopatry, or that rapid speciation was made impossible by the presence of a competing euryhaline ichthyofauna.

Aside from the fish that were in the August and November catch, fishermen identified a catfish (*Clarias batracus?*) and an eel (*Anguilla mauritana?*) as important seasonal elements of the catch. The composition of the catch in 1971 and reports of local fisherman are at variance with the observations of MANACOP (1937), who lists several marine species among the fishes he found.

Only one crocodile was sighted during the sampling. Crocodiles were once numerous, particularly in a swampy portion of the Tubay River, but they have been rapidly exterminated as modern weapons have become available.

9. Summary

Lake Mainit is located on northeastern Mindanao, 27 m above sea level. The lake covers 141 km^2, occupies a rather deep basin that is apparently of tectonic origin, and is probably quite old. The climate, although tropical, shows a seasonal trend toward higher rainfall and cooler weather from November through February. The lake was thermally stratified in both August and November, but the dilute nature of the deepest water indicates that deep mixing occurs during the cool season. The lake is moderately well-buffered and contains slightly more sodium than calcium.

Two measurements of C-14 uptake showed that Lake Mainit is highly productive (1–2 gC/m^2/day). Carbon uptake is vertically distributed in a manner reminiscent of temperate oligotrophic lakes, so that the lake is transparent despite its high productivity. Phytoplankton standing crop was 28 g/m^2 in August and 18 g/m^2 in November. Dominant algal genera include *Anabaena*, *Lyngbya*, *Synedra*, *Cryptomonas*, *Peridinium*, and *Gymnodinium*. Protozoa comprised a substantial portion (15–50%) of the total zooplankton biomass. Cyclopoid copepods dominated the standing crop of larger zooplankton. Rotifers and Cladocera were present but not diverse. The ratio of phytoplankton to zooplankton biomass was 2.3 in August and 0.86 in November. There is evidence for a strong upward nocturnal migration in the last six copepod stages, but most rotifers species were present in large numbers at the surface both in the evening and at midday. The fish fauna is primarily composed of small euryhaline species that are likely to be effective zooplankton predators.

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