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STRUCTURE AND FUNCTION OF THE ZOOPLANKTON COMMUNITY OF MIRROR LAKE, NEW HAMPSHIRE[1]

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Abstract. An intensive study of the zooplankton community of Mirror Lake, New Hampshire, was undertaken over a 3-yr period. Our objectives in the lake study have included measurements of a number of attributes of the zooplankton community that integrate structure and function at the ecosystem level; among these are dispersion, biomass, productivity, respiration, and nutrient cycling.

Eight species of rotifers and 3 species of cladocerans were successfully cultured. Generation time for planktonic rotifers was ≈8–10 days (17°C). The effect of higher food levels on rotifers was to shorten generation time and to increase brood size. In cladocerans, high food levels caused an increase in length and brood size.

A curvilinear relationship existed between zooplankton community respiration and temperature in Mirror Lake. Mean monthly zooplankton community respiration ranged from 96.0 kg C/ha/mo in June of 1969 to a low of 20.5 kg C/ha/mo in April of 1970. Over a 3-yr period, respiration was 79.9% of assimilation.

The 0 to 4.5-m strata (≈epilimnion) contributed 68.5% and 46.5% of the annual zooplankton production and biomass. Zooplankton community production ranged from 22.3 kg C/ha/yr to 29.3 kg C/ha/yr with a 3-yr mean of 25.2 kg C/ha/yr. The annual zooplankton biomass ranged from 1.4 to 2.6 kg C/ha with a 3-yr mean of 2.0 kg C/ha.

A linear relationship was found to exist between net phytoplankton and zooplankton production in various lakes of the world. Ecological efficiency apparently increases with the trophic status of the lake. It is recommended that the term ecological efficiency be refined to include both autochthonous and allochthonous inputs of reduced carbon into the lake.

Rotifers assume a major role in intrasystem nutrient cycling and energy transfer within the lake ecosystem. Of the total amount of P incorporated into the organic matter of zooplankton community each year, 33.5% is assimilated in rotifer tissue. The annual turnover rate of P by rotifers is 30.9 and is high compared to crustaceans (10.1).

Copepods comprise 55.4% of the total zooplankton biomass. However, the copepods, with their slow growth over an entire year, represent only 19.3% of the zooplankton production, while rotifers account for 39.8% of the zooplankton production annually in Mirror Lake. Also, evidence is presented that rotifers play a major role in energy transfer in lakes of varying trophic status (oligotrophic to eutrophic).

Key words: biomass; community; ecosystem; efficiency; New Hampshire; niche; nutrients; phosphorus; production; respiration; structure; zooplankton.

INTRODUCTION

The northern hardwood forest and the oligotrophic lake ecosystem of the Hubbard Brook Valley, New Hampshire, are the subject of continuing ecological studies. In spite of a voluminous literature on zooplankton, the role of zooplankton, particularly rotifers, is inadequately understood in an aquatic ecosystem. Our objective in the study of the zooplankton community of the lake is to integrate structure and function at the ecosystem level. Thus, we discuss our measurements of the zooplankton populations of Mirror Lake, New Hampshire in relation to dispersion, biomass, productivity, respiration, and nutrient cycling.

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The study area

Mirror Lake has apparently been nutrient poor and relatively unproductive throughout its 12 000-yr history (Likens and Davis 1975). Currently, Mirror Lake is an oligotrophic, usually dimictic lake with a maximum depth of 11 m, a mean depth of 5.75 m, and a theoretical water residence time of 1.0 yr. The outlet of the lake flows into Hubbard Brook just before the latter joins the Pemigewasset River. The water is slightly acid (pH 5.5–6.8) with a dissolved solid content of 15–20 mg/l. Secchi disk readings are generally 6 to 7 m during the summer. The vertical oxygen distribution in summer may by described as positive heterograde (Åberg and Rodhe 1942).

The Bacillariaphyceae, Cryptophyta, and Cyanophyta are nearly always present. In the spring and

summer, the Chrysophyceae have the highest species diversity and always comprise a significant fraction of the phytoplankton biomass (Gerhart 1973). Nitrogen and P simultaneously limit phytoplankton productivity (Gerhart 1975). Annual net phytoplankton productivity is estimated as 37 g C/m² (Jordan and Likens 1975). Macrophyte productivity (1.7 g C/m²) has been determined by Moeller (1975). Only 5 species of fish, *Perca flavescens, Esox niger, Ictalurus nebulosus, Catostomus commersoni,* and *Micropterus dolomieui* are found in the lake (Mazsa 1973) along with 1 newt *Notopthalmus v. viridescens* (Burton 1973). Benthic invertebrates have been investigated by Walter (1976). An organic C budget has been developed for the lake by one of us (Jordan and Likens 1975).

Materials and Methods

General limnological methods.—Zooplankton samples were collected from a fixed station (Central) at weekly intervals during late spring, summer, early autumn, and at monthly intervals the rest of the year from October 1968 to September 1971. Between 1000 h and 1200 h, at 0, 3, 6, and 9 m, 11.88 litres of water were collected, filtered on the lake, and preserved with 5% buffered formalin. After 17 May 1970, only 2.97 litres of water were filtered at each depth.

Phytoplankton samples, oxygen and temperature measurements, secchi disk readings, and water chemistry samples were concurrently taken on each sampling date. Water samples were obtained at metre intervals with a Ruttner sampler. Oxygen was determined by the azide modification of the Winkler Method (American Public Health Association 1960). At 0, 3, 6, and 9 m, 100 ml of water from the Ruttner sampler were preserved with acid-Lugols solution in brown bottles for phytoplankton analysis.

Horizontal distribution.—Zooplankton samples were collected randomly at 3-m intervals from 8 stations throughout the lake. Total collection time was 90 min.

Zooplankton sampling device.—Samples were collected by a water-bottle technique (Likens and Gilbert 1970). A Van Dorn bottle was lowered to the desired sampling depth and closed immediately. Closing the water bottle immediately is imperative if a quantitative sample of the larger, more motile zooplankton is desired (Smyly 1968). After the bottle was hauled into the boat, the water was filtered through a plankton funnel equipped with a 35-μm mesh net (prior to June 1969, a 48-μm mesh net was used).

Likens and Gilbert (1970) have demonstrated this sampling procedure to be a quantitative procedure for estimating rotifer density. There was a question as to whether this procedure was quantitative for Cladocera and Copepoda in Mirror Lake. To answer this, an Isaac-Kidd, Clarke-Bumpus, and a 0.5-m vertical tow net were compared to the Likens-Gilbert (1970) procedure.

Serious functional problems may occur in metered devices if fine mesh nets are used, giving inaccurate results (Tranter and Smith 1968). McNaught (1971) recommends not using a net finer than 363 μm (#2 net) in productive waters. Because Mirror Lake is unproductive and many researchers have employed a 158-μm mesh net, a #10 (158 μm) net was used in the Isaac-Kidd, Clarke-Bumpus, and 0.5-m vertical tow net. We believe, therefore, that these conditions were optimal for use of the metered devices in Mirror Lake. The plankton funnel was equipped with a 35-μm mesh net.

Within a period of 90 min, 3 tows or hauls were made with each device. The Clarke-Bumpus, Isaac-Kidd, and water-bottle samples were taken at a depth of 3 m. For comparison with the 0.5-m vertical tow, water-bottle samples were taken at 0, 3, 6, and 9 m, counted, and appropriately weighted for volume at each depth to obtain a value for the whole water column. The water-bottle samples were counted totally; the other samples were subsampled and counted in a Sedgewick-Rafter cell.

All species of zooplankton in the towed devices were found in the water-bottle sample (Table 1). In all cases except 1, the water bottle caught more of the larger, more motile Cladocera and Copepoda than the other devices. More *Daphnia catawba* were caught by the Clarke-Bumpus apparatus than the water bottle; however, the means were not significantly different ($P = .05$). The number of rotifers and nauplii missed with a #10 mesh net is particularly striking.

Counting procedures and associated errors.—Prior to June 1970, rotifers and copepod nauplii were counted in a Sedgewick-Rafter cell on 1-ml subsamples taken with a Stempel pipet. The mean was calculated from counts of 5 individual subsamples. Total samples were counted for copepods and cladocerans during this period. After June 1970, samples were totally counted for all species by the inverted microscope method (Utermöhl 1958, Nauwerck 1963).

The total error involved with taking a sample, counting it, and expanding it to the rest of the lake can be divided into 3 components: counting error, site sampling error, and lake sampling error. Counting errors for both the inverted microscope method and the Sedgewick-Rafter approach are generally low, with the settling technique providing a more precise count (Table 2). Five samples taken at the same station provided an estimate of the site sampling error (Table 3). Because we were able to consistently catch all the rotifers and probably most of the crustaceans, and because the site sampling error was generally $<10\%$, we feel that samples are quantitative at 1 station (Central) in the lake. However, because of the contagious dispersion of many organisms (Table 4) and the small number (1) of stations sampled in the seasonal studies, the error statement for the total number of organisms in the lake is large (Table 3b).

TABLE 1. Comparison of the catching efficiencies of a Clarke-Bumpus Sampler (#10 net, 158 μm), Isaac-Kidd Sampler (#10 net), 0.5-m vertical tow (#10 net), and a Likens-Gilbert Sampler

Species	Likens-Gilbert ($\bar{x}$ ± SE)/m³	Isaac-Kidd ($\bar{x}$ ± SE)/m³	Clarke-Bumpus ($\bar{x}$ ± SE)/m³	0.5-m vertical tow ($\bar{x}$ ± SE)/m³ for the entire water column	Likens-Gilbert ($\bar{x}$ ± SE)/m³ for the entire water column
Bosmina longirostris	505 ± 84	81 ± 34	231 ± 34	378 ± 27	682 ± 84
Holopedium gibberum	1052 ± 126	72 ± 72	872 ± 92	599 ± 95	1043 ± 115
Daphnia catawba	5598 ± 295	1910 ± 230	8243 ± 1008	2465 ± 628	5416 ± 390
Cyclops scutifer	2315 ± 547	562 ± 463	1750 ± 390	775 ± 144	2858 ± 339
Diaptomus minutus	6397 ± 673	1828 ± 93	3416 ± 1377	4588 ± 181	6906 ± 421
Copepod nauplii	20 059 ± 1667	87 ± 87	1015 ± 34	4598 ± 1180	44 792 ± 483
Polyarthra vulgaris	62 062 ± 4024	0.0	0.0	116 ± 21	76 850 ± 2811
Keratella cochlearis	9705 ± 572	0.0	88 ± 88	26 ± 19	35 608 ± 807
Kellicottia longispina	11 599 ± 1035	1336 ± 873	8029 ± 509	2676 ± 457	12 183 ± 620
Asplanchna priodonta	1052 ± 126	0.0	0.0	249 ± 12	1139 ± 137
Kellicottia bostoniensis	0.0	0.0	0.0	2615 ± 425	11 106 ± 295

Production.—Cladocera and Copepoda production was estimated by the method of Winberg et al. (1965):

$$P = \frac{N_I W_I}{T_I} + \frac{N_{II} W_{II}}{T_{II}} + \frac{N_{III} W_{III}}{T_{III}} + \ldots,$$

where P = production; N_n = number in the size class; T_n = development time of the size class; and W_n = change in weight during time T_n, where n = size class.

The rotifers are not susceptible to size classification because of their small size and meager growth after hatching. The doubling-time method (Galkovskaya 1965), a method suitable for rotifers, was used in this study. This method is based upon the inverse relationship of the daily individual growth increment to generation time:

$$P = \frac{\bar{N}\bar{W}}{T_{e+p}},$$

where P = production; $\bar{N}$ = average number of individuals over a given time period; T_{e+p} = development time from hatching of the parent rotifer to the hatching of its offspring; and $\bar{W}$ = average weight increment.

Development time, generation time, and culturing methods

Copepoda.—The growth curves of 3 species *Diaptomus minutus, Cyclops scutifer,* and *Mesocyclops edax* were developed from actual measurements of individuals from field samples (Fig. 1). With the exception of copepod eggs, the change in length and development time of a size class was determined from these growth curves. Development times for copepod eggs were determined from Schindler's (1972) equation:

$$\frac{1}{D} = 0.0426 + 0.0008T^2,$$

where D = development time and T = temperature (°C).

Cladocera.—Unlike the copepods, the cladocerans in Mirror Lake are continuously reproducing with a resultant overlap in cohorts. To develop the growth curve from the field data, it was necessary to separate the cohorts of each species with time. Because it was not possible to do this for *Daphnia catawba, Holopedium gibberum,* or *Bosmina longirostris,* the growth curves were obtained by culturing the organisms. With the exception of the arbitrary division of the growth curve into 5 size classes, development time and change in length of a size class were estimated from the growth curve in the same manner as for the copepods. Ovigerous females and individuals from the

TABLE 2. Counting error associated with the (A) settling technique and (B) Sedgewick-Rafter Cell

	$\bar{x}$	SE
(A) Settling technique (n = 3)		
Keratella taurocephala	17.0	0.00
Keratella cochlearis	304.7	1.33
Keratella crassa	95.0	1.53
Polyarthra vulgaris	259.0	6.66
Kellicottia longispina	148.0	1.00
Copepod nauplii	130.7	0.67
Daphnia catawba	24.7	0.33
Diaptomus minutus	66.7	0.67
Cyclops scutifer	12.0	0.00
(B) Sedgewick-Rafter Cell (n = 5)		
Keratella cochlearis	55.2	4.0
	15.2	0.9
	15.6	3.3
Kellicottia longispina	2.4	0.7
Polyarthra vulgaris	90.4	6.0
	18.6	2.8
Conochiloides dossuarius	19.6	5.7
	44.2	4.6
Keratella taurocephala	5.6	0.9
	12.6	1.4
Kellicottia bostoniensis	12.6	1.8

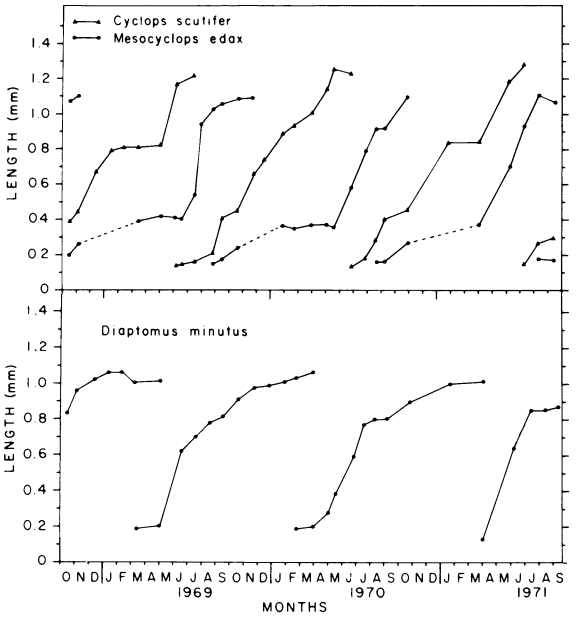

FIG. 1. Seasonal growth curves for *Cyclops scutifer*, *Mesocyclops edax*, and *Diaptomus minutus*. Dotted lines indicate absence of nauplii in the water column.

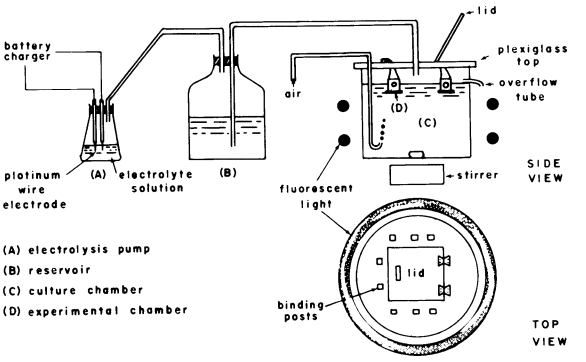

FIG. 2. Diagram of chemostat used in culturing cladocerans. A series of potentiometers may be added to control amperage.

TABLE 3. Site sampling (A) and lake sampling (B) error for selected zooplankton in Mirror Lake, New Hampshire, USA

A. Site sampling error (n = 5)

	$\bar{x}$	SE
Keratella taurocephala	91.8	10.9
Keratella cochlearis	85.2	8.3
Polyarthra vulgaris	447.2	16.3
Copepod nauplii	88.4	4.2
Daphnia catawba	31.0	4.4
Mesocyclops edax	14.8	1.1
Diaptomus minutus	6.8	0.4

B. Lake sampling error—Mean for several stations is compared to estimate at Central.

	Strata	Stations (n)	$\bar{x}$ ± 95% confidence level	$\bar{x}$ for Central ± 95% confidence level (n = 3)
Polyarthra vulgaris	0	8	49.9 ± 54.3	29.0 ± 28.4
	3	7	314.8 ± 317.8	213.3 ± 46.1
	6	3	78.7 ± 697.1	88.7 ± 12.4
Kellicottia longispina	0	8	1.0 ± 1.0	1.3 ± 1.43
Keratella taurocephala	0	8	34.2 ± 11.4	43.5 ± 16.3
Cyclopoidae	0	8	5.5 ± 2.9	3.5 ± 2.2
Diaptomus minutus	0	8	1.9 ± 1.7	2.7 ± 6.6
Daphnia catawba	3	7	3.0 ± 2.0	7.0 ± 7.4

last size class, the asymptote of the growth curve, were used to calculate the maximum length.

Because food abundance affects the growth of *Daphnia* (Hall 1964) and, thereby, development time and change in length for a size class, cladocerans were cultured at 2 food levels: unenriched and enriched. Two continuous culture devices driven by electrolytic pumps were constructed (Fig. 2). Glass Pyrex jars (16–20 litres) served as the culture vessels. Overflow tubes, inserted in holes bored through the side of each flask, maintained the culture volume at ≈12–14 litres, depending on which culture vessel was used. Each morning, water in the reservoir was emptied, and fresh, unfiltered water was added from the 3-m depth of the lake. As a result, the culture medium was not a monoculture but contained all the phytoplankton species normally found in the lake. Light was provided by two 40-watt Sylvania Circline fluorescent lamps surrounding each culture vessel. Temperature changes due to the light-dark cycle were minimized (e.g., 17.8 ± 1.2°C) by a fan blowing directly on the culture vessel. The culture water was kept mixed by a magnetic stirrer and by air bubbled slowly from the bottom. Once a week, the culture vessel was emptied, wiped clean with a Kimwipe, and rinsed with deionized water 3 times before refilling with unfiltered lake water.

The experimental chamber in which each organism was actually housed was made of a 2.54-cm section of plexiglass tubing, 2.54 cm long with a 0.35-cm thick plexiglass bottom (Fig. 3b). The culture medium flowed through the experimental chamber from four 1.27-cm holes covered with 252-μm mesh (Nitex) netting. The experimental chamber was easily lifted from the culture chamber by cotton string attached to the binding posts. By this procedure, the organism could be observed on a dissecting scope with minimal disturbance. Every other day the organism would be transferred with a small pipet to a clean chamber.

For enriched cultures, N (sodium nitrate) and P (so-

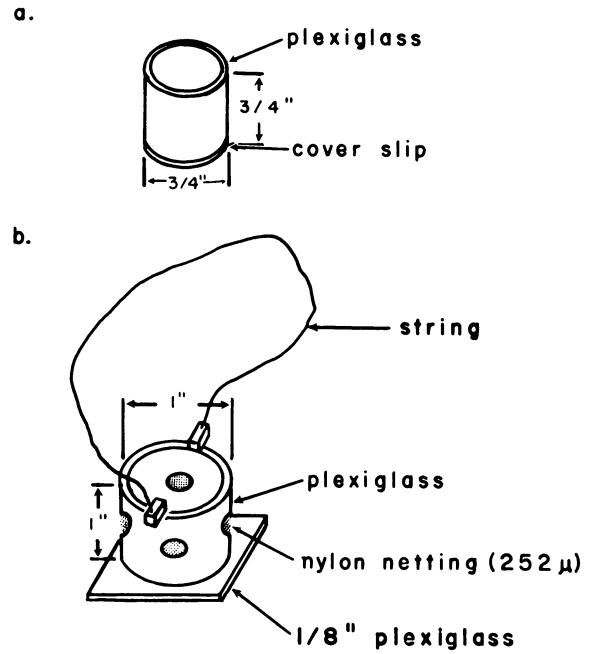

FIG. 3. Experimental chamber for rotifers (a) and cladocerans (b). 1 inch = 2.54 cm.

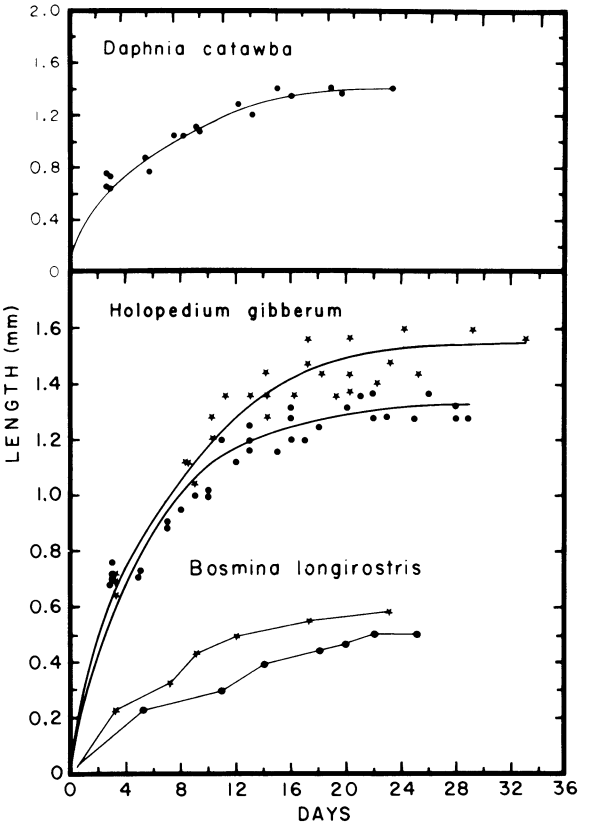

FIG. 4. Growth curves of *Holopedium gibberum*, *Bosmina longirostris*, *Daphnia catawba* in enriched (stars) and unenriched (circles) cultures. *Holopedium gibberum*—Enriched: Chl *a* = 4.8 parts per billion (ppb), Mean life span (MLS) = 21.8 days, Mean brood size (MBS) = 3.93, *n* = 5, Temperature (T) = 18.0 ± 0.7. Unenriched: Chl *a* = 1.7 ppb, MLS = 24.8 days, MBS = 1.80, *n* = 5, T = 18.8 ± 1.2. *Bosmina longirostris*—Enriched: Chl *a* = 4.3 ppb, MLS = 23.2 days, MBS = 2.0, *n* = 2. Unenriched: Chl *a* = 1.53 ppb, MLS = 24.2 days, MBS = 1.25, T = 18.0 ± 0.7. *Daphnia catawba*—Unenriched: Chl *a* = 1.7 ppb, MLS = 17.0 days, MBS = 2.83, T = 18.3 ± 1.2, *n* = 4. The line fitted to *H. gibberum* and *D. catawba* is a significant fit ($P < .05$).

dium phosphate) were added to each reservoir to stimulate phytoplankton production (Gerhart 1975). It was assumed that increases in chlorophyll standing crop reflected an increase in the phytoplankton population. By increasing or decreasing flow (washout) or by changing nutrient concentrations, chlorophyll levels were adjusted in the enriched culture vessel to ≈5 ppb. Chlorophyll values of 5 ppb or greater have been observed during the summer in the hypolimnion (Gerhart 1973).

A problem arises as to which growth curve, enriched or unenriched, should be used for estimating change in length and development time of a size class. The effect of an increased food supply on a cladoceran is to increase the size of the organism and increase the number of eggs in the brood pouch (Fig. 4; Hall 1964). As Hall (1964) suggested, the maximum length and the brood size of the individuals of a natural population are indirect measures of food supply. We determine which growth curves should be used for production estimates by comparing brood size and maximum length of the organism in the field with laboratory data at different food levels. When data on maximum length and brood size were not available for a month (Tables 5 and 6), the curve developed from the unenriched culture was employed.

With this approach, growth curves for *Bosmina longirostris* from enriched cultures were used only in November 1969 and March 1970. In December of 1969 and January of 1970, growth curves from unenriched cultures were used (Table 5a). During the 3 yr of the study, this was the only winter during which *Bosmina* was prevalent in the lake. During this period (November 1969–January 1970) the use of the enriched curves and the high concentration of *Bosmina* reflect the high phytoplankton biomass not found in other years (Fig. 5). *Bosmina longirostris* was not cultured in the continuous culture device (See next section—Rotatoria).

Enriched curves were employed for *Holopedium gibberum* in the fall of 1968 and 1969 (Table 5). The unenriched curve was used for *D. catawba* (Table 6).

Rotatoria.—Because of their small size, rotifers and *Bosmina longirostris* were cultured in 1.91-cm × 1.91-cm plexiglass chambers (Fig. 3a). To prevent *B. longirostris* from being caught on the surface film, the chamber was capped carefully with a glass coverslip so as not to introduce an air bubble. Every 12 h, the

TABLE 4. Horizontal distribution of zooplankton. C = contagion, R = random, and U = uniform. See Elliot (1971) for methods

Species	Depth (m)	$\bar{x}$	s^2	χ^2	Dispersion
Polyarthra vulgaris	0	59.4	1014	119.6	C
	3	362.0	32 168	533.0	C
	6	93.0	3845	84.0	C
Kellicottia longispina	0	1.52	1.59	2.09	R
	3	7.45	14.77	6.00	R
	6	10.3	11.5	4.47	R
Conochilus unicornis	0	49.6	67.9	95.7	C
	3	25.6	186.6	51.02	C
	6	2.37	0.72	1.53	R
Keratella taurocephala	0	36.0	144.8	28.2	C
	3	24.3	266.0	65.7	C
	6	2.31	0.49	0.85	R
Keratella cochlearis	0	2.00	2.7	9.5	R
	3	8.51	62.0	43.7	C
	6	125.3	369.1	11.8	C
Copepod nauplii	0	26.2	210.3	562	C
	3	58.3	144.2	14.8	C
	6	42.4	1162.0	27.0	C
Cyclopoidae	0	5.52	11.8	14.9	R
	3	23.1	27.6	7.2	R
	6	16.9	41.0	9.7	R
Diaptomus minutus	0	2.9	14.5	34.0	C
	3	4.7	4.8	6.1	R
	6	26.1	735.0	112.5	C
Daphnia catawba	0	1.2	2.8	19.0	C
	3	3.0	4.8	9.6	R
	6	3.5	1.8	2.0	R

organism was transferred into a clean experimental chamber containing fresh lake water from the 3-m region. For the enriched culture, water enriched with N and P to stimulate phytoplankton production was taken from a circular polyethylene column (diameter = 0.8 m, length = 4.6 m) located in the lake (see Gerhart 1975 for details on this procedure). *Conochiloides dossuarius* and *Kellicottia bostoniensis* were cultured in unenriched hypolimnetic water (9 m) because they possessed only 1 major population pulse during the summer in the hypolimnion, a region already high in chlorophyll concentration.

Eight species were successfully cultured. Only 1, the colonial rotifer *Conochilus unicornis*, was not successfully cultured. The mean generation time of the 8 other species was used for *C. unicornis*.

Because of the difficulty in measuring changes in length in the rotifers and their tendency to carry only 1 egg, the use of the brood size–maximum length approach to determine the relative effect of quantity of food on the reproductive capacity of the rotifers could not be employed. However, the ratio of eggs per female is an indicator of the reproductive potential of a population. Generally, the higher the algal standing crop, the higher the egg ratio, the higher the reproductive capacity of the population (Edmondson 1962, 1965), or the higher the turnover rate of the population. For individuals, a higher standing crop of algae means a decrease in generation time and possibly an increase in brood size: factors which are reflected in the population by a higher egg ratio and an increase in the turnover rate.

TABLE 5. Mean maximum length and brood size of selected monthly field samples and laboratory specimens of *Bosmina longirostris* (A), and *Holopedium gibberum* (B). Values given are the mean ± SE

	Maximum length (mm)	Brood size	Growth curve employed
A. *Bosmina longirostris*			
Laboratory culture (enriched)	0.59	2.00 ± 0.32	...
Laboratory culture (unenriched)	0.50	1.25 ± 0.25	...
November 1969	0.56 ± 0.01	1.83 ± 0.17	enriched
December 1969	0.48 ± 0.01	1.00 ± 0.00	unenriched
January 1970	0.45 ± 0.01	1.00 ± 0.00	unenriched
March 1970	0.61 ± 0.03	1.82 ± 0.13	enriched
B. *Holopedium gibberum*			
Laboratory culture (enriched)	1.55	3.93 ± 0.26	...
Laboratory culture (unenriched)	1.34	1.80 ± 0.37	...
October 1968	1.37 ± 0.02	2.20 ± 0.20	unenriched
October 1969	1.52 ± 0.05	4.00 ± 0.07	enriched
November 1968	1.55 ± 0.03	3.25 ± 0.95	enriched
March 1969	1.30*	2.00*	unenriched
May 1972	1.30*	2.00*	unenriched
June 1971	1.33 ± 0.01	1.00 ± 0.00	unenriched
August 1971	1.37 ± 0.03	1.75 ± 0.25	unenriched

* 1 individual.

TABLE 6. Mean maximum length and brood size of selected monthly field samples and laboratory specimens of *Daphnia catawba*. Values given are the $\bar{x} \pm$ SE

	Maximum length (mm)	Brood size
Laboratory (unenriched)	1.40	2.90 ± 0.59
October	1.36 ± 0.02	2.11 ± 0.20
November	1.35 ± 0.03	2.14 ± 0.23
December	1.38 ± 0.06	2.14 ± 0.14
January	1.31 ± 0.01	3.00*
March	1.35 ± 0.03	2.16 ± 0.15
June	1.40 ± 0.02	2.54 ± 0.12
July	1.41 ± 0.03	2.13 ± 0.26
August	1.39 ± 0.04	1.61 ± 0.18
September	1.44 ± 0.02	1.80 ± 0.37

* 1 individual.

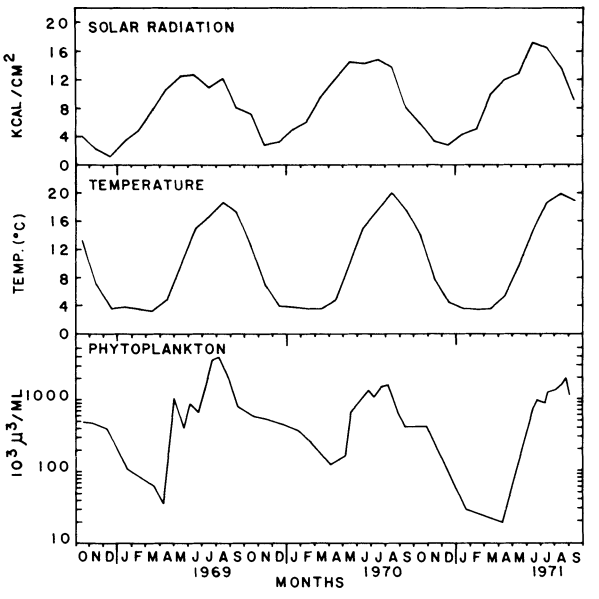

FIG. 5. Seasonal variation in solar radiation, temperature, and phytoplankton biomass in Mirror Lake, New Hampshire, USA. Phytoplankton biomass values are daily means weighted for depth at Station Central. Temperature values are monthly means weighted by volume of each 1-metre stratum of the entire lake. Solar radiation values represent the total amount of solar radiation impinging on the lake per month.

As noted earlier, rotifers were cultured in water low (unenriched—June) and high (enriched) in chlorophyll. The mean egg ratio of the field samples and the associated generation time of a rotifer for the month of June was used as an indicator of the reproductive capacity of the population. If for any depth or month the egg ratios were twice the June mean, the generation times from the enriched cultures were used in calculating production. By this technique, generation times from enriched cultures were generally employed in the fall, spring, and during the winter of 1969–1970. This indicates either higher quantities of food, better quality food, or both.

Temperature.—In cladocerans, food level affects the size of the organism and brood size, while temperature alone may be utilized to predict duration of egg development and physiological life span (Hall 1964). The generation time of a rotifer decreases with increases in food level or temperature. The effect of temperature and food have been assumed to act independently on generation times of rotifers. In general, rate processes in poikilotherms are increased or decreased with increasing or decreasing temperatures. Thus, the annual fluctuation in temperature of a lake affects the physiological life span, generation time, and the production of zooplankton.

The effect of temperature on rate processes in poikilotherms may be obtained by simply culturing at various temperatures. However, when working with a large number of species such as in Mirror Lake, this approach becomes impractical. The dependence of a rate process on temperature can be calculated utilizing coefficients from Krogh's normal curve (Winberg 1971, Edmondson and Winberg 1971). A comparison between the observed life span and the predicted life span at different temperatures is given in Table 7. Generally, agreement is found between the predicted and the observed life spans. In cases where ranges are given, predicted values overlap with the measured value.

Production calculations.—The mean monthly production and biomass of zooplankton were calculated by the following formula:

$$\text{Production} = \left[V_1 \cdot \frac{(D_1 W_1)}{DT_1} + V_2 \cdot \frac{(D_2 W_2)}{DT_2} + \cdots + V_n \cdot \frac{(D_n W_n)}{DT_n}\right] T;$$

$$\text{Biomass} = V_1 D_1 W_1 + V_2 D_2 W_2 + \cdots + V_n D_n W_n.$$

For production in the crustaceans, W is the change in dry weight of a size class while in the rotifers it is the mean dry weight. With biomass, W is the mean weight of a size class (crustaceans) or an organism (rotifers); D is the weighted monthly mean density of a size class or an organism; development times (DT) were adjusted according to Krogh's normal curve by the mean monthly heat content of each strata; T is the number of days in a month, while n is the size class.

Based on sampling depth and length of the water bottle (0.75 m), the lake was arbitrarily divided into 4 strata: 0–2 m, 2–4.5 m, 4.5–7.5 m, 7.5–10.9 m. The actual volume (V) of water in each stratum is calculated by a computer program based on the morphometry of the lake basin, ice thickness, and water height at a gaging station at the outflow of the lake (Fig. 6).

Length-weight relationships.—Utilizing a Cahn Gram Electrobalance, length-weight relationships were developed for *Daphnia catawba, Holopedium*

TABLE 7. Comparison of observed with predicted life spans utilizing Krogh's normal curve (Winberg 1971, Edmondson and Winberg 1971). D.T. = development time

	Temperature (°C)	Observed development time (days)	Temperature (°C)	Observed development time (days)	Temperature (°C)	Predicted development time (days)
Daphnia mendotae (Hall 1964)	20	60–80	11	150	11	168[a]
Daphnia pulex (Knutson 1970)	9 ± 2	21.0 ± 0.92[b]	20 ± 2	9.13 ± 0.20	20 20	6.9 10.5[c]
Moina macrospora (Brown 1929)	20	111.1 h	25	66.7 h	25	73.3 h
Kellicottia longispina (Galkovskaya 1965)	15	6.67	18	5.0	18	4.2
Lecane inermis (Finesinger 1926)	18	10	29–35	4 or 5	29	4.41
Daphnia magna (MacArthur and Baillie 1929)	18	38.62 ± 0.22[b] Maximum = 92	8	107.94 ± 2.81 Maximum = 179	8	112.0
	8	107.94 ± 2.81	10	89.67 ± 2.07	10	82.8
	8	107.94 ± 2.81	18	38.62 ± 0.22	18	37.2

[a] Based on 70 days.
[b] ±SE.
[c] Based on: temperature = 11°C; D.T. = 19 days.

gibberum, Diaptomus minutus, Cyclops scutifer, and *Mesocyclops edax* (Fig. 7). Because of the small amount of growth in *Bosmina longirostris, Tropocyclops prasinus,* and the rotifers, only mean dry weights were measured (Table 8). Depending on the weight of the organism, 2–150 organisms were individually selected from preserved samples, rinsed in distilled water, measured with an ocular micrometer if a length-weight relationship was to be developed, placed on tared aluminum foil pans, and dried 24–48 h at 60°C. Samples were allowed to cool at least 1 h in a desiccator before being weighed.

Chemical analysis of zooplankton tissue.—Chemical analyses were done on *D. catawba, H. gibberum, D. minutus,* a mixed cyclopoid sample (*M. edax, C. scutifer*), and a mixed rotifer sample. Zooplankton collected with a Clarke-Bumpus sampler was filtered through a series of stacked filters possessing (from top to bottom) 308-μm, 253-μm, 86-μm, and 53-μm mesh Nitex® nets. By filtering the concentrated Clarke-Bumpus samples through the separation filters when a species population pulse was occurring, it was possible to collect large amounts of relatively monospecific material for chemical analysis.

After removal from the filter, the samples were examined microscopically and extraneous matter or undesirable species were removed. All samples were thought to be at least 90% pure. The samples were then placed in evaporating dishes and allowed to dry at a temperature of 60°C.

Dry weights were determined after drying at 60°C for 48 h. Triplicate subsamples of ≈0.1 g from the thoroughly mixed sample were analyzed for Ca^{++}, Mg^{++}, K^{+}, Na^{+}, and Zn^{++}. Procedural details and method employed for the analysis for these elements may be found in Likens and Bormann (1970).

Samples analyzed for C, N, and P were homogenized in a ball mill and vacuum desiccated for 16 h prior to weighing into silver foil cups. Analyses for carbon and nitrogen were made with a Carbo-Erba Model 1102 Elemental Analyser modified to provide 2 channels for the simultaneous determination of C and N (Hauser 1973). The acid digestion method of Stainton et al. (1974) was employed for P determinations. Six determinations for C, N, and P were made, with each replicate consuming ≈1.5 mg of sample material in total.

TABLE 8. Mean dry weight of *Bosmina longirostris, Tropocyclops prasinus,* and 9 species of rotifers. The weights of rotifer and *B. longirostris* eggs are based on the volume of the egg (6.70×10^4 μm³, rotifers; 6.57×10^5 μm³, *B. longirostris*) and the mean dry weight density of eggs of *Daphnia catawba* (4.28×10^{-7} μg/μm³), *Diaptomus minutus* (6.44×10^{-7} μg/μm³), and *Cyclops scutifer* (1.17×10^{-7} μg/μm³)

Species		Dry weight (μg) ($\bar{x}$ ± SE)
Keratella taurocephala		0.096 ± 0.007
Keratella crassa		0.090 ± 0.001
Keratella cochlearis		0.070 ± 0.008
Kellicottia bostoniensis		0.066 ± 0.012
Kellicottia longispina		0.100 ± 0.015
Asplanchna priodonta		0.212 ± 0.003
Polyarthra vulgaris		0.060 ± 0.002
Conochilus unicornis		0.082 ± 0.005
Conochiloides dossuarus		0.119 ± 0.009
Rotatoria egg		0.027
Bosmina longirostris	adult	1.17 ± 0.088
	egg	0.26
Tropocyclops prasinus		1.20 ± 0.057

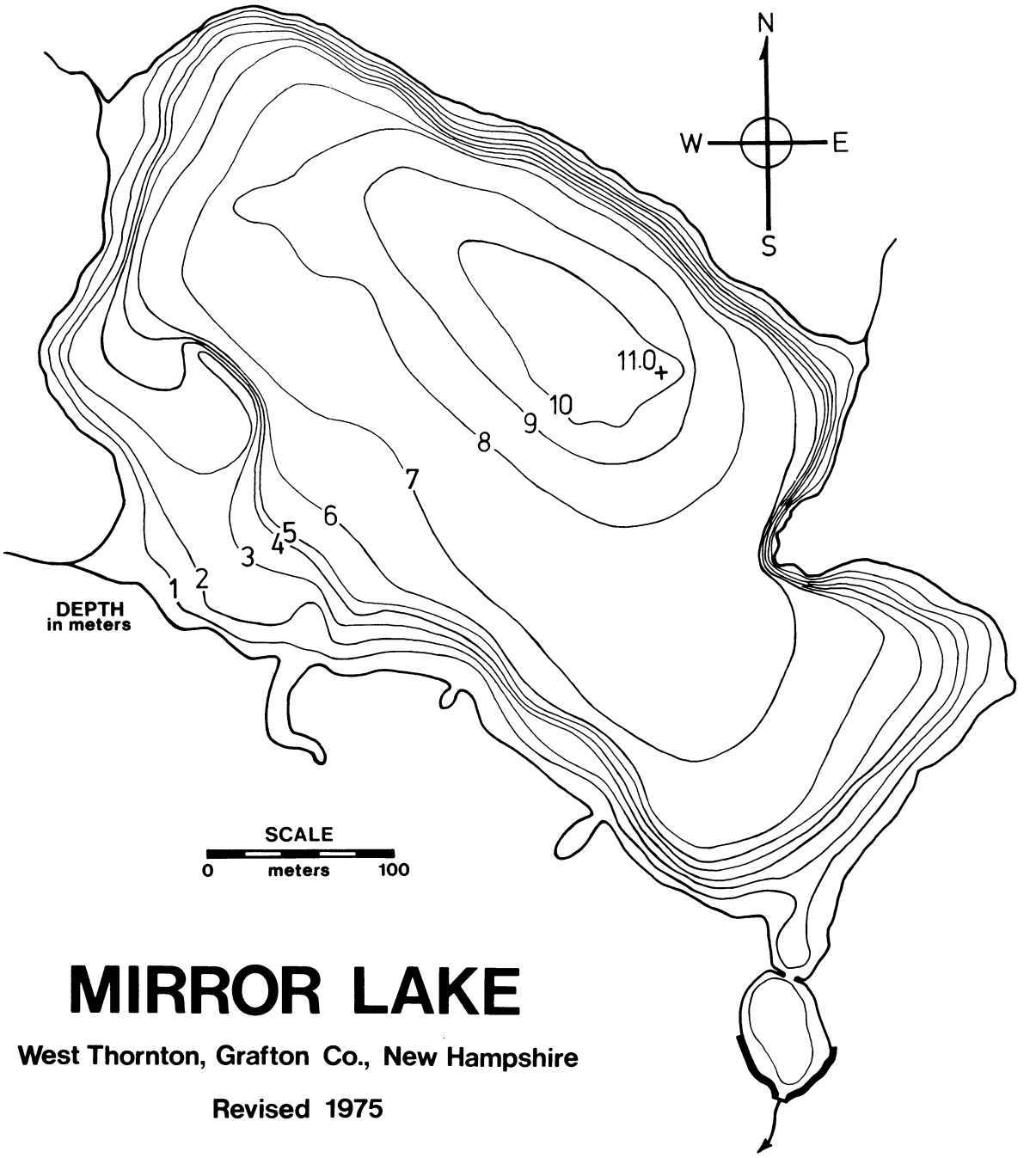

FIG. 6. Bathymetric map of Mirror Lake, New Hampshire, USA.

A Parr Adiabatic Bomb Calorimeter equipped with a AC5E Semimicro Bomb was used for caloric analyses. Corrections for the heat of formation of nitric acid and combustion of the fuse were made. In all samples, the nitric acid correction was insignificant.

A comparison of the different species and groups analysed reveals a similar chemical composition except for *Diaptomus minutus* (Table 9). This species has the highest energy and C content and consistently the lowest cation concentration.

Respiration.—Zooplankton respiration was measured by the large volume, mixed species technique after consideration of the effects of microbial respiration, photosynthesis, bottle size, and incubation

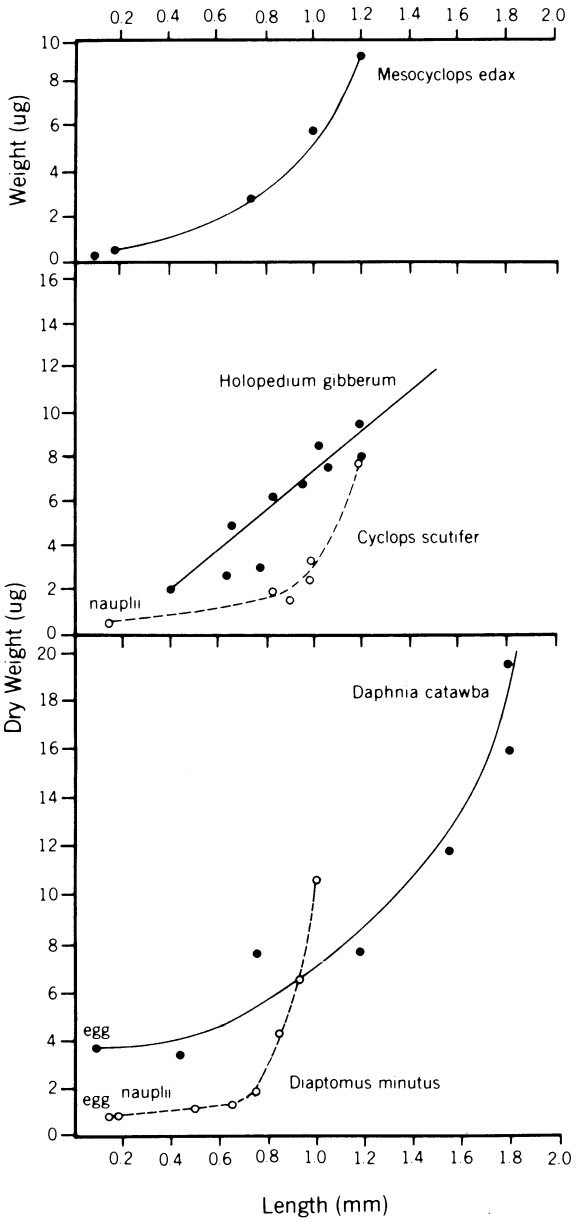

FIG. 7. Length–dry weight relationships for *Holopedium gibberum, Daphnia catawba, Cyclops scutifer, Mesocyclops edax,* and *Diaptomus minutus.* Curves fitted by eye.

time on zooplankton respiration. Microbial respiration and photosynthesis or both may bias estimates of zooplankton oxygen consumption. However, careful studies indicate that microbial respiration or photosynthesis or both would not significantly affect our measurements of zooplankton respiration in Mirror Lake (Makarewicz 1975). A high respiratory rate was found during the 1st few h of incubation (Fig. 8), presumably due to handling (Raymont and Gauld 1951). For this reason, the concentrated samples of zooplankton in biochemical oxygen demand (BOD) bottles were allowed to equilibrate in the lake for 2 h before the initial bottles were analyzed for oxygen. By using a 300-ml BOD bottle, bottle effects on zooplankton respiration were minimized (Table 10). The effect of density of zooplankton on rates of respiration were minimized by using zooplankton concentrations of approximately 5 mg dry weight/bottle (Table 11).

General procedure for estimating zooplankton respiration.—Rates of oxygen consumption were estimated for animals captured with a Clarke-Bumpus tow (#10 net) at a depth of 4 m. The contents of each Clarke-Bumpus haul were carefully placed into a large, plastic bucket. After a large number of zooplankton were captured (8–12 hauls), the contents of the bucket were quickly filtered through a 86-μm mesh net. The plankton were immediately immersed in lake water which had been filtered (Millipore HA 0.45 μm). The concentrated zooplankton solution was thoroughly mixed and siphoned into darkened 300-ml BOD bottles. The contents of at least 3 bottles were preserved and counted to determine the mean weight of zooplankton in each bottle. Total dry weight in a bottle was determined from the counts by summing the weights of the individuals.

At least 6 bottles, 3 initial and 3 experimental, were incubated in the lake. After equilibrating for 2 h, the initial bottles were analysed for dissolved oxygen. Six to 8 h later, the experimental bottles were analysed for dissolved oxygen. Subtracting the oxygen concentration of the experimental bottle from the oxygen concentration of the initial bottle gave zooplankton community respiration. Respiration was measured on 5 dates throughout the year (ranging from the winter to the summer). By measuring community zooplankton respiration with season, the respiratory measurements are compensated for different size classes of a species, temperature effects, and seasonal changes in zooplankton composition.

In Mirror Lake, the effect of temperature on zooplankton oxygen consumption is a curvilinear relationship (Fig. 9) with a temperature coefficient of 2.7. A Q_{10} in the range of 2–3 has often been reported for many investigations (Vollenweider and Ravera 1958). On a per unit weight basis, respiration rates of zooplankton in Mirror Lake and Cayuga Lake in New York are also very similar (Table 12).

Results and Discussion

General time, life span, and growth.—In total, 8 rotifers were successfully cultured. In the unenriched culture, 1 amictic egg is carried during the life span of the organism. With higher food levels, the brood size of *Polyarthra vulgaris* increased from 1 to 2, i.e., 2 eggs developing at the same time. Also, a significant decrease in generation time occurred with increased quantities of food. Thus, the effect of increased food supply on reproduction of rotifers in Mirror Lake is

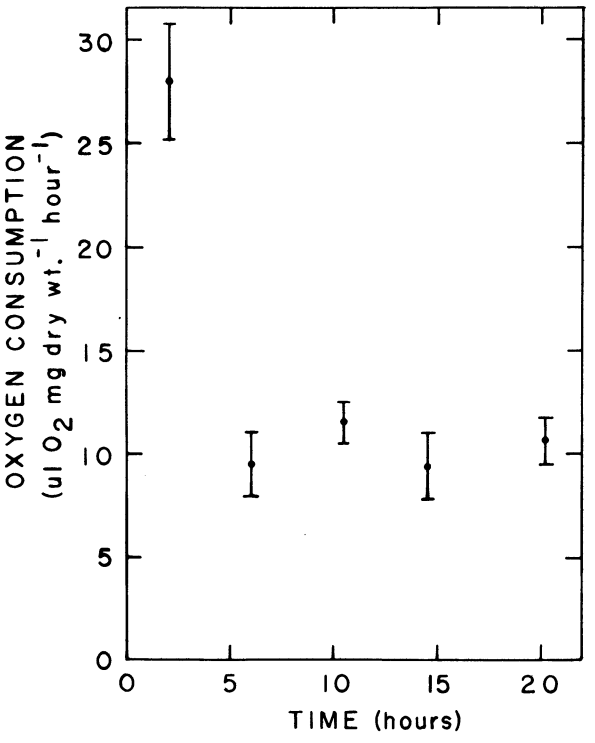

FIG. 8. Oxygen consumption of zooplankton with time ($\bar{x}$ ± SE).

TABLE 10. Oxygen consumption (STP) by zooplankton with varying bottle sizes. Included is an analysis of variance and the calculated least significant difference. $P = .01$; $\overline{Smd}$, standard deviation of the mean difference

Bottle size (ml)	Oxygen consumption (μl of O_2/mg dry weight of zooplankton/h) Replicates 1	2	3	4	5	$\bar{x}$
125	39.68	30.87	41.66	35.17	36.63	36.80
300	27.29	21.60	22.67	25.34	21.38	23.66
1 200	26.00	24.67	31.41	24.46	28.83	27.07

Source of variation	df	Sum of squares	Mean square	F
Total	14	597.0		
Between bottles	2	465.0	232.5	21.04**
Error (within)	12	132.6	11.05	

Least significant difference, L.S.D. = $\overline{Smd} + t^{.05}_{n(k-1)}$ = 9.47.

to decrease generation time and possibly increase brood size (Table 13).

Hutchinson (1967) reports the life span of many rotifers to lie between 5.6 and 11.3 days, which is similar to the range found for Mirror Lake rotifers (Table 13). However, the generation times of rotifers in Mirror Lake are longer than values reported for similar species in Lake Naroch (Galkovskaya, 1965). Hutchinson (1967) also reports the life span of *Rotaria rotaria* and the sessile *Cupelopagis vorax* to be 35–40 days. By including these very long life spans, Hutchinson (1967) suggests that a life span of 22 days is typical of rotifers. Considering both the Mirror Lake and Lake Naroch data, the average life span of planktonic rotifers should be revised downward to 8–10 days (17°C).

The life span and brood size of *B. longirostris, D. catawba,* and *H. gibberum* are given in Fig. 4. Initial growth of the organisms was rapid but slowed by the 12th to 16th day. Growth rate and maximum length of poikilotherms are considered to be a function of food supply (Hall 1964, McLaren 1965). This was the case in Mirror Lake. The effect of increasing food supply was to increase brood size and the length of the organism. Even though generation time decreased, the life span appeared not to decrease significantly with

TABLE 9. Chemical composition and caloric values for zooplankton from Mirror Lake. Values given are means and standard deviations of the mean based upon dry weight analysis of composite samples collected during the spring and summer. PPM = parts per million

Species	Sample Ca	Mg	K	PPM Na	Zn	Sample percent P	N	C	Calories/g	Percent ash
Daphnia catawba	425.5 ±4.1	18.6 ±0.44	78.6 ±3.4	101.2 ±6.0	3.22 ±0.12	1.57 ±0.02	8.6 ±0.15	47.1 ±1.26	5653.3 ±127.8	18.0
Holopedium gibberum	298.3 ±4.1	26.9 ±0.24	96.0 ±3.0	196.5 ±11.1	4.39 ±0.063	1.43 ±0.02	6.2 ±0.07	38.0 ±0.22	5608.0 ±100.0	23.0
Diaptomus minutus	41.8 ±1.0	10.2 ±2.20	61.8 ±0.79	53.6 ±1.7	1.58 ±0.081	.95 ±0.02	6.7 ±0.12	51.7 ±0.47	6877.6 ±61.3	7.5
Cyclops	198.9 ±5.1	24.7 ±0.11	127.7 ±0.81	164.7 ±5.3	4.73 ±0.48	1.47 ±0.02	7.2 ±0.12	41.8 ±0.23	5781.6 ±130.0	17.7
Rotifer	123.3 ±0.5	24.7 ±0.31	58.9 ±1.4	76.2 ±3.8	4.02 ±0.092	.96 ±0.03	7.7 ±0.25	40.4 ±0.27	. . . . .	19.7
Chaoborus	103.5 ±2.5	26.8 ±0.46	174.4 ±3.6	91.9 ±3.5	2.87 ±0.12	1.58 ±0.02	8.2 ±0.10	44.3 ±0.11	6101.39 ±142.97	20.0

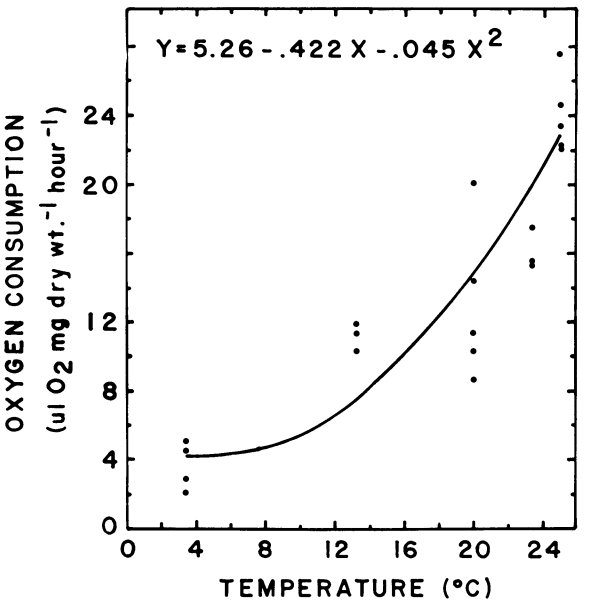

FIG. 9. Oxygen consumption rates of zooplankton with temperature. The line is significant for curvilinearity ($P < .05$).

the increase of food supply. Hall (1964) observed similar results on *Daphnia galeata mendotae* with increased food supply. This suggests the increase in length and brood size and the decrease in generation time with increasing food supply may be a general phenomenon associated with the cladocerans.

Relative abundance of species.—An ordination of species rank against percent of production describes a dominance-diversity curve with 4 distinct groups (Fig. 10). The first group, consisting only of the dominant species *Daphnia catawba*, represents 29% of the total zooplankton production. Those organisms that have consistently high densities each year and are generally found in each season of the year comprise the second group. This group of 8 species accounts for 59.5% of the zooplankton production. Thus, 9 zooplankton species (Group 1 and 2) represent 88.5% of the annual zooplankton production. Three of the species are rotifers.

Unlike the second group, the third group consists of organisms present in 1 yr in relatively high densities or relegated to areas of the lake where temperature and oxygen were low. For example, *Kellicottia longispina* and *B. longirostris* were prevalent only in the 2nd yr of the study, while *K. bostoniensis* and *C. dossuarus* are found only in the cold hypolimnion during summer stratification.

In the last group are rare organisms. These organisms, together with those in Group 3, represent a reservoir of species that could become prevalent in the lake with eutrophication or with changes in predation pressure.

In Mirror Lake the ordination of species rank against production is not a significant fit to the log normal distribution. However, a significant fit probably would not be expected with a sampling effort restricted to 1 station with a small sample area (33 cm²) (Colinvaux 1973).

In older, established equilibrium communities, Goulden (1966) and Tsukada (1967) have shown the abundance and rank order of the chydorid Cladocera will approach a MacArthur type-1 distribution. Mirror Lake has not experienced any major catastrophes over its 12 000-yr history (Likens and Davis 1975). Comparison of the actual abundance and rank order of Mirror Lake zooplankton with expected values from MacArthur's type-1 distribution indicates a significant fit (Fig. 10). If the omnivores and/or predators are ranked separately from the herbivores, they appear to concentrate their dominance in 1 species: their rank abundance distribution approaches a geometric series, while the remaining herbivores still fit the MacArthur type-1 distribution (Fig. 11).

Division of the niche hyperspace.—In Makarewicz and Likens (1975, 1978), we report how species of zooplankton divide the niche hyperspace of Mirror Lake.

Respiration.—Community zooplankton respiration varied from a high of 122 kg C/ha/yr in the 2nd yr to a low of 96 kg C/ha/yr in the 3rd yr of the study. For

TABLE 11. Oxygen consumption (STP) by zooplankton with varying concentration of zooplankton. A normal weight represents ≈5 mg (dry weight) of zooplankton

Zooplankton biomass	Oxygen consumption (μl of O_2/mg dry weight of zooplankton/h) Replicates		
	1	2	3
Normal × 2	15.30	17.11	16.11
Normal	14.25	16.17	14.37
Normal × 0.5	19.22	15.08	16.59

Source of variation	df	Sum of squares	Mean square	F
Total	8	19.04	2.38	
Between concentration	2	6.30	3.15	1.49
Error (within)	6	12.73	2.12	

TABLE 12. Comparison of zooplankton respiration rates in Mirror Lake and Cayuga Lake

	Temperature (°C)	Oxygen consumption (μl O_2/mg/h)
Cayuga Lake (Bishop 1968)	18–20	14.2 ± 0.48
	4	3.8 ± 0.50
Mirror Lake	19.0	13.5
	3.4	3.7

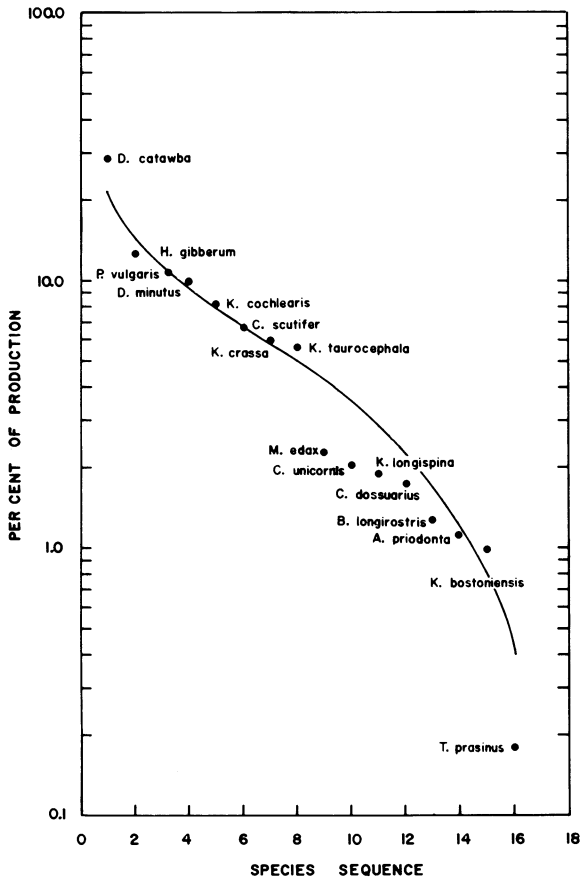

FIG. 10. Rank–species abundance curve of the zooplankton community. The MacArthur type-1 distribution is a significant fit at $P = .10$ according to the chi-square ($\chi^2 = 5.58$, DF = 14) and Kolmogorov-Smirnov (Massey 1951) test. The lognormal was not a significant fit at $P = .10$ ($\chi^2 = 11.17$, DF = 6).

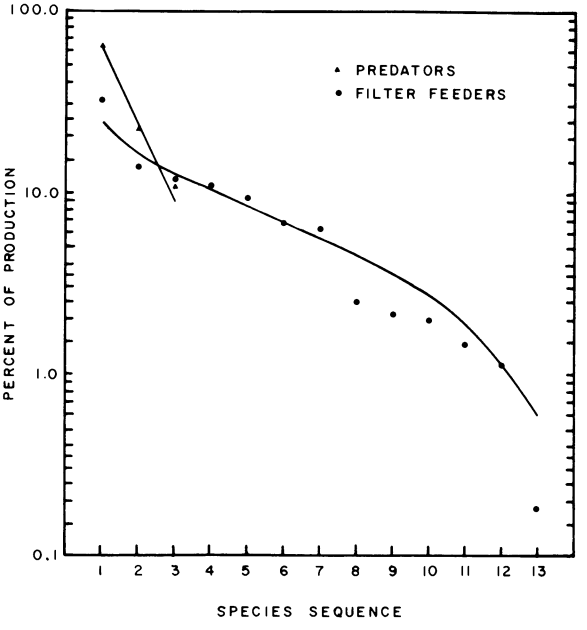

FIG. 11. Rank–species abundance curve of omnivores-predators and herbivores. The MacArthur type-1 distribution is a significant fit to the herbivore distribution at $P = .10$ according to the chi-square ($\chi^2 = 3.14$, DF = 9) and Kolmogorov-Smirnov test. C = 0.38 for the geometric series.

the 3-yr period, the mean monthly zooplankton respiration ranged from 20.5 kg C/ha/mo in June of 1969 to 3.0 kg C/ha/mo in April of 1970. Over a 3-yr period, zooplankton community respiration was 79.9% (range = 79.1–80.6%) of assimilation. Cummins (1971) observed respiration to be 90% of assimilation for a population of *Leptodora kindtii*.

There is a seasonal periodicity of zooplankton com-

TABLE 13. Generation time and life span of rotifers in enriched and unenriched cultures. Enriched (E) cultures have been fertilized with nitrogen and phosphorus. Unenriched (U) cultures contain lake water from the 4-m depth. Culture temperature = 16.8°C

Species	Number of replicates	Culture type	Development time: Egg (days)	Development time: Post embryonic (days)	Development time: Generation time ± SE (days)	Development time: Life span ± SE (days)
Polyarthra vulgaris	8	U	3.5	8.5	12.0 ± 0.71	12.9 ± 0.77
	3	E	2.7	6.0	8.7 ± 0.88	. . .
Kellicottia longispina	2	U	2.8	12.3	15.1	. . .
	6	E	2.5	8.3	10.8 ± 0.57	11.8 ± 0.57
Kellicottia bostoniensis	9	9 m water	2.3	7.3	9.6 ± 0.38	10.7 ± 0.38
Conochiloides dossuarius	7	9 m water	2.5	4.8	7.3 ± 0.62	8.3 ± 0.62
Keratella cochlearis	7	U	2.1	8.3	10.4 ± 0.20	11.4 ± 0.20
	3	E	2.2	7.0	9.2 ± 0.17	. . .
Keratella crassa	5	U	2.4	9.4	11.8 ± 0.93	12.8 ± 0.93
	3	E	2.5	7.7	10.2 ± 0.44	. . .
Keratella taurocephala	7	U	2.4	10.1	12.5 ± 0.41	14.1 ± 0.55
	3	E	2.0	8.0	10.0 ± 0.29	. . .
Asplanchna priodonta	7	U	1.6	5.9	7.5 ± 0.28	7.5 ± 0.28

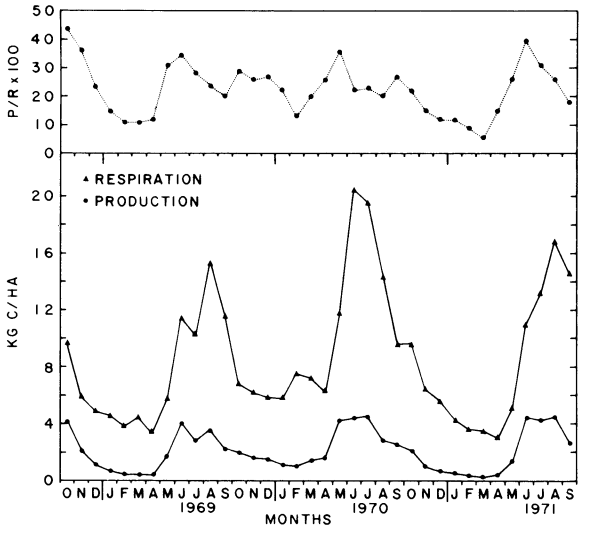

FIG. 12. Mean monthly community zooplankton production and respiration. A respiratory quotient of 0.83 was employed for the carbon equivalent of a given rate of oxygen uptake.

munity respiration described annually by a unimodal curve (Fig. 12). Respiration increases during the spring and reaches a peak in the summer. As zooplankton biomass and temperature decreases, respiration falls off to a minimum in winter. With spring, the cycle begins again. A similar zooplankton respiration cycle exists for zooplankton of Lago Maggiore and Mergozzo (Vollenweider and Ravera 1958).

Production-respiration.—Information on the functioning of a zooplankton community may be obtained by following seasonal production-respiration (P/R) ratios (Fig. 12). In the spring, when the lake is cool, the P/R ratio increases, indicating more energy from trophic level I is diverted into the synthesis of new organic matter. In the summer, the ratio decreases, with a larger fraction of energy being used in respiration to maintain the organism in the warmer lake

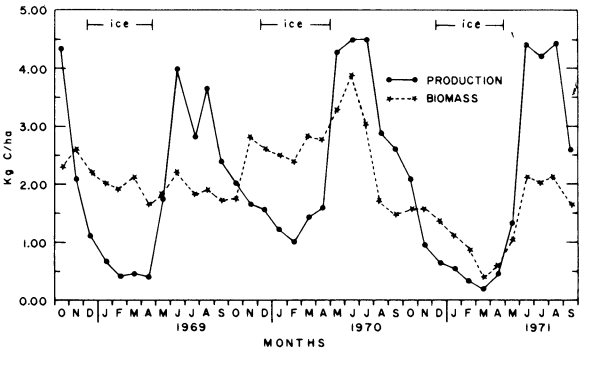

FIG. 13. Mean monthly community zooplankton production and biomass.

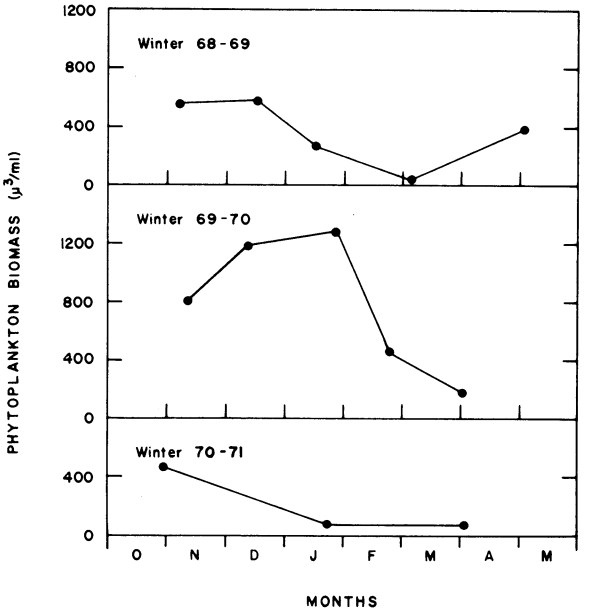

FIG. 14. Biomass of selected algal species during the winters of 1968–1971. *Cryptomonas erosa, Cryptomonas marssonii, Cryptomonas pulsilla, Katablepharis ovalis, Chrysococcus* spp., *Erkenia subaequiciliata, Monochrysis aphanagter.*

water. With cooler water temperature in the fall, there is an increase in the ratio with more energy again being utilized in the production of new organic matter. As the winter progresses, the decrease reflects the larger decrease in production than in respiration. Because of the minimal thermal and food conditions imposed on the community, the synthesis of new matter almost ceases, with the energy available being utilized to maintain the organisms present. This cycle repeats itself each year.

Production-biomass.—The 0 to 4.5-m strata (~epilimnion) contributed 68.5% and 46.5% of the annual zooplankton production and biomass. The 4.5 to 7.5-m strata (~metalimnion) accounted for 26.3% and 27.9% of the annual zooplankton production and biomass; the 7.5 to 10.9-m region (~hypolimnion) contributed only 5.1% and 7.1% of the zooplankton production and biomass. The low contribution of the hypolimnion to lake production and biomass is due to the morphometry of the Mirror Lake basin; the hypolimnion represents only 6.9% of the total volume of the lake. When production and biomass are not weighted for volume of each strata and compared on a concentration basis (mg C/m^3), the hypolimnion contributes 16.3% and 25.9% of the zooplankton production and biomass.

A cyclic periodicity of zooplankton community production and biomass is apparent in Mirror Lake (Fig. 13) similar to the seasonal zooplankton cycle observed in Clear Lake, Ontario (Schindler 1972). This seasonal

TABLE 14. Annual biomass and production of Rotifera, Cladocera, and Copepoda for a 3-yr period in Mirror Lake

Biomass	Rotifera	Cladocera	Copepoda	Total
October 1968–September 1969				
kg C/ha	0.26	0.51	1.26	2.03
Percent	12.8	25.1	62.1	
October 1969–September 1970				
kg C/ha	0.48	0.56	1.54	2.58
Percent	18.6	21.7	59.7	
October 1970–September 1971				
kg C/ha	0.24	0.52	0.61	1.37
Percent	17.5	38.0	44.5	
Mean percent	16.3	28.3	55.4	
Production				
October 1968–September 1969				
kg C/ha/yr	8.26	10.09	5.69	24.04
Percent	34.4	42.0	23.7	
October 1969–September 1970				
kg C/ha/yr	13.59	9.08	6.60	29.27
Percent	46.4	31.0	22.5	
October 1970–September 1971				
kg C/ha/yr	8.60	11.08	2.59	22.27
Percent	38.6	49.8	11.6	
Mean percent	39.8	40.9	19.3	

cycle in Mirror Lake is correlated with the seasonal pattern of phytoplankton biomass, solar radiation, and the weighted mean lake temperature (heat content) (Fig. 5).

Zooplankton community production ranged from 22.3 kg C/ha/yr to 29.3 kg C/ha/yr with a 3-yr mean of 25.2 kg C/ha/yr. The annual zooplankton biomass ranged from 1.4 to 2.6 kg C/ha with a 3-yr mean of 2.0 kg C/ha (Table 14).

During the winter of 1969–1970, a much higher phytoplankton biomass was evident than in other years. Similarly, a higher zooplankton biomass and production was evident during this winter. Seven edible phytoplankton species in particular were present in high densities, unlike other winters, and apparently accounted for the increase in zooplankton production (Fig. 14).

Indirect evidence (i.e., the occurrence of clear, hard ice; the lack of a snow cover on the lake; and the occurrence of oxygen supersaturation just below the ice, presumably due to photosynthesis) indicates that greater amounts of solar radiation were penetrating into the water column during the winter of 1969–1970. Although the data are indirect and not conclusive, they do suggest that solar radiation and temperature are limiting primary production in the winter. Nitrogen and P are known to be limiting primary production in the summer (Gerhart 1975).

Production-biomass ratio.—The ratio of production to biomass (P/B) is an estimate of the turnover rate of the community. For example, in Mirror Lake, the daily P/B ratio for crustaceans during May through September is 0.04, a biomass turnover time of 25 days. Similar daily crustacean P/B ratios for the same time period have been observed in Clear Lake (P/B = 0.05), Lake 239 (P/B = 0.04), and Lake Naroch (P/B = 0.06) (Patalas 1970).

TABLE 15. Rotifer production-biomass (P/B) ratios for a vegetative period, which is assumed to be the "ice-free" period

	Source	P/B
Lake Krivoe	Alimov et al. 1972	8.2
Lake Krugloe	Alimov et al. 1972	14.0
Lake Naroch	Winberg et al. 1972	85.7
Lake Batorin	Winberg et al. 1972	62.3
Lake Myastro	Winberg et al. 1972	64.6
Mirror Lake	This study	26.3

The daily rotifer P/B ratios from May through September in Clear Lake and Lake 239 are 0.37 and 0.35, respectively. These values are considerably > the P/B ratio of 0.11 observed for Mirror Lake rotifers during the same time period. Similar differences in rotifer P/B ratios exist between many Russian lakes and between these lakes and Mirror Lake (Table 15).

Differences in the rotifer P/B ratios may be due to differences in rotifer species composition in these lakes. In the 3 lakes Winberg et al. (1972) investigated, *Asplanchna priodonta* represented >50% of the rotifer production. In Mirror Lake (Table 16), Lake Krivoe, and Lake Krugloe, lakes with lower rotifer P/B ratios, *A. priodonta* is only a minor constituent of the total zooplankton productivity.

In Clear Lake and Lake 239, *A. priodonta* is also a minor constituent of the total zooplankton productivity. However, the daily rotifer P/B ratios are still high relative to Mirror Lake. Production estimates not weighted for depth and volume of each strata in Clear Lake and Lake 239 may have caused these differences. The lower P/B values from the cold hypolimnion would tend to lower the higher ratios from the epilimnion.

TABLE 16. Production-biomass (P/B) ratios for the zooplankton community in various lakes during the vegetative period. Net phytoplankton production = g/C/m² per vegetative period

	Krugloe[a]	Krivoe[a]	Mirror	Naroch[b]	Myastro[b]	Batorin[b]
Primary Production	3.2	12	37	43	140	156
Zooplankton production / Zooplankton biomass	12.7	10.1	10.1	18.4	16.2	19.1

[a] Alimov et al. (1972).
[b] Winberg et al. (1972).

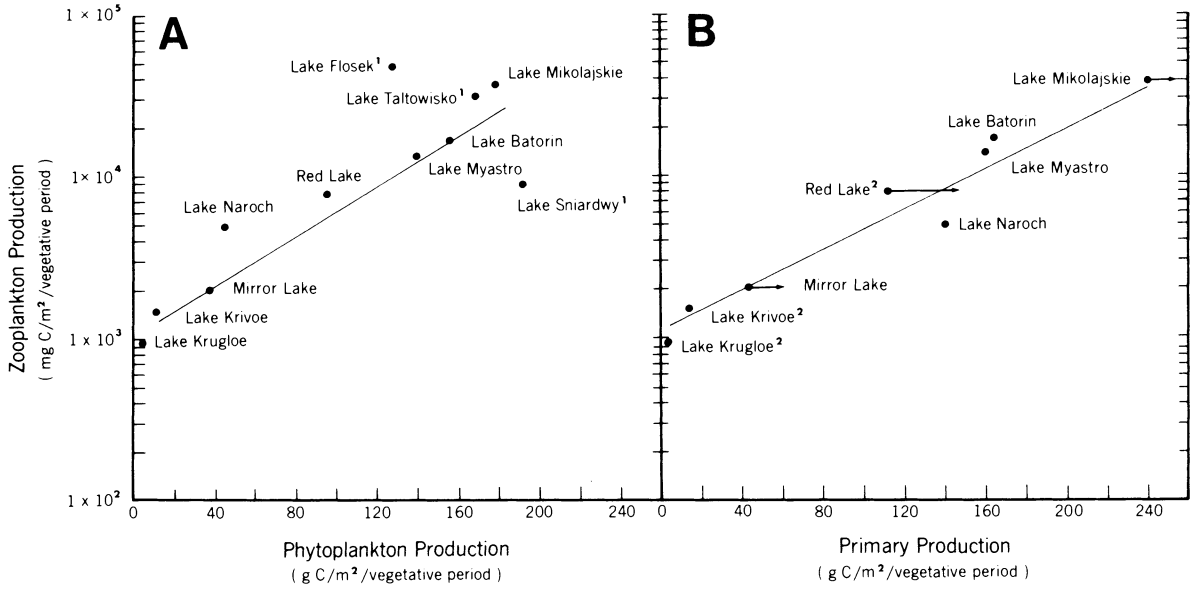

FIG. 15. Zooplankton production vs. (A) net phytoplankton production and (B) net primary production of phytoplankton, periphyton, and macrophytes in various lakes. Line in panel A is fitted by eye. In panel B, Y = antilog 3.032 + 0.0063 X, r = .88, n = 8. [1]Represents net phytoplankton production for the pelagic region. [2]Represents net phytoplankton plus macrophyte production only. Arrows indicate the amount of allochthonous inputs of reduced carbon.

There is a tendency for the zooplankton community P/B to increase with the productivity of the lake (Table 16; Patalas 1970). One would expect, with eutrophication, an increase in the availability of food to zooplankton. An increase in food should increase brood size and growth rate and decrease generation time. These factors, accompanied with the warmer temperatures generally expected in a eutrophic lake relative to an oligotrophic lake, should increase the turnover rate of the biomass, i.e., increase the P/B ratio.

However, the relationship presented is not a strong one. At least 2 factors may be the cause of it: quality of food and total food available. With eutrophication there is a tendency for blue-green algae to dominate lakes. Blue-greens are not readily assimilated by zooplankton (Porter 1977) and appear to increase zooplankton generation times (Makarewicz 1976). This would tend to lower P/B ratios.

Lake Naroch has a relatively high P/B ratio considering its low phytoplankton production. However, when macrophyte and periphyton production are considered, the total primary production of Lake Naroch is 3× the value given (Winberg 1972). Considering the total reduced C produced and potentially available to zooplankton through detritivore food chains, the P/B ratio for this lake becomes more reasonable.

Production and ecological efficiency.—Intuitively, we expect a direct relationship between phytoplankton net production and zooplankton production, but rarely are actual data available to show it. In Fig. 15a, we plot net phytoplankton production per vegetative period vs. zooplankton production for various lakes throughout the North Temperate Zone. A straight line appears to be a good fit to most of the points, with 3 exceptions. Lake Flosek and Lake Naroch have a higher zooplankton production, while Lake Sniardwy has a lower zooplankton production than would be expected on the basis of net phytoplankton production. However, Lake Flosek is dystrophic with probable high inputs of allochthonous organic material (Kajak et al. 1972, Hillbricht-Ilkowska et al. 1972), while in Lake Naroch, macrophytes and periphyton each produce organic C in amounts equivalent to the net phytoplankton production (Winberg et al. 1972). When the primary production of Lake Naroch is tripled, the point falls close to the line (Fig. 15a). Similarly, in Lake Flosek, a large input of organic material will move the point toward the line.

The slope of the line (Fig. 15a) suggests that ecological efficiency in these lakes (zooplankton production/net phytoplankton production) increases with eutrophy. This is not necessarily what would be expected. For example, blue-green algae often dominate the phytoplankton in eutrophic waters and they are not readily assimilated by herbivorous zooplankton (Porter 1977). Because of this inability to utilize a part of the phytoplankton production, a decrease in ecological efficiency might be expected.

However, with increasing eutrophy, there usually is a general increase in phytoplankton production or alternatively, an increase in production of macrophytes and periphyton. Also, there may be an increase in organic matter inputs (dissolved or particulate matter or both) from the drainage area. Each of these

TABLE 17. Standing crop matter, standing crop turnover rate, turnover time, and annual flux of phosphorus in the Cladocera, Copepoda, and Rotatoria. Values represent the mean for 3 yr

	Mean annual standing crop (mg P/m²)	Turnover rate (turnovers/yr)	Turnover time (days)	Annual phosphorus flux (Standing crop × turnover rate) (mg P/m²/yr)
Rotatoria	0.78	30.9	11.8	24.1 (33.4%)
Cladocera	1.80	19.3	18.9	34.7 (48.1%)
Copepoda	2.97	4.5	81.1	13.3 (18.5%)

TABLE 18. Percentage of production of Cladocera, Copepoda, and Rotatoria in various lakes

	Krivoe[a]	Krugloe[a]	Naroch[b]	Myastro[b]	Batorin[b]	239[c]	Mirror
Rotatoria	15.2	19.2	43.5	23.9	29.3	67.2	39.8
Cladocera	36.1	71.8	31.2	47.6	45.5	5.4	40.9
Copepoda	48.7	8.9	25.2	28.6	25.1	27.4	19.3

[a] Alimov et al. (1972).
[b] Winberg et al. (1972).
[c] Schindler (1972).

sources of reduced organic C represents potential food for zooplankton, either by direct ingestion or through detrital food webs. These additional sources of food may offset the development of relatively inedible blue-green algae in the plankton of eutrophic waters and may account for the apparently paradoxical condition of increased ecological efficiency with increasing phytoplankton production in eutrophic waters.

For example, Saunders (1969) has suggested that bacteria often dominate the planktonic biomass during a bloom of blue-green algae and, at such times, the bacteria provide a concentrated and important food source for zooplankton. Peterson and Hobbie (1978) have shown that *Daphnia* do utilize bacteria as a food source under natural conditions. Such other potential sources of food (e.g., macrophytes, periphyton, bacteria utilizing reduced C) for zooplankton are not included in the relationship shown in Fig. 15a and may account for the wide scattering of points. Consideration of macrophyte and periphyton production with phytoplankton production (Fig. 15b) strengthens the linear relationship between zooplankton and primary producers. This suggests that the ratio of zooplankton to net primary production does increase with increasing trophic status.

Actual energetic relationships between aquatic trophic levels are often obscured because all of the potential food sources are not considered or evaluated according to availability and quality. Various workers have shown that phytoplankton productivity may not adequately reflect the metabolic status of an aquatic ecosystem (cf. Likens 1972). From an ecosystem point of view, the total amount of reduced C available to the ecosystem from all autochthonous and allochthonous sources must be considered. This C has been termed Ecosystem Source Carbon (Likens 1972). Likewise, the total amount of reduced C available to a trophic level should be considered in determining the ecological efficiency of that trophic level. Because of complexities and "reuse" of C in detritivore food webs, it is usually very difficult to quantitatively determine ecological efficiency under field conditions. At a minimum, we propose that the concept of ecological efficiency include both autochthonous and allochthonous inputs of reduced C, i.e., ecological efficiency = zooplankton production/Ecosystem Source Carbon.

Importance of the Rotatoria.—From the Mirror Lake data, it is clear that rotifers can assume a major role in intra-system nutrient cycling and transfer of energy within the lake ecosystem (Tables 14 and 17). Of the total amount of P incorporated into organic matter by the zooplankton community each year, 33.4% is found in rotifer tissue. However, not only is a relatively large amount of P incorporated into rotifer tissue each year, but the turnover rate of P within this group is high (mean turnover time of 11.8 days). The reason for the high turnover rate is the short generation time of rotifers as compared to cladocerans and copepods. It is evident that rotifers with their fragile, easily decomposed body tissue are incorporating P as organic matter, dying, and releasing P at a faster rate than the crustacean population.

It is commonly thought the rotifers are relatively unimportant in lakes (Brooks 1969, Porter 1977) and that copepods often dominate oligotrophic lakes such as Mirror Lake. In fact, copepods do comprise ≈55% (3-yr average) of the total zooplankton biomass. However, the copepods, with their slow growth over an entire year, represent only ≈19% of the zooplankton production, while rotifers account for ≈40% of the zooplankton production annually in Mirror Lake.

The high production rates of rotifers in Mirror Lake (as compared to other North American lakes studied) are due to high turnover rates of rotifers as compared to the crustaceans and to the relatively high biomass of rotifers. The high biomass value in Mirror Lake is due to the use of sampling equipment with fine mesh nets (48 μm or less). Any sampling scheme not employing nets as fine as 48-μm mesh is of doubtful value as a quantitative measure of rotifer density and thus, zooplankton biomass and production in aquatic ecosystems.

Rotifers play a major role in energy transfer in many lakes of the world (Table 18). Because these lakes range in trophic status from extreme oligotrophy (Krugloe) to eutrophy (Batorin), the important role of rotifers in lake metabolism may be a much more common phenomenon than previously thought.

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