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Protozoan abundances in the plankton of two tropical lakes

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With 2 figures and 1 table in the text

Abstract

Quantitative counts were made of protozoans in the euphotic zone of Lake Valencia, Venezuela, over a two-year interval and in Lake Lanao, Philippines, over a one-year interval. In Lake Lanao, the annual average abundance of protozoans was 1900 individuals per cc, corresponding to 260,000 μ^3/cc. Over 75 % of individuals and of biomass was accounted for by very small flagellates. Large flagellates, ciliates, and amoeboid forms accounted for the remainder of the protozoans in Lake Lanao. In Lake Valencia, the average protozoan abundance was 350 individuals per cc, corresponding to 109,000 μ^3/cc. Ciliates and amoeboid forms dominated in Lake Valencia. Comparison of protozoan biomass with the known phytoplankton turnover rates in the two lakes indicates that protozoans cannot be an important source of phytoplankton mortality. Protozoans may have important effects on bacterial populations in Lake Lanao, but these effects seem less likely in Lake Valencia.

Introduction

A number of authors have recently pointed out that protozoans have been inadequately studied by comparison with other planktonic organisms (e. g., Hutchinson 1967; Canter & Lund 1968; Porter et al. 1979; Pace & Orcutt 1981; Beaver & Crisman 1982). Both zooplankton specialists and phytoplankton specialists have consistently considered protozoans to be outside their fields of interest. Furthermore, the zooplankton specialists, who would most logically study these small heterotrophs, typically rely on net samples and, since protozoans pass through nets, have thus not been able to quantify protozoan abundances. Phytoplankton samples are quantitatively suitable for protozoan counting, but phytoplankton specialists typically only deal with the autotrophs and thus typically do not record the microheterotrophs. The result is that the literature gives a very poor idea of the overall quantitative importance of protozoans in various kinds of lakes.

Although the general data base on protozoan abundances in plankton environments is poor, a number of recent studies have included quantitative treatments of protozoans. For example, the comprehensive temperate-zone studies by Nauwerck (1963), Rigler et al. (1974), and Pace & Orcutt (1981) provide quantitative information on protozoan abundances in selected lakes.

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BEAVER & CRISMAN (1982), in one of the most comprehensive quantitative studies to date, provide information on protozoan abundances on an annual basis in 20 different Florida lakes. HECKY & KLING (1981) have published quantitative estimates of protozoan abundances in Lake Tanganyika. The purpose of the present work is to contribute to this small but growing list of recent quantitative estimates of protozoan abundances. Data reported here are for Lake Lanao, Philippines, and Lake Valencia, Venezuela.

Study site and methods

Lake Lanao is located at 8° N in the southern Philippines. The general properties of the lake are given by LEWIS (1979) and the references cited therein. The lake is warm monomictic; it has a predictable mixing season beginning in December and lasting through March. Over the rest of the year, the lake is stratified, although the thickness of the upper mixed layer varies much more than it would in a temperate lake. The lake is highly productive (LEWIS 1974). Annual average standing stock of phytoplankton is about $1.6 \times 10^6 \mu^3$/cc in the euphotic zone (LEWIS 1978). The zooplankton community contains significant numbers of calanoid copepods, cyclopoid copepods, cladocerans, and rotifers. In the early part of the mixing season, phytoplankton biomass and productivity are suppressed by light deprivation caused by deep mixing. During the stratification season, phytoplankton biomass can be depressed by nutrient deprivation. Phytoplankton biomass is divided among the blue-greens and diatoms as dominants and secondarily among the greens, cryptophytes, and dinoflagellates.

Lake Valencia, which is located at 10° N latitude near the Caribbean Sea in Venezuela, is also a warm monomictic lake (LEWIS 1983). The mixing season for Lake Valencia falls between December and February or March; the lake is stratified the rest of the year. In Lake Valencia, phytoplankton and zooplankton biomass are not always depressed by seasonal mixing, as in Lake Lanao. Because of artificial enrichment, Lake Valencia supports a higher average phytoplankton standing stock than Lake Lanao (a mean of $19 \times 10^6 \mu m^3$/cc for 1977—78: LEWIS 1985). Blue-green algae dominate the phytoplankton biomass in Lake Valencia, although occasionally diatoms and selected other taxa make a quantitatively significant appearance. The zooplankton composition is similar to that of Lake Lanao.

The data to be presented here for Lake Lanao were taken between July 1970 and July 1971. The data for Lake Valencia are based on the interval January 1977 through December 1978. For both lakes, the samples were taken at weekly intervals. For Lake Lanao, an integrated sample was taken of the upper 15 m by means of a tube. The samples were preserved in the field with Lugol's solution and counted quantitatively at high magnification by the inverted microscope method (UTERMÖHL 1958). Replicate counts were made of samples from two separate stations. Studies of both the phytoplankton and the zooplankton have shown that between-station variation is minor by comparison with temporal variation (LEWIS 1979), so only the mean protozoan abundances from all replicates at the two stations will be presented here. Since high magnification was used (1400×), even the smallest flagellates could be counted quantitatively.

Lake Valencia samples were also collected in replicate at a midlake station. Integrated samples over 5-meter increments of the water column were taken from the top of the lake to the bottom. In order to make the numbers comparable to those presented for Lake Lanao, the average counts for the upper 15 meters are reported here.

No attempt was made to identify the protozoans in Lake Lanao or in Lake Valencia. However, the organisms were placed into categories as they were counted (flagellates, ciliates, amoeboid).

Results

Table 1 summarizes the mean abundances of protozoans in Lake Lanao and Lake Valencia. In Lake Lanao, the most abundant protozoans were of the small flagellate category. Many of these had a body length in the vicinity of 5 μm and were similar in appearance to the genus *Bodo*. Large flagellates were also present; these had body lengths in the vicinity of 20 μm. Ciliates and amoeboid forms, whose longest dimension was typically in the vicinity of 20 μm, were even less abundant.

In Lake Valencia, the small flagellates were not nearly so important as they were in Lake Lanao. Large flagellates were also present in minor amounts. Ciliates were the most abundant, particularly in terms of biomass. Amoeboid forms were steadily abundant and, although less important than the ciliates, accounted for a significant proportion of total individuals.

Table 1. Average standing stock of protozans in Lake Lanao (1970–71) and Lake Valencia (1977–78).

	Number		Volume	
	indiv. per cc	%	μm^3/cc	%
Lake Lanao				
Small Flagellates	1763	92	212,000	81
Large Flagellates	120	6	40,000	15
Ciliates & Amoeboid Forms	28	2	9,000	4
Total Protozoa	1912	100	261,000	100
Lake Valencia				
Small Flagellates	18	5	2,000	2
Large Flagellates	4	1	2,000	2
Ciliates	218	62	98,000	90
Amoeboid Forms	111	32	7,000	6
Total Protozoa	351	100	109,000	100

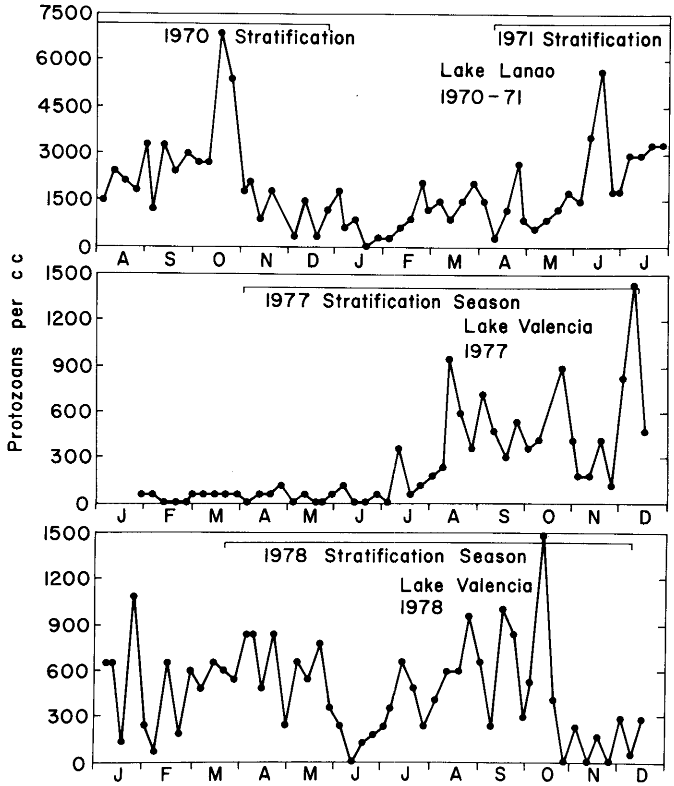

Fig. 1. Abundance patterns of protozoans in the euphotic zone of Lake Lanao and Lake Valencia.

Contrary to intuition, the protozoan standing stock of Lake Lanao was considerably greater than that of Lake Valencia, despite the much higher standing stock of algae in Lake Valencia.

Fig. 1 shows the variations in total numbers of individuals in both Lake Lanao and Lake Valencia. Regular patterns of abundance are not really evident in either of the lakes. In Lake Lanao, protozoan abundance was suppressed in the period of most intense mixing, as were phytoplankton and zooplankton abundances. However, major variations in abundance also occurred during the stratification season. There is no obvious explanation for the low abundance of protozoans in Lake Valencia for the first half of 1977. Ciliates appeared in greater numbers after June of 1977, which is a proximate explanation for the change, but the reason for the increase in ciliate abundance is unknown. In neither lake did the protozoan abundance show a clear correlation to phytoplankton biomass or phytoplankton composition.

Discussion

Protozoans can be important in the plankton in at least two ways: (1) they may consume significant quantities of phytoplankton, or (2) they may consume significant quantities of bacteria and thus constitute a link between the bacteria and the macrozooplankton (PORTER et al. 1979).

In general, it appears that protozoans are only likely to have a quantitative effect on phytoplankton mortality in oligotrophic lakes. The studies by RIGLER et al. (1974) of Char Lake and HECKY & KLING (1981) of Lake Tanganyika both show surprisingly high proportions of total heterotroph biomass in the protozoan category. Any tendency toward herbivory among the protozoans of these lakes could thus directly affect phytoplankton populations. On the other hand, protozoan populations in more productive lakes, although probably higher in absolute terms than those in oligotrophic lakes, seem less likely to be important in relation to other sources of mortality (e.g., NAUWERCK 1963; BEAVER & CRISMAN 1982).

The data on Lakes Lanao and Valencia reinforce the impression that protozoans are not likely to be important sources of phytoplankton mortality in productive lakes. Exact calculations are very difficult to make because the feeding habits of the protozoans are unknown. In all likelihood, the smaller size classes are bacterial feeders (FENCHEL 1980). Some taxa of larger protozoans may feed steadily on phytoplankton, however. In both Lake Lanao and Lake Valencia, direct evidence of phytoplankton feeding, which would have been evident at high magnification for taxa feeding steadily on phytoplankton, was

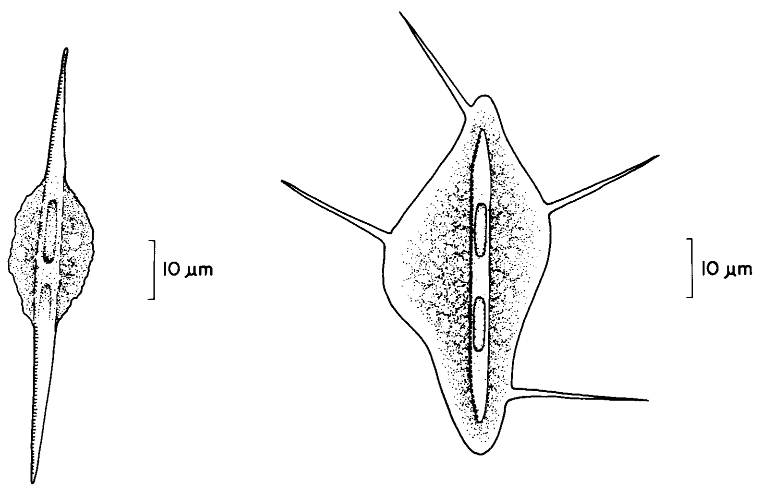

Fig. 2. Evidence of predation on diatoms by amoeboid protozoans as seen through the light microscope.

only seen in the amoeboid forms. In both Lake Valencia and Lake Lanao, amoeboid forms consumed diatoms even in instances where the size of the protozoan was considerably less than that of its food (Fig. 2). In neither lake, however, was there evidence that more than a few percent per day of the diatoms were ever consumed by protozoans.

An upper bound for the significance of phytoplankton feeding can be obtained by some approximations. FENCHEL (1980) estimates that the larger protozoans, which are most likely to feed on phytoplankton, have a ration of 10 to 30% per hour, or roughly 5 times body weight per day. Applying this ration to the large flagellates, ciliates, and amoeboid forms in Lake Lanao, one would estimate the upper bound of average phytoplankton consumption to be roughly 250,000 μ^3/cc/day, or about 15% per day of the average phytoplankton standing stock. This allowance is almost certainly too liberal insofar as it assumes that the large protozoans are entirely herbivorous, whereas there is every reason to suspect that bacteria and detritus make up a large proportion of their foods. Even so, given the rapid turnover of phytoplankton biomass in Lake Lanao, protozoans would not be the major cause of mortality.

A similar calculation applied to Lake Valencia produces qualitatively similar results. The standing stock of large protozoans in Lake Valencia is about double that seen in Lake Lanao. However, the phytoplankton standing stock is considerably higher, so the potential phytoplankton consumption is only a few percent of the average standing stock per day.

In light of the apparently low ratio of protozoan food consumption to phytoplankton turnover in these two lakes, protozoans may actually the more important in relation to bacteria and detritus than in relation to phytoplankton. With respect to bacteria, even approximate calculations are impossible because of the great uncertainties surrounding bacterial biomass turnover. In Lake Valencia, where the bacterial populations may exceed 10^6 cells per cc according to counts made by epifluorescence microscopy, the relatively low standing stocks of protozoans seem unlikely to be very influential. In Lake Lanao, which has substantial populations of very small heterotrophic flagellates, the situation may be different.

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Zusammenfassung

Quantitative Zählungen der Protozonen wurden zwei Jahre lang im Valenciasee, Venezuela, und eine Jahresperiode im Lanaosee, Philippinen durchgeführt. Im Lanaosee betrug die jährliche Protozoen-Durchschnittsmenge 1900 Einzelzellen pro cc, oder 260000 μ^3/cc. Über 75% der Einzelzellen und der Biomasse bestand aus sehr kleinen

Flagellaten. Große Flagellaten, Ciliaten und Amöbenformen stellen den Rest der Lanaosee-Protozoen dar. Im Valenciasee betrug die jährliche Protozoendurchschnittsmenge 350 Einzelzellen pro cc oder 109 000 μ^3/cc. Im Valenciasee waren Ciliaten und Amöbenformen überwiegend. Ein Vergleich der Protozoenbiomasse mit den bekannten Erneuerungsraten von Phytoplankton in den zwei Seen deutet darauf hin, daß Protozoen keine wichtige Ursache der Phytoplankton-Sterblichkeit darstellen können. Es mag sein, daß Protozoen die Bakterienpopulationen im Lanaosee beträchtlich beeinflussen. Im Valenciasee scheint das aber weniger wahrscheinlich.

References

BEAVER, J. E. & CRISMAN, T. L. (1982): The trophic response of ciliated protozoans in freshwater lakes. — Limnol. Oceanogr. **27:** 246—253.

CANTER, H. M. & LUND, J. W. G. (1968): The importance of protozoa in controlling the abundance of plankton algae in lakes. — Proc. Linn. Soc. London **179:** 203—219.

FENCHEL, T. (1980): Suspension feeding in ciliated protozoa: functional response and particle size selection. Feeding rates and their ecological significance. — Microbial Ecology **6:** 1—11, 13—25.

HECKEY, R. E. & KLING, J. (1981): The phytoplankton and protozoan plankton of the euphotic zone of Lake Tanganyika. — Limnol. Oceanogr. **26:** 548—564.

HUTCHINSON, G. E. (1967): A Treatise on Limnology. Vol. **II,** Introduction to Lake Biology and the Limnoplankton. — Wiley, New York. 1—1115.

LEWIS, W. M., Jr. (1974): Primary production in the plankton community of a tropical lake (Lake Lanao, Philippines). — Ecol. Monogr. **44:** 377—409.

— (1978): A compositional, phytogeographical, and elementary structural analysis of the phytoplankton in a tropical lake. — J. Ecol. **66:** 213—226.

— (1979): Zooplankton Community Analysis. — Springer, New York. 1—163.

— (1984): A five-year record of the thermal and mixing properties of a tropical lake (Lake Valencia, Venezuela). — Arch. Hydrobiol. **99:** 340—346.

— (1985): Phytoplankton succession in Lake Valencia, Venezuela. — In: Seasonality of Freshwater Phytoplankton. J. TALLING and M. MUNAWAR, Eds. Junk, The Hague. (in press).

PACE, N. L. & ORCUTT, J. P., Jr. (1981): The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. — Limnol. Oceanogr. **26:** 822—830.

PORTER, K. G., PACE, N. L. & BATTEY, J. F. (1979): Ciliate protozoans as links in freshwater planktonic food chains. — Nature **277:** 563—565.

RIGLER, F. H., MACCALLUM, N. E. & ROFF, J. C. (1974): Production of zooplankton in Char Lake. — J. Fish. Res. Bd. Canada. **31:** 637—646.

UTERMÖHL, H. (1958): Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. — Internat. Verein. Theor. Angew. Limnol. Mitt. **9:** 1—38.

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