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Plankton dynamics in a high mountain lake (Las Yeguas, Sierra Nevada, Spain). Indirect evidence of ciliates as food source for zooplankton

L. Cruz-Pizarro[1], I. Reche[2] & P. Carrillo[2]
[1] *Instituto de Agua, Universidad de Granada, 18071 Granada, Spain;* [2] *Departamento Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, 18071, Granada, Spain*

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Abstract

A detailed sampling programme during the ice-free season (July–September) in the oligotrophic lake Las Yeguas (Southern Spain) has shown a well-defined time lag between phytoplankton and zooplankton maximum standing stocks, the former displaying a peak (23 μgC l^{-1}) just after the ice-melting, and the latter by the end of September (80 μgC l^{-1}).

A ratio of autotrophs to heterotrophs lower than 1 which lasted more than two thirds of the study period may suggest a high algal productivity per unit of biomass. The estimated strong top-down regulation of phytoplankton by zooplankton indicates an efficient utilization of resources.

A comparative analysis between the available food supply and the critical food concentration that is necessary to maintain the population of *Daphnia pulicaria* (which constitutes up to 98% of the heterotrophic biomass) proves this species to be food-limited in the lake under study.

To explain the dominance (and development) of such large-bodied cladoceran population, we discuss the possibility of the utilization of naked protozoan ciliates (Oligotrichidae) as a complementary high quality food source, and the exploitation of benthic resources through a coupled daily migration behaviour.

Introduction

Oligotrophy promotes the existence of small sized phytoplankton species with high metabolic rates (Reynolds, 1984; Rott, 1988; Psenner & Zapf, 1990). At the same time it promotes large-bodied zooplankton with low metabolic rates per unit weight (Taylor, 1984). This results, among others, in a simplification of the planktonic community which makes such systems suitable to study complex interactions (Neill, 1988).

The activity of the microbial components in the recycling of nutrients in the euphotic zone of these nutrient-limited ecosystems is likely to be crucial for support of the growth and production of all components in the pelagic community (Axler *et al.*, 1981; Scavia & Laird, 1987; Stockner & Porter, 1988).

In this sense, bacterivory of ciliates that can bypass at least one step in the bacteria to flagellate to ciliate microbial loop (Azam *et al.*, 1983), has been considered very important in providing the feedback of nutrients and making a substantial proportion of the bacterial production available to higher order consumers (Sherr & Sherr, 1987).

In this paper we describe the seasonal variations in the structure of the planktonic community in an oligotrophic high mountain lake and discuss the role of ciliates as a link, moving picoand nanoplankton carbon to macrozooplankton, thus allowing the maintenance of a high heterotrophic biomass dominated by large cladocerans.

The possibility of a diel feeding rhythm coupled with the vertical migration of the zooplankton (Lampert & Taylor, 1985) is also considered.

Study site

Las Yeguas is a small (2530 m^2) and shallow (maximun depth: 8 m) oligotrophic lake (chlorophyll concentration range: 0.6–1.76 $\mu g\ l^{-1}$, TP under 30 $\mu g\, l^{-1}$ and high transparency) located at 2800 m in the Sierra Nevada (Southern Spain).

In the early sixties a dam was built to use the lake as a drinking water supply reservoir for a nearby ski station and despite this it failed in increasing the water storage because of some leakage problems, which was presumably responsible for a change in the water quality and phytoplankton composition (Sanchez-Castillo *et al.*, 1989). In fact, Reche (1991) has detected alkalinity values close to 1 meq l^{-1}, far from the range of concentrations measured for the whole Sierra Nevada lakes (between 50 and 400 μeq l^{-1}: Morales-Baquero *et al.* 1992).

Biological communities are rather simple. *D. pulicaria* dominates, in terms of biomass in the zooplankton, whereas the population of *Mixodiaptomus laciniatus* is poorly represented, in contrast with its specific dominant status in more than 70% of the lakes in the Sierra Nevada. Green algae, particularly *Chlorella*, *Oocystis*, *Chlamydomonas* and *Chlorogonium* species all account for about 40–70% of the autotrophic biomass. There are no fish.

Materials and methods

The plankton samples were taken at 2 m intervals from surface to bottom with a double Van Dorn bottle (8 litres each) at a deep central station ($z = 8$ m). Samples were taken twice a week, during the ice-free period of 1986.

A 100 ml subsample from the water bottle was preserved with acid Lugol's solution for the analysis of phytoplankton and protozoans. 50 ml subsamples were sedimented for 48 hours in a 2.6 cm diameter compound chamber, and cells counted in 100 randomly selected fields of view at a magnification of 1000 × under an inverted microscope as Sandgren & Robinson (1984) recommend.

For every sample 20 cells of each species were measured to estimate cell volume from the appropriate geometric shape. Biovolume ($\mu m^3\ ml^{-1}$) for each individual taxon was thus determinated by multiplying mean cell volume by cell population density (Vanni, 1987). To get biomass (wet weight) values, a specific gravity of 1 for the phytoplankton, and 1.025 for ciliates (Sorokin & Paveljeva, 1972), was assumed.

The carbon content of the phytoplankton community was estimated using the equations of Strathmann (1967), that from Smetacek (1975) for armoured dinoflagellates, and that proposed by Sorokin & Paveljeva (1972) for the ciliates.

The abundance of zooplankton was obtained by sieving 8 l of water through a 45 μm mesh size net; zooplankton was immediately preserved in 4% formaldehyde. Counting for whole samples was done under an inverted microscope at 150 × magnification.

Zooplankton biomass was estimated using length-weight regressions, following Dumont *et al* (1975) and Botrell *et al.* (1976) and then expressed in terms of carbon using the conversion factors proposed by Lampert (1984).

For calculating whether or not food availability was limiting to zooplankton growth, we have followed the method provided by Huntley & Boyd (1984) who suggest that below some critical particulate carbon concentration (C_c:$\mu gC\ l^{-1}$) food would be insufficient to support the predicted maximum growth rate of zooplankton not limited by food availability.

Results

As observed in most of similarly nutrient limited systems, the period just after the ice-melting is characterized by a peak in the phytoplankton biomass (Carrillo, 1989; Carrillo *et al.*, 1990) promoted by both improvements in the physical (increased irradiation) and chemical (readily available nutrients accumulated on the snow during the winter) conditions (Barica & Armstrong, 1971; Larson, 1973).

During the ice-free period the evolution of the algal abundance and biomass depict a well defined pattern, showing a gradual and sustained decrease of such parameters from 11 000 cell ml^{-1} and 23 μgC l^{-1} down to values close to 50 cell ml^{-1} and 0.8 μgC l^{-1} respectively (Fig. 1)

The autotrophic community was dominated at the early stages of the study period by small, non-motile cells belonging to the genus *Chlorella* (2–4 μm) and *Oocystis* (6–8 μm) which contributed between 78 and 90% to the photosynthetic biomass (Fig. 2).

Flagellates were present throughout the entire period and showed little variations both in density and in biomass, although at the end of the summer they accounted for more than 90% of carbon available for zooplankton (Fig. 1). In this sense, Fig. 2 shows a more realistic image, since it demonstrates that flagellates did not contribute significantly to the plankton biomass.

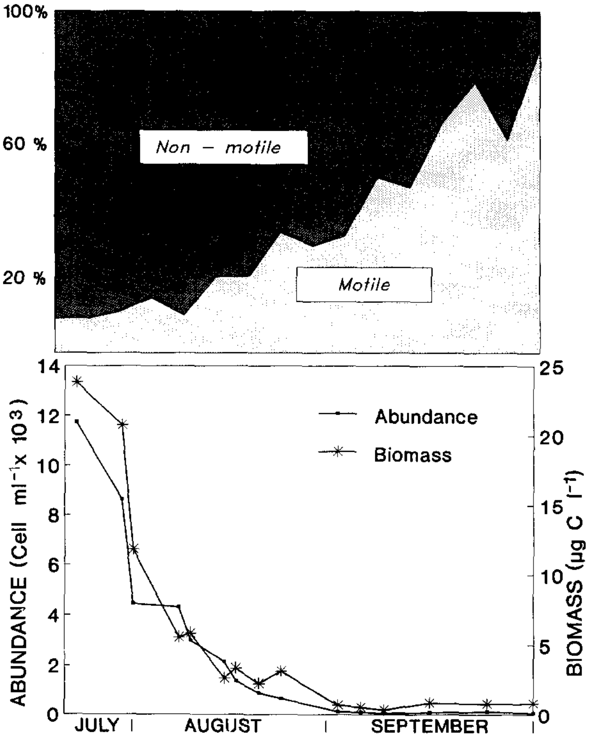

Fig. 1. Evolution of the contribution by motile and non-motile algal fraction to the autotrophic carbon content (top) and of the phytoplankton abundance and biomass (down) in the study period.

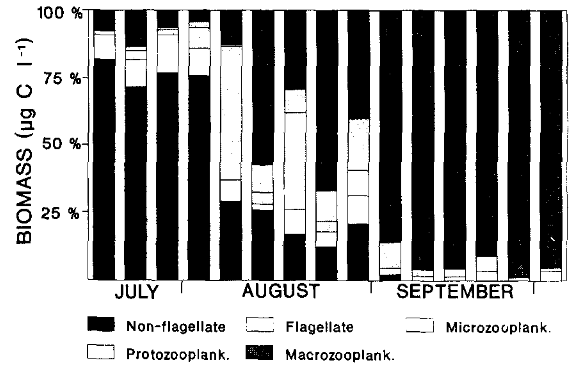

Fig. 2. Relative contribution of the different functional and size groups to the total biomass.

The development of the zooplankton biomass basically performed a reversed pattern to that described by algae, rising to the maximum values (80 μgC l^{-1}) by the end of September (Fig. 3a).

A detailed analysis of the heterotrophic community allows to establish a clear seasonal succession for the different groups involved. In the first period, and for about two to three weeks, rotifer populations (*Hexarthra bulgarica* and *Euchlanis dilatata*) did develop, reaching biomass values up to 8 μgC l^{-1}, just coinciding with the greatest decrease of the algal populations (Figs 3b and 1).

A second stage was dominated by the protozooplankton, mainly small (10–25 μm) naked oligotrichidae ciliates, at cellular densities (2–10 cell ml^{-1}) within the range usually found in similar oligotrophic environments (Gates & Lewg, 1984; Carrick & Fahnenstiel, 1990), which in terms of carbon (up to 7 μgC l^{-1}) represent an important contribution to the actual biomass.

Finally, during September, the heterotrophic community was largely dominated by the macrozooplankton, increasing in biomass throughout the ice-free period from 1 μgC l^{-1} in July to 79 μgC l^{-1} at the end of September, thus resem-

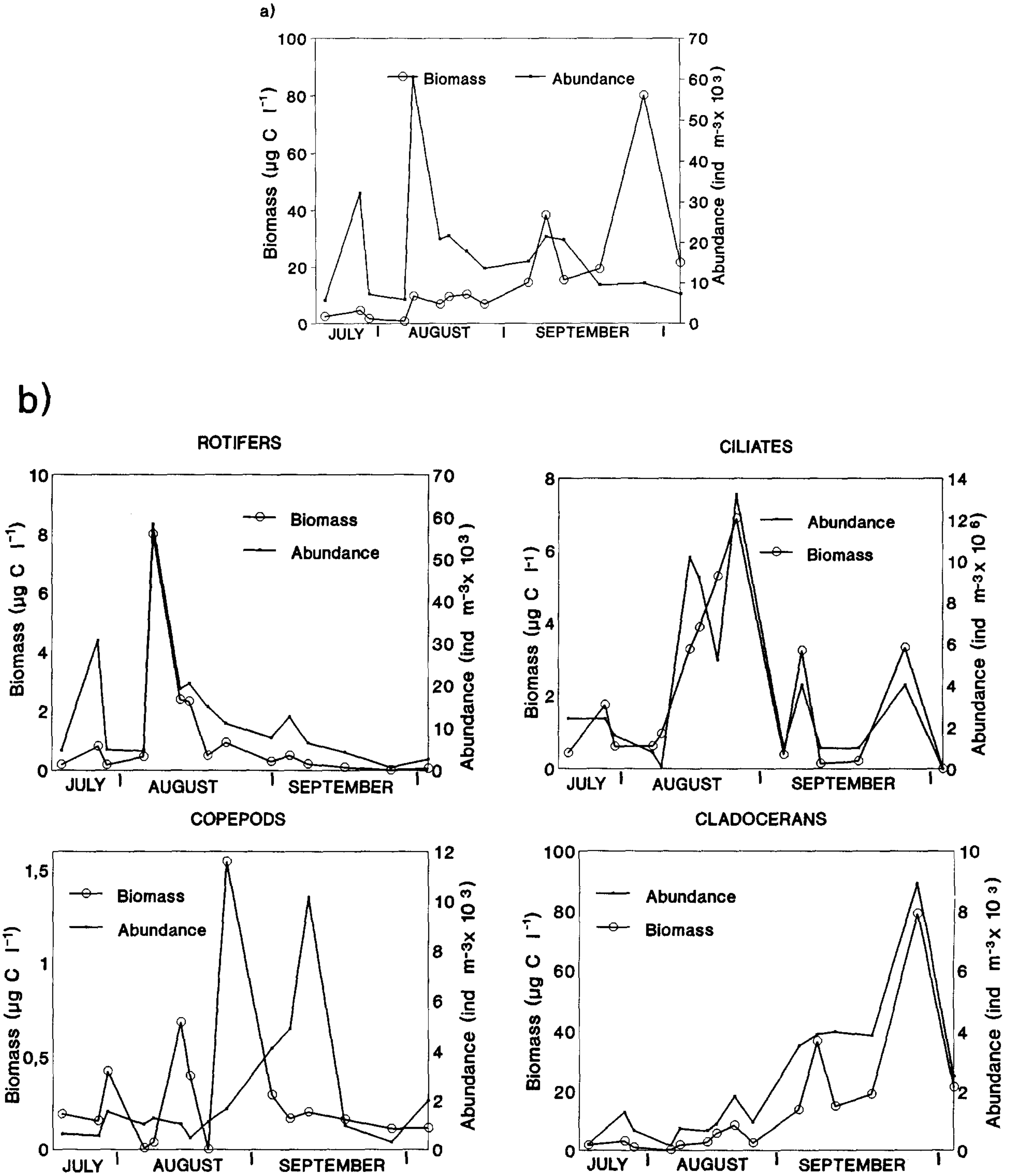

Fig. 3. Changes in the total zooplankton biomass and abundance (microzooplankton + macrozooplankton) (a), and of the different taxonomic groups (b) during the ice-free period.

bling the pattern described for the whole zooplanktonic assemblage.

This fraction, comprised in more than 90% by great sized cladocerans (*D. pulicaria*) accounted, during the study period, for between 5 and 90% of the particulate pelagic carbon (Fig. 2) and between 18 and almost 98% if only the zooplankton community is taken into account.

The only two copepod species in the lake (*Mixodiaptomus laciniatus, Eucyclops serrulatus*) are poorly represented. In fact, the former one, which dominates the zooplankton biomass during most of the ice-free period in other Sierra Nevada lakes (Carrillo, 1989) never surpassed 10% of the heterotrophic biomass in lake Las Yeguas.

Discussion

The analysis of the changes in biomass and in the trophic structure of the pelagic community during the investigation period has shown that for more than two-thirds of this time the autotrophs: heterotrophs ratio was lower than 1 (see for instance Figs 1 and 3a). This is indicative of a phytoplankton assemblage with relatively low standing stock and high turnover rates (Stegmann & Peinert, 1984), but to explain the rather high increase in the carbon content (three and fourfold) between both trophic levels, a high zooplankton efficiency should be addressed.

In fact, the zooplankton biomass (independent var.) *vs* phytoplankton biomass (dependent var.) regression analysis, shows a reverse and highly significant relationships between both variables (Fig. 4), suggesting a control of the algal biomass by the zooplankton, i.e. a top-down mechanism seems to be the main factor responsible for the primary producers regulation. These results agree with those predicted for oligotrophic systems (McQueen *et al.*, 1986) and for environments dominated by large cladocerans (McQueen *et al.*, 1989).

Even accepting such high phytoplankton turnover and zooplankton efficiency rates it is still difficult to approve that the development of *Daphnia pulicaria*, a species with high food requirements (Kasprzak *et al.* 1986), may only be maintained by such scarce resources.

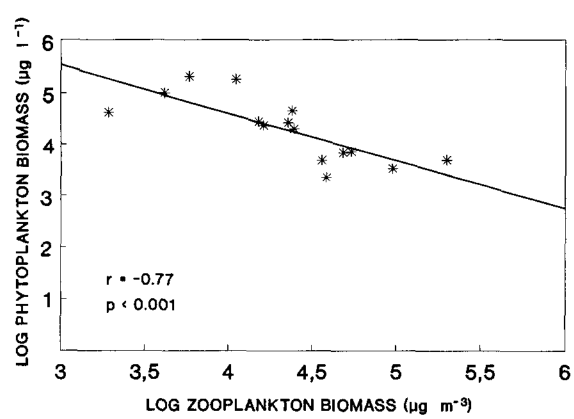

Fig. 4. Regression of phytoplankton biomass on zooplankton biomass (log-log).

In Fig. 5 we have compared the calculated critical food concentration required for this species (while considering an exclusive herbivorous behaviour) and the food amount available from the autotrophic fraction. According to our data, *D. pulicaria* should be food limited except for the time immediately after thaw.

Ciliated protozoans have been considered as an important link in aquatic systems by feeding on size particles not efficiently grazed by large zooplankton and serving, in turn, as readily as-

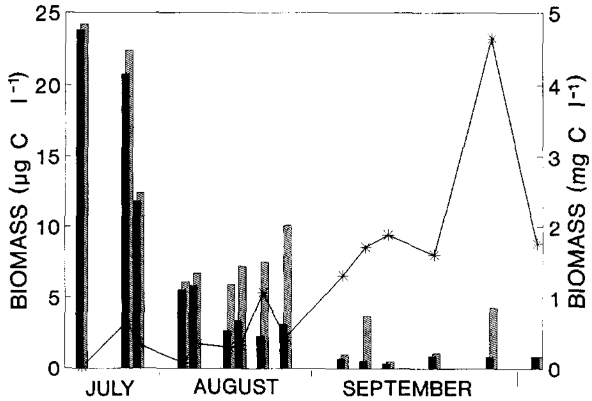

Fig. 5. Critical food concentration estimated for Daphnia pulicaria (mg C l^{-1}, solid line) and available food quantity (μg C l^{-1}, black bars: algae, striped bars: algae + ciliates) during the study period.

similated prey for such grazers (Porter *et al.*, 1979; Beaver & Crisman, 1982).

In lake Las Yeguas the protozoan contribution to the available carbon source for consumers was highest in the second half of August. Even then it did not exceed 70% (between 3 and 7 μgC l^{-1}), very far from the estimated critical food concentration for *D. pulicaria* (between 0.43 and 1.1 mgC l^{-1}) in the same period (Fig. 5).

The importance of protozoans as prey, however, may be seen in their high nutritional value: high energy and protein content (Stoecker & Capuzzo, 1990; DeBiase *et al.*, 1990; Gifford, 1991).

D. pulicaria is probably the only large macrozooplankter in the lake that can effectively utilize all components of the microbial communities ranging in size from 1–50 μm (Stockner & Porter, 1988), thus being able to outcompete calanoids which, in such oligotrophic lakes, cannot effectively graze on picoplankton or very small nanoplankton particles (Scavia & Laird, 1987). In this respect, the lack of ability of cladocerans species to use taste to discriminate food quality should also be considered (DeMott,1986).

In contrast, the high transparency of the water and the shallowness of the lake allow the development of an important epipelic community consisting of Diatoms, Euglenophyceae together with some Zygnematales species which have represented up to 4.6 mgC l^{-1} in samples taken close to the maximum depth of the lake, after disturbing the bottom (Reche, in prep.). This extremely high food reservoir might be available for *Daphnia* as Echevarria *et al.*(1990) suggest, through a coupled diurnal feeding rhythm and a vertical migration, widely described for this species in a rather similar ecosystem (Cruz-Pizarro, 1978; 1981; Carrillo *et al.*, 1991).

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