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Phytoplankton responses to experimental enhancement of grazing pressure and nutrient recycling in a small Andean lake

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SUMMARY

1. Three series of field experiments with different zooplankton species composition and biomass were performed in a small lake in the south Andes. We attempted to measure the responses of phytoplankton species resulting from grazing mortality and stimulation of growth by nutrient recycling.
2. Nanoflagellates contributed substantially to total phytoplankton cell abundance. *Chrysochromulina parva* represented 93.4%, 92.2% and 95.9% of total phytoplankton density in December, January and February, respectively. This fraction was reduced in all treatments with increasing zooplankton biomass.
3. A negative relationship was obtained between *C. parva* cell numbers and increase in dissolved P. On the other hand, a significant positive relationship between the abundance of the diatom *Aulacoseira granulata* and P concentration was observed. These results indicate that the ungrazed diatom was able to capitalise on the increase in nutrient availability.
4. As a net result of the increase or decrease of algal species we observed a change in the nano:net phytoplankton relationship. The outcome of three-day incubations with increased zooplankton biomass was an increasing importance of net phytoplankton.
5. The results indicate the importance of the indirect effects of zooplankton (through nutrient recycling) in the increase in diatoms, and the role of grazing as a growth-limiting factor for the flagellate *C. parva*.

Introduction

Phytoplankton–zooplankton interactions involve two contrasting processes working simultaneously. Zooplankton consume phytoplankton and thus influence algal populations directly by increasing loss rate (Porter, 1977). However, at the same time, algal growth is stimulated by the regeneration of the limiting nutrients, phosphorus and nitrogen (Lehman, 1980; Urabe, 1993, 1995; Carrillo *et al*., 1995). within the pelagic ecosystem, therefore, the net result of this interaction is a balance between consumption and stimulation.

Zooplankton grazing usually results in a decrease in phytoplankton biomass. However, due to selective feeding by zooplankton (Burns, 1968; Gliwicz, 1969; Porter, 1977; DeMott, 1990), algal species differ in the extent to which they suffer ingestion loss. This reduction of algal density or biomass increases the *per capita* availability of nutrients for other algae (Sterner, 1990).

Zooplankton nutrient release, mainly as soluble forms of N and P, constitutes a substantial proportion of the nutrient required for phytoplankton growth (Lehman, 1980; Urabe, Nakanishi & Kawabata, 1995). These nutrients are released according to the relative elemental contents of the food and grazer tissues (Hessen & Andersen, 1992; Urabe, 1993; Urabe *et al*.,

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1995); thus, zooplankton can alter the nutrient availability for phytoplankton growth.

The importance of the zooplankton regenerating effect is increasingly recognised in relation to the trophic status of the system (Axler, Redfield & Goldman, 1981; McQueen, Post & Mills, 1986; Carrillo, Reche & Cruz-Pizarro, 1996). Rates of turnover of N and P are faster in oligotrophic than in eutrophic waters as the nutrient pool sizes are smaller, and thus oligotrophic waters appear to be more dependent on internal recycling (Harris, 1986). In fact, at these lower trophic levels, zooplankton regulate the relative quantity of nutrient release via excretion and thereby change the turnover rate (Elser *et al*., 1988; Urabe, 1993).

South Andean lakes are oligotrophic (Pedrozo *et al*., 1993), and small bodied zooplankton are characteristic of the area (Balseiro & Modenutti, 1990; Modenutti & Balseiro, 1991). Previous field and experimental studies on the zooplankton–phytoplankton interaction in these lakes (Balseiro, Modenutti & Queimaliños, 1992; Queimaliños, 1993; Queimaliños & Modenutti, 1993) have shown that small flagellated algae are heavily selected by the small-bodied zooplankton (i.e. *Bosmina longirostris* (O.F. Müller)). Recent experimental studies have revealed a positive relationship between released nutrient (N and P) and zooplankton biomass (Balseiro, Modenutti & Queimaliños, 1997). This situation was enhanced when zooplankton biomass was dominated by crustaceans such as the calanoid copepod *Boeckella gracilipes* Daday and the cladoceran *B. longirostris*, compared with the zooplankton dominated by the rotifer *Polyarthra vulgaris* Carlin.

In this study, we performed a series of field experiments over gradients in zooplankton biomass. In three series of incubation experiments with different zooplankton species composition we attempted to measure the responses of algal species to the reduction of the edible algal population by grazing, and also to increased nutrient recycling.

Materials and methods

Study site

The study was carried out in lake El Trébol (Río Negro, Argentina, 41°2′ S; 71°4′ W). The lake lies at 764 m above sea level and has a surface area of 0.3 km^2 and a maximum depth of 12 m. The climate of the region is classified as temperate (mean annual temperature 8.7 °C), with dominant rainfall in winter (1200 mm yr^{-1}). The lake tends to be dimictic as it freezes during hard winters, otherwise its behaviour is warm monomictic. Direct stratification occurs during spring with a thermocline at 5–6 m. During the summer, the mixed layer occupies the whole lake. A pelagic station was fixed in the middle of the lake where the water was 11 m deep.

Dissolved nutrient release rates and phytoplankton concentrations were examined by *in situ* incubation experiments for 3 days with different zooplankton densities in polycarbonate bottles in the mixed layer of the lake.

The lake was sampled 1 or 2 days before and on the initial day of each experiment. In each sample, water transparency was measured using a Secchi disk and vertical profiles of water temperature, dissolved oxygen and conductivity were obtained by means of a thermistor, an oxygen meter and a conductivity meter. Water for chemical analysis, phytoplankton and duplicate zooplankton samples were collected with a Ruttner bottle and a Schindler–Patalas trap.

Incubation experiments

In situ experiments of grazer density gradients were run on three dates: 5–8 December 1995 (expt 1); 16–19 January 1996 (expt 2) and 12–15 February 1996 (expt 3). Each experiment was started at 11.00 h.

The experimental design consisted of four treatments with three replicates each. One treatment had no zooplankton and in the other three, increasing zooplankton concentrations (100–4000 μg DW L^{-1}) were added. These three treatments were called 1×, 2× and 3×, respectively. It should be noted that 1× concentration was not equivalent to the natural concentration, being only relative to the other treatments. Acid-washed 2-L polycarbonate bottles were used as experimental units.

Lake water was collected at a depth of 5 m using a Schindler–Patalas trap and filtered through a 55-μm-mesh net. The filtered water was placed in four isolated tanks. About one hour before the start of the experiments, zooplankton were collected using a 40-cm-diameter conical plankton net with 55-μm mesh size. After sampling, the live zooplankton were rinsed with filtered lake water and acclimatised in 1-L beakers containing filtered lake water. To initiate the experiment, filtered lake water was poured into the 2-L

bottles and the increasing concentrations of zooplankton were added to each bottle using a wide-bore pipette.

A total of forty-eight experimental units were prepared, twelve of which (four treatments, three replicates each) were carried to the lab to quantify the initial conditions. The remaining thirty-six bottles were incubated in a frame at a depth of 5 m at the pelagic lake station. Twelve bottles (four treatments, three replicates each) were removed after 24 h, another twelve after 48 h and the rest after 72 h of incubation (day 1, day 2 and day 3, respectively).

Laboratory methods

In all cases, the experimental units were carried to the laboratory within half an hour of removal from the frame, in darkness and in an insulated container to prevent temperature changes. In the laboratory, 150 mL from each bottle were separated and fixed with acid Lugol solution for phytoplankton counting. For determination of ammoniacal nitrogen (NH_4^+–N); total dissolved phosphorus (TDP-P) and SRP-P, the water from each bottle was filtered through a GF/F filter after removing zooplankton with a 55-μm mesh. The zooplankton was immediately preserved in 4% formaldehyde; the filter was used for chlorophyll *a* determination. The concentration of NH_4^+-N was measured with the Indophenol blue method. For TDP, samples were digested with potassium persulfate at 125 °C at 1.5 atm for 1 h. SRP and TDP concentrations were measured by the ascorbate-reduced molybdenum blue method. Chlorophyll *a* concentration was measured using extraction with 90% ethanol following Nusch (1980).

Phytoplankton were quantified in an inverted microscope in 50 mL Utermöhl chambers after 48 h of sedimentation. For each sample, 20 cells per species were measured to estimate the cell volume according to the most appropriate geometric shape. The algal biovolume concentration ($\mu m^3\,mL^{-1}$) for each species was determined by multiplying the mean cell volume by the population density.

Rotifer species were counted under a compound microscope in a 1-mL Sedgwick–Rafter chamber. Crustacean species were counted under a dissecting microscope in a 5-mL Bogorov chamber. At least thirty individuals of each species from each experimental unit were counted. Zooplankton biomass was estimated on the basis of the length–mass regressions of Bottrell *et al*. (1976).

Growth rates of phytoplankton (g) were calculated between day 0 and day 3 as follows:

$$g = \frac{LnN_t - LnN_0}{t}$$

Zooplankton phosphorus release rates were estimated following the calculations of Carrillo *et al*. (1995) based in Peters's (1975) model:

$$E_i = \frac{1}{2}\ (0.032 \cdot e^{0.39T} W_i^{-0.38} + 0.079 \cdot e^{0.39T} W_i^{-0.38})$$

where T = temperature (°C) and W_i = animal dry weight (mg)

This model assumes that the specific excretion rate of phosphorus ($\mu g\ P\ mg^{-1}\ DW\ h^{-1}$) is a function of mean individual dry weight (mg) and water temperature (°C). The sum of size, biomass and species release rate gave an estimate of the potential phosphorus release ratio for the community. In addition, P released by zooplankton during experiments was calculated as P release rate multiplied by incubation time in hours.

Differences between treatments were assessed using ANOVA. The proportions were transformed to the arcsin of the square root before the analysis.

Results

Field study

Vertical profiles of water temperature showed a tendency towards direct stratification in December and almost isothermal conditions in January and February, as a consequence of strong winds (Fig. 1). Water temperature reached 20 °C at the surface during January decreasing to 17.5 °C in February; dissolved oxygen concentration showed an almost homogeneous distribution in the water column (Fig. 1) and transparency, measured using a Secchi disk, was 5 m in December, 7 m in January and 8 m in February indicating a euphotic zone which extended down to the lake bottom. Total dissolved solids varied neither within the water column nor between experiments (conductivity: 65 $\mu S\ cm^{-1}$). Chlorophyll *a* concentrations were 1.0, 0.5 and 1.0 $\mu g\ L^{-1}$, in December, January and February, respectively.

Phytoplankton was represented by fifteen species:

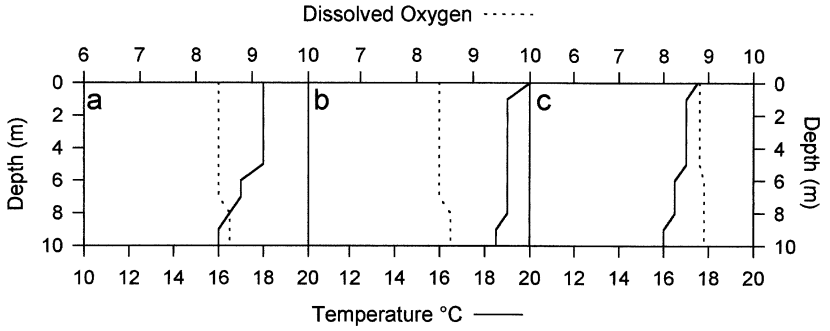

Fig. 1 Vertical profiles of temperature and dissolved oxygen concentrations in lake El Trébol. (a) 5 December 1995; (b) 16 January 1996 and (c) 12 February 1996.

three chlorophyceans, five bacillariophyceans, three dinophyceans, three chrysophyceans and one cryptophycean. However, only one species contributed substantially to total cell abundance. The nanoflagellate *Chrysochromulina parva* Lackey (3–6 μm GALD, Greatest Axial Linear Dimension) represented 93.4%, 94.2% and 95.9% of total phytoplankton cell abundance in December, January and February, respectively. The net phytoplankton fraction (> 20 μm GALD) was dominated by the dinoflagellate *Gymnodinium mirabilis* Stein (55–78 μm GALD) and the diatom *Aulacoseira granulata* (Ehr.) Simonsen (36–47 μm GALD) in December and by *A. granulata* in January and February. Although this fraction represented less than 5% of total phytoplankton numbers, it reached 48% of total phytoplankton biovolume.

In December, two crustacean zooplankton species, the calanoid copepod *Boeckella gracilipes* and the cladoceran *Bosmina longirostris*, represented up to 99% of the total zooplankton biomass. In January, *B. longirostris* was the dominant species (up to 99% of the total zooplankton biomass), while in February the rotifer *Polyarthra vulgaris* was dominant and *B. longirostris* was present only at a moderate density (representing 5% of the total abundance, but 50% of total zooplankton biomass).

Experimental study

During the first experiment (expt 1, December) the zooplankton was made up of two species: *B. gracilipes* (> 80% of total zooplankton biomass) and *B. longirostris* (< 20% of total zooplankton biomass) (Fig. 2a). Manipulation of zooplankton biomass as treatments in this experiment was successful (ANOVA: $P < 0.001$). The initial phytoplankton concentrations in the four treatments did not show significant differences (ANOVA: $P > 0.05$). We observed that *C. parva* decreased in density from days 1 to 3, with increasing zooplankton biomass (ANOVA: day 1 $P < 0.05$; days 2 and 3 $P < 0.001$). This resulted in a steady decrease in growth rates from day 0 to day 3 (Fig. 3a, left). In the filtered treatment, the density of *C. parva* increased with time.

In the second experiment (expt 2, January), the zooplankton was dominated by *B. longirostris* representing 99% of the total zooplankton biomass (Fig. 2b). The manipulations of zooplankton biomass (ANOVA: $P < 0.001$) resulted in the greatest value of our three experiments, ranging from 0 (filtered lake water) to 4.3 mg L^{-1} (Fig. 2b). Phytoplankton initial condition did not differ between the four treatments (ANOVA: $P > 0.05$). We observed a significant decrease in *C. parva* density with increasing zooplankton biomass (treatments) (ANOVA: $P < 0.001$ in all cases). These differences were enhanced with incubation time (days). On the third day (72 h incubation), *C. parva* abundance was reduced to very low levels in all three treatments with zooplankton, resulting in high and negative growth rates (Fig. 3a, centre). In the treatments without zooplankton (filtered), *C. parva* did not increase significantly as in expt 1 (Fig. 3a).

During our third experiment (expt 3, February) we started with a zooplankton community made up of *P. vulgaris* and *B. longirostris*, representing 50% of the total zooplankton biomass each (Fig. 2c). Although total zooplankton biomass manipulation was successful (ANOVA: $P < 0.001$); a change in zooplankton structure was observed during the 3 days of incubation. At the end of 72 h of incubation, zooplankton was dominated by *Bosmina* and there had been a clear decrease in *Polyarthra* biomass, especially in the 3× treatment (Fig. 2d). The initial phytoplankton concentrations were not significantly different between the four treatments (ANOVA: $P > 0.05$). On each of the three days of incubation, the dominant phytoplank-

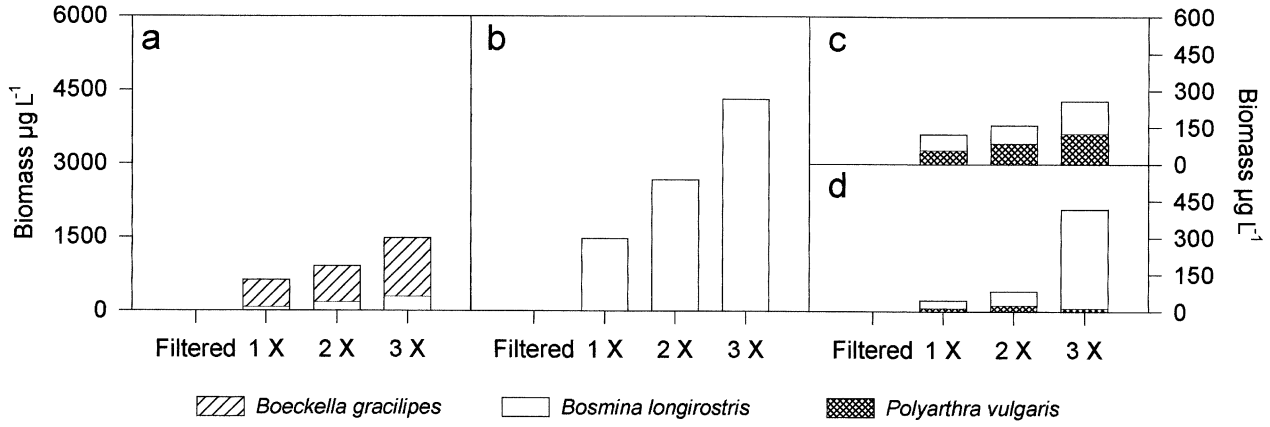

Fig. 2 Zooplankton biomass and species composition of the different treatments: filtered water (without zooplankton); 1×, 2× and 3× (1-, 2- and 3-fold zooplankton biomass). (a) Expt 1, December 5–8 1995 (initial and final condition); (b) Expt 2, 16–19 January 1996 (initial and final condition); (C) Expt 3, 12 February 1996, initial condition and (d) Expt 3, 15 February 1996, final condition.

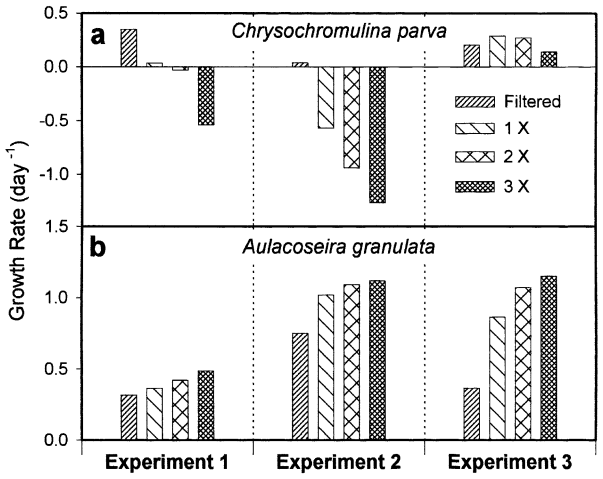

Fig. 3 Growth rates of the dominant phytoplanktonic species from day 0–3. Treatments: Filt: Filtered water (without zooplankton); 1×; 2× and 3× (1-, 2- and 3-fold increase in zooplankton biomass). (a) *Chrysochromulina parva;* (b) *Aulacoseira granulata.*

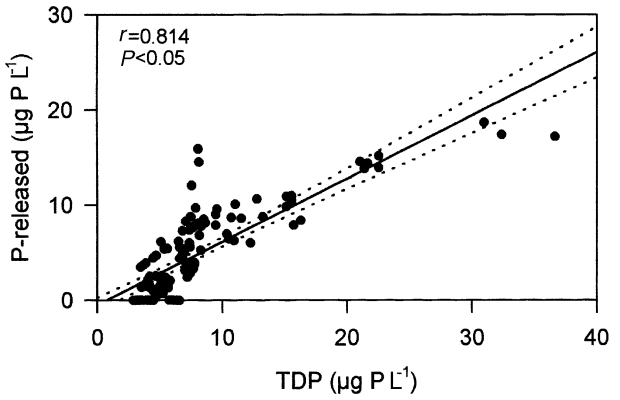

Fig. 4 Relationship between TDP-P and P released by zooplankton during the three experimental series, estimated through Peters' (1975) model.

tonic species, *C. parva*, showed different responses. After 24 h incubation, we found a significant decrease in cell concentration with increasing zooplankton biomass (ANOVA: $P < 0.001$). On the second day (48 h incubation), no significant result was obtained (ANOVA: $P > 0.05$), and on the third day, significant differences were obtained again (ANOVA: $P < 0.05$). However, on this third day, *C. parva* did not show a further decrease with increasing zooplankton biomass, but rather did show an increase which resulted in a net positive growth rate over the three days (Fig. 3a, right).

On the other hand, we observed that the ungrazed diatom *A. granulata* showed positive growth rates, which were higher in those treatments with increased zooplankton biomass (Fig. 3b).

In all three experiments, zooplankton manipulation (treatments) resulted in increases in nutrient (TDP-P and NH_4^+-N) availability within the experimental units (Balseiro *et al.*, 1997). The increase in P resulted from high nutrient recycling produced by the same zooplankton, as shown in Fig. 4, where P released was estimated through Peters's (1975) model. The observed relationship between P-released (estimated) and TDP (measured), indicates that zooplankton biomass was responsible for the observed increase in P concentrations. However, *C. parva* did not show an increase in density according to the increase in P; moreover, *C. parva* density decreased as P increased (Fig. 5a–c). This observed negative relationship was the result of high herbivory, because an increase or no

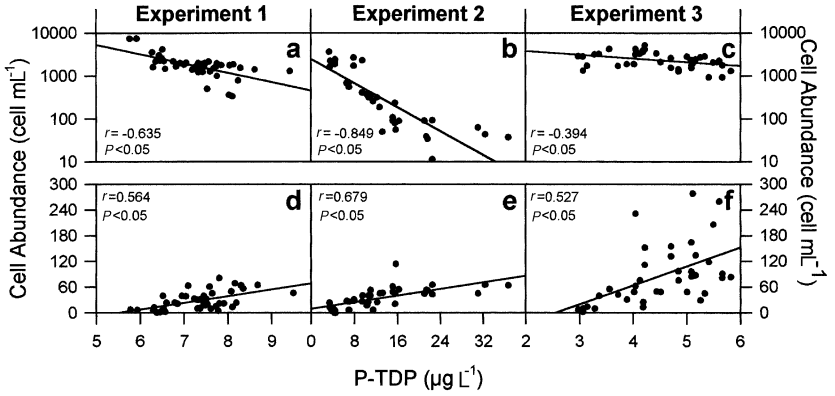

Fig. 5 Relationship between TDP-P and specific algal cell abundance during the experiments. (a)–(c) *Chrysochromulina parva*; (d)–(f) *Aulacoseira granulata*.

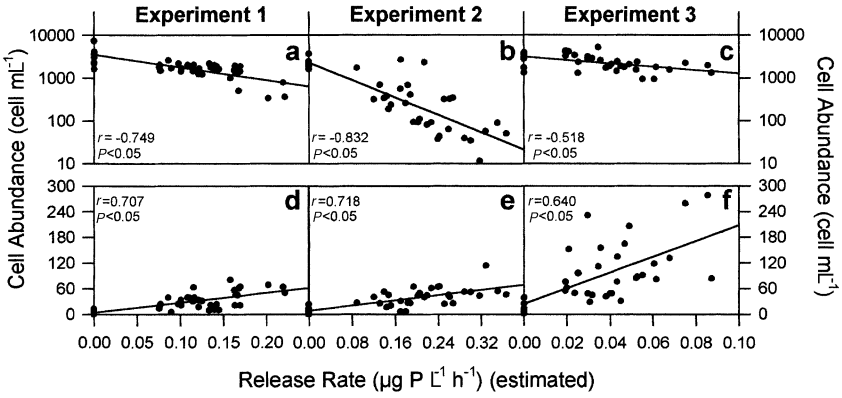

Fig. 6 Relationship between P release rates (estimated through Peters', 1975 model), and specific algal cell abundance during the experiments. (a)–(c) *Chrysochromulina parva*; (d)–(f) *Aulacoseira granulata*.

changes in *C. parva* density were observed in the treatments without zooplankton (filtered) during the 3 days of incubation (Fig. 3a). In our short incubation experiments, reduction in density due to grazing outstripped the increase due to cell reproduction, despite the high nutrient concentration. We therefore observed a negative relationship between *C. parva* and the estimated P release rates (Fig. 6a–c).

On the other hand, we obtained a significant positive relationship between *Aulacoseira* cell numbers and P concentration (Fig. 5d–f), and a similar positive relationship was obtained when the nutrient (P) was estimated as P release rates (Fig. 6d–f). These results indicate that the ungrazed diatom *A. granulata* was able to capitalize on the increase in nutrient availability.

Finally, as an ultimate result of the increase or decrease in algal species, we observed a change in the nano:net phytoplankton relationship (Fig. 7). The outcome of the three days of incubations and the increase in zooplankton biomass was a significant change towards an increase in the importance of the net phytoplankton fraction (ANOVA: $P < 0.001$ for expts 1 and 2 and $P < 0.05$ for Expt 3).

Discussion

Herbivorous zooplankton affect phytoplankton directly by grazing, but also indirectly by regenerating nutrients (Sterner, 1986, 1989). Thus, zooplankton influence species composition and succession patterns in algal communities (Bergquist, Carpenter & Latino, 1985; Carrillo *et al.*, 1995).

In oligotrophic lakes dominated by large-bodied zooplankton, the reproduction rates of a phytoplankton community mainly composed of small algae, are equalled or even surpassed by consumption by zooplankton (Gliwicz, 1985; Sterner, 1989). Although south Andean lakes are dominated by small-bodied zooplankton, an increase in zooplankton biomass nevertheless results in strong grazing pressure on edible phytoplankton. However, nutrient recycling provides a stimulus for algal growth, evidenced in the netphytoplankton since it is composed of species which are large enough to have a refuge from grazing.

The seasonal succession of phytoplankton in small Andean lakes is characterized by dominance of nanoflagellates in spring and early summer which are then

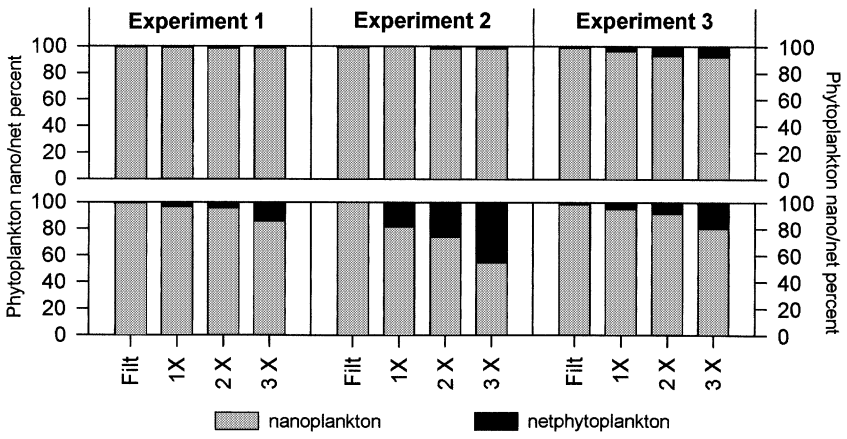

Fig. 7 Changes in the nano–netphytoplankton relationship during the three experiments. Upper panel: initial conditions (day 0); lower panel: final conditions (day 3). Treatments: Filt, filtered water (without zooplankton); 1×; 2× and 3× (1-, 2- and 3-fold increase in zooplankton biomass).

partially replaced by diatoms in late summer and autumn (Díaz & Pedrozo, 1993; Queimaliños, 1997). It is clear that this replacement follows the pattern based on size changes from nanoplankton to netphytoplankton in midsummer as was described by Sommer *et al*. (1986), but with some time delay. The chemical composition of Andean lakes corresponds to a very dilute solution of silica and calcium bicarbonate (Pedrozo *et al*., 1993). Silica concentration in these lakes is higher than in other lakes of the world (Díaz & Pedrozo, 1993); such that, in nutrient enrichment bioassays, no significant responses to silica addition have been observed (Díaz & Pedrozo, 1996).

Our experimental data from lake El Trébol support the idea that this replacement pattern is the net result of both positive and negative effects of zooplankton on phytoplankton. Empirical evidence for zooplankton grazing on *C. parva* is considerable, as it is a small, unicellular, naked species (Sterner, 1989; Queimaliños, 1993). The results obtained in our experiments clearly show that the most important factor regulating *C. parva* is grazing by herbivorous zooplankton (Fig. 3a). This situation brings about the negative relationships obtained for *C. parva* cell numbers to P released or to TDP over the three days of incubation (Figs 5 and 6), and decreasing growth rates with increasing zooplankton biomass (Fig. 3a). This relationship does not indicate an independence of *C. parva* growth from P loading. On the contrary, in our experiments, P increased with the increase of zooplankton biomass (Balseiro *et al*., 1997), which simultaneously implies an increased grazing pressure. Therefore, we observed a net loss of *C. parva* cell abundance which was particularly clear in expt 2 which included the strongest biomass manipulation with the lowest (negative) growth rates (Figs 3a, 5b and 6b).

On the other hand, we observed an increase in *A. granulata*, with positive growth rates, in our three experimental series with different zooplankton species composition (Figs 3b and 7). In our experiments, the abundance of diatoms showed a dependence on the mineral phosphorus excreted by the zooplankton (Fig. 5d–f and 6d–f), implying that diatoms are able to capitalise on this recycled P. Grazers provide a low Si : P supply ratio because, while P is released in a bioavailable form, Si is not. The presence of herbivores should therefore disfavour diatom competitive dominance (Sterner, 1989). Our results, however, indicate an opposite outcome, since diatoms were favoured in the increased zooplankton biomass experiments. Silica availability in these Andean lakes is very high (Díaz & Pedrozo, 1996). Thus the diatoms have a competitive advantage in exploiting phosphorus supplies during heavy grazing conditions, since Si is not a limiting nutrient. Many diatom species are superior phosphorus competitors compared with naturally co-occurring algal species (Tilman *et al*., 1986).

Although the general trends in the responses of *C. parva* and *A. granulata* in expt 3 were similar to the other experiments (Fig. 5c,f, 6c,f), it is clear that some kind of physiological complexities occurred during this experiment. First, during the three days of incubation, a change in zooplankton population structure occurred in the experimental units (Fig. 2c,d). Second, as a consequence of such changes, the response of *C. parva* density was different on days 1, 2 and 3.

In expts 1 and 2, the zooplankton was composed of crustaceans, but in expt 3 the rotifer *P. vulgaris* represented half of the zooplankton biomass. The relationships between biomass, grazing rate and excretion rate may be quite different in *P. vulgaris* to that in crustaceans, and this difference may be reflected in

the algal response. Also, the zooplankton structure changed during the experiment, with the increase of *Bosmina*, especially on day 3 in treatment 3× (Fig. 2d). This change makes more difficult to clarify the effect that *P. vulgaris* could have on *C. parva.*

Our three series of incubation experiments under manipulated zooplankton conditions, performed in lake El Trébol, indicate that the composition of phytoplankton is regulated simultaneously by loss due to grazing and stimulation due to nutrient recycling. However, these two processes may affect different algal species and seem to be more evident when zooplankton are dominated by crustaceans. The results obtained outline the importance of the indirect effects of the zooplankton (by nutrient recycling) to explain the development of diatoms, and the role of grazing as a growth-limiting factor for *C. parva* abundance, in spite of the small body size of the zooplankton of Andean Lakes.

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