

# Short-term responses of phytoplankton to nutrient enrichment and planktivorous fish predation in a temperate South American mesotrophic reservoir

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**Abstract** Top-down and bottom-up mechanisms have been proposed as potential regulators of the phytoplankton biomass of aquatic ecosystems. We evaluated the effect of nutrient enrichment and planktivorous fish predation through a mesocosm experiment conducted at a polymictic system (Peñuelas reservoir, Chile). Results show that phytoplankton biomass increased, while diversity decreased, in nutrient-enriched treatments. Planktivorous fish predation did not have a significant effect on phytoplankton biomass but led to a reduction of bigger zooplankton abundance. These results are an indication that these reservoir systems would be preferentially influenced by resource availability in short-term manipulations.

**Keywords** Top-down · Bottom-up · Nutrients additions · Zooplanktivory · Southern hemisphere · Oceanic climate

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## Introduction

Phytoplankton biomass can be regulated by abiotic and biotic factors such as nutrients, light, herbivory, sedimentation and, in the case of reservoirs, by large water volume losses (Thornton et al., 1990; Wetzel, 2001). The discussion about its regulation can be traced back to the assertion by Hairston et al. (1960) that phytoplankton biomass is regulated by resources or *bottom-up* control. Later on, Carpenter et al. (1985) proposed that a *top-down* control by predators could have cascading impacts on primary producers as well. McQueen et al. (1986), combining top-down/bottom-up effects, predicted that there would be a strong control from resources at the base of the food web (primary producers) that decreases as it goes from one trophic level to the next, and a strong predator control at higher trophic levels. Their concept incorporates the trophic state of the ecosystem, predicting that top-down effects or fish predation (Lampert & Sommer, 1997) would have a significant impact on the primary producers of oligotrophic systems, while regulation by predators would not be important in eutrophic systems.

Jeppesen et al. (2003), differing from McQueen et al. (1986), using empirical data, provided evidence that the trophic cascade is higher in nutrient-rich lakes than in oligotrophic ones. Furthermore, they stated that predator control of large-bodied zooplankton tends to be higher in shallow lakes compared to deep ones.

While the bottom-up and top-down impacts are traditionally conceived as compatible with each other; the results of Gliwicz (2002, 2003) in field population-density data suggest that the nature of the two impacts is different. Rates of change, such as the rate of individual body growth, rate of reproduction, and each species population growth rate, are bottom-up controlled. Other variables, such as biomass, individual body size, and population density, are top-down controlled and are fixed at a specific level, regardless of the rate at which they are produced.

In South America, the results found in short-term mesocosm experiments have shown a top-down control by zooplanktivorous fish reducing thus, grazing pressure by large zooplankton on phytoplankton biomass (Northcote et al., 1990; Boveri & Quiros, 2002).

It is of importance to consider that lake ecosystems in the southern and northern hemispheres at similar latitude differ with regard to their physical and biological characteristics, such as thermal stratification, seasonal temperature amplitude, and differences in community composition, especially zooplankton and fish. Compared to the northern temperate region, Chilean lakes at corresponding latitudes in the southern hemisphere are warm monomictic or polymictic with narrower thermic amplitude because of the Pacific Ocean moderating influence (Geller, 1992; Vila et al., 2006). They are also characterized by higher richness of zooplanktivorous fishes and lower number of piscivorous ones than northern hemisphere sites (Soto & Zúñiga, 1991). Likewise, these systems have a lower richness of zooplanktonic species which are dominated by calanoid copepods and small size cladocerans (Zúñiga, 1988; Soto & Zúñiga, 1991). These physical and biotic differences can lead to major ecological disparity between northern and southern ecosystems. On the basis of the previous characteristics, the issues related to phytoplankton control in Chilean lentic ecosystems would be important for both ecosystem functions and management.

To study this, mesocosm field experiments were conducted in a polymictic mesotrophic reservoir system in central Chile. The controlling variables were: (a) presence of fish and zooplankton, and (b) nutrient enrichment. The main goal was to evaluate the direct and indirect effects of resource availability and fish zooplanktivory on the control of

phytoplankton biomass in order to test the relative importance of top-down versus bottom-up pathways in central Chilean lentic ecosystems.

## Methods

### Study area

Peñuelas reservoir (33°10' S–71°29' W) is a dendritic, polymictic temperate reservoir in central Chile, constructed at the beginning of the last century as a drinking water supply. The reservoir is located in the Peñuelas Lake National Reserve at 347 m elevation and with a surface area of 19 km<sup>2</sup>. It has a maximum depth of 15 m and mean depth of 5 m. The maximum water volume recorded was 75 × 10<sup>6</sup> m<sup>3</sup> and the minimum was 9.8 × 10<sup>6</sup> m<sup>3</sup>. Rainwater is the only inflow, and the outflow is regulated by the drinking water plant (Schmid-Araya & Zúñiga, 1992). During the experiments, the reservoir was mesotrophic with total phosphorus concentration (mean ± SD) of 16.54 ± 2.37 µg l<sup>-1</sup>, total nitrogen from 588.10 ± 75.23 µg l<sup>-1</sup>, with a TN:TP ratio of 36, and chlorophyll *a* of 10.43 ± 0.96 µg l<sup>-1</sup>. All mean values were measured 0, 2, 4, 6, 8 m, in the deepest zone of the reservoir and enclosing sites.

### Experimental design

The experiment was carried out in 18 enclosures in Peñuelas Reservoir from 7–25 May, 2004 (austral autumn). The enclosures were installed near the dam, which was the deepest area of the reservoir. They were made of 0.1 mm thick polyethylene (2 m height × 0.7 m in diameter), containing an approximate volume of 0.8 m<sup>3</sup>, and fixed to a PVC floating frame extending 30 cm over the water surface to avoid water entry. Mesocosm inside walls did not show periphyton development during the experimental period. A 2 × 3 factorial design was used with natural and nutrient-enriched conditions, crossed with three different community compositions: (1) only phytoplankton, (2) phytoplankton and zooplankton, and (3) phytoplankton, zooplankton and zooplanktivorous fish.

The enclosures were filled with reservoir water filtered through a 64 µm mesh. During the filling

process,  $\text{NH}_4\text{Cl}$  and  $\text{H}_2\text{KPO}_4$  were added to each enclosure designated as the nutrient treatment, with an initial concentration of  $1027 \mu\text{g l}^{-1}$  TN and  $40.78 \mu\text{g l}^{-1}$  TP in the enrichment treatments. Zooplankton from the reservoir was concentrated by vertical hauls with a  $60 \mu\text{m}$  net. After gentle homogenization 14 individuals per liter were added to the zooplankton treatments similar to the concentration found in the reservoir. Fishes were collected at the reservoir two days before the experiment. Three fish specimens of *Cheirodon interruptus* (Jenyns) with similar size, normal swimming activity, and without any evident damage were added to the treatments with fish presence at a biomass near  $7.0 \text{ g m}^{-3}$ , which corresponds to the natural fish biomass of this system. The fish survival was monitored twice a week and during the experiment only one fish had to be replaced.

Water samples were collected every four days to measure phytoplankton and every 8 days for zooplankton. Phytoplankton was sampled by plunging a  $134 \times 2 \text{ cm}$  cylinder from surface to bottom of the enclosure to obtain an integrated sample (Elliott et al., 1983; Hanazato et al., 1990; Wetzel & Likens, 1991). Phytoplankton samples were preserved with Lugol solution and identified with an inverted microscope (Utermöhl, 1958). Zooplankton was sampled three times during the experiment with the same device used for the phytoplankton sampling, but the sampler was plunged six times in each enclosure to obtain three liters of water which were filtered with a  $70 \mu\text{m}$  mesh and preserved with the sucrose-formalin solution of Haney & Hall (1973). Chlorophyll *a* was determined spectrophotometrically by filtering 500 ml of water with GF/F filters and extracted in 90% acetone (APHA, 1992).

Bottom-up effects were analyzed using each species population growth rate and top-down effects as changes of population density and biomass (chlorophyll *a*).

The effects of nutrient enrichment and fish on phytoplankton over time were tested using a repeated-measure ANOVA. Data were log-transformed before analyses to achieve normality. Simpson's diversity index was estimated for the phytoplankton community in each enclosure, since this index places weight on the common species and is therefore sensitive to changes in the more abundant species (Simpson, 1949; Krebs, 1999).

## Results

The initial concentration of TP and TN of enrichment enclosures were  $40.78 \mu\text{g l}^{-1}$  and  $1027 \mu\text{g l}^{-1}$  respectively and the TN: TP relationship equalled 25. In non-enrichment treatment the initial concentration of TP and TN were  $18.78$  and  $516.48 \mu\text{g l}^{-1}$ . At the end of the experiment, these values were  $39.67$  and  $541.37 \mu\text{g l}^{-1}$  of TP and TN respectively in the enrichment enclosures and  $21.4$  and  $345.4 \mu\text{g l}^{-1}$  respectively in non-enrichment treatments.

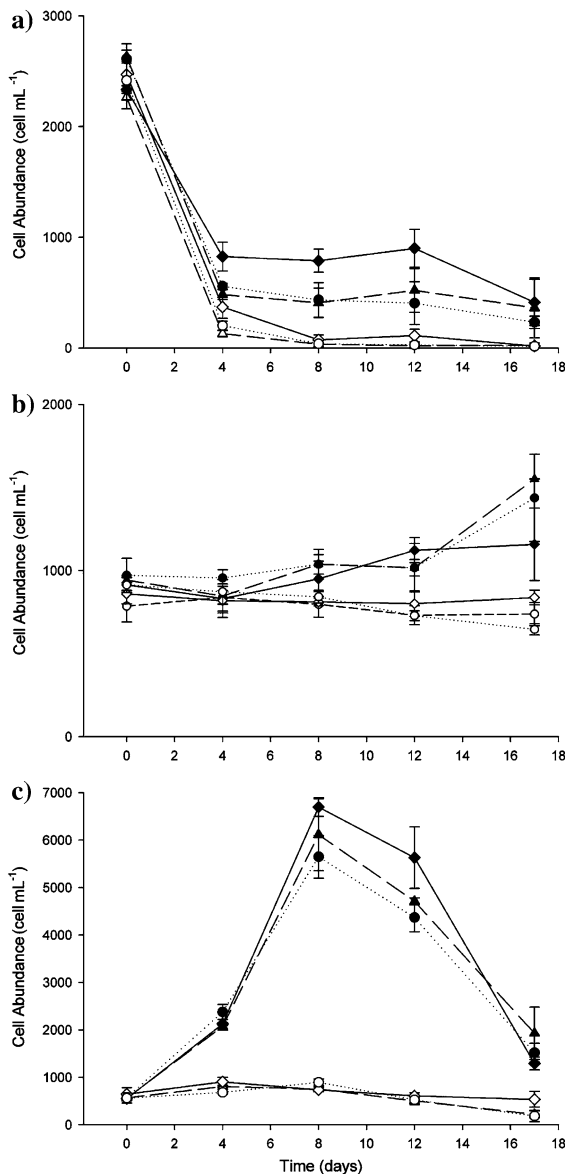
The phytoplankton assemblage community from the reservoir comprised nearly 40 species, but only three dominant taxa accounted for 74% of total phytoplankton abundance. At the beginning of the experiment, the assemblage was dominated by *Scenedesmus quadricauda* (Turpin) Brébisson. *Tetraedron minimum* (A. Braun) Hansgirg and *Synedra* sp. *S. quadricauda* abundance decreased in all enclosures from day four, being replaced by *Synedra* sp. between days 4 and 12 (Fig. 1).

Phytoplankton diversity was significantly lower in the nutrient-enriched treatments relative to the non-enriched, the zooplankton and the fish did not generate an effect on diversity and significant enrichment  $\times$  time interactions (Table 1).

Rotifers represented the major abundance of zooplankton community with *Brachionus calyciflorus* Pallas, *Keratella* sp. and *Polyarthra* sp. with *B. calyciflorus* exceeding almost threefold the size of the other rotifers. The cladocerans *Bosmina longirostris* (O. F. Müller) and *Ceriodaphnia dubia* Richard were the least abundant of the zooplanktonic community.

Nutrient additions sustained higher growth rates of *S. quadricauda* ( $F_{1,7} = 36.80$ ,  $P < 0.001$ ), *T. minimum* ( $F_{1,7} = 7.81$ ,  $P < 0.05$ ), and *Synedra* sp. ( $F_{1,7} = 43.41$ ,  $P < 0.001$ ) (Fig. 2). Enrichment treatments only increased the growth rates of *B. calyciflorus* ( $F_{1,4} = 42.08$ ,  $P < 0.01$ ) and had no effects on cladocerans ( $F_{1,4} = 3.26$ ,  $P > 0.1$ ) and *Keratella* sp. ( $F_{1,4} = 0.43$ ,  $P > 0.5$ ). However, *Polyarthra* sp. had a higher growth rate in non-enrichment treatments ( $F_{1,4} = 19.74$ ,  $P < 0.05$ ).

As top-down effects, zooplankton and fishes did not show effect in phytoplankton biomass (Fig. 3; Table 1) and abundance of *S. quadricauda* ( $F_{2,7} = 1.43$ ;  $P > 0.05$ ), *T. minimum* ( $F_{2,7} = 1.43$ ;  $P > 0.05$ ), and *Synedra* sp. ( $F_{2,7} = 2.33$ ;  $P > 0.05$ ) (Fig. 1). Fishes significantly decreased the abundance



**Fig. 1** Mean ( $\pm 1$  SE) abundance of (a) *Scenedesmus* (b) *Tetraedron minimum* and (c) *Synedra* sp. in enclosures during the experiment. Nutrient enrichment (black figures), no enrichment (white figures), fish, zooplankton and phytoplankton (diamonds), zooplankton and phytoplankton (triangles) and only phytoplankton (circles)

of *B. calyciflorus* ( $F_{1,4} = 15.36$ ;  $P < 0.05$ ) and total cladocerans ( $F_{1,4} = 7.81$ ;  $P < 0.05$ ) (Fig. 4). The small rotifers *Keratella* sp. and *Polyarthra* sp. (Fig. 5) did not change with fishes presence ( $F_{1,4} = 2.03$ ;  $P > 0.1$ ) and ( $F_{1,4} = 0.17$ ;  $P > 0.1$ ), respectively. Nevertheless, significant fish  $\times$  time interactions ( $F_{2,8} = 5.2$ ;  $P < 0.05$ ) in *Keratella* sp. were found,

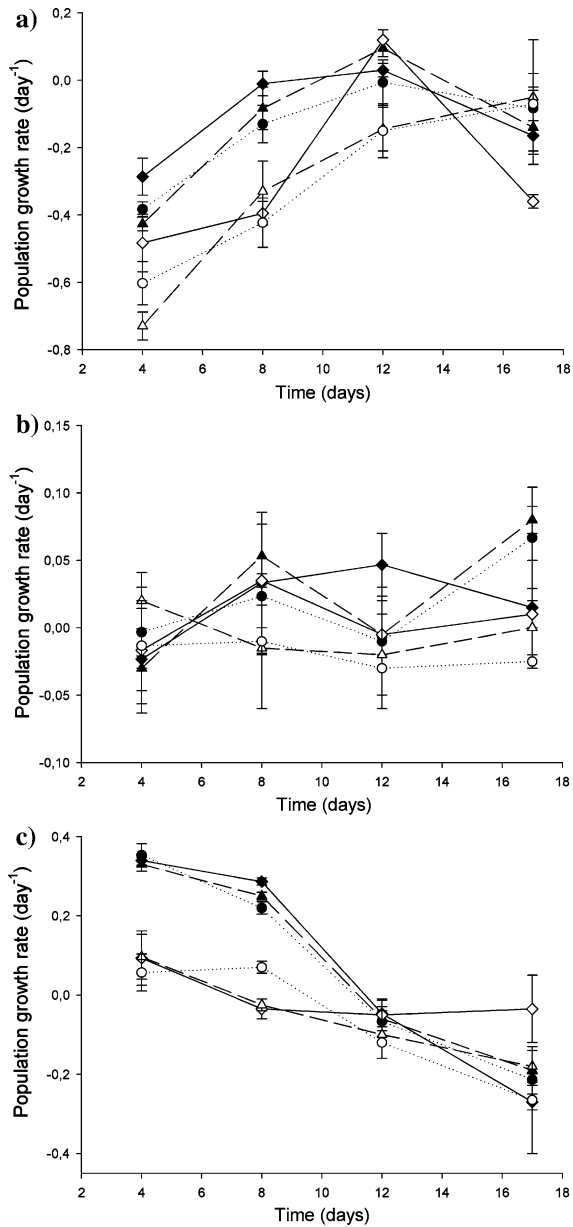
**Table 1** Results of repeated measures ANOVA testing the effects of nutrient enrichment (Nutrient) and food web structure (Web) on chlorophyll *a* concentration and Simpson's diversity index over time

	d.f.	<i>F</i>	<i>P</i> -value
<b>Chlorophyll <i>a</i></b>			
Treatment effects			
Nutrient	1	324.90	<0.001
Web	2	1.32	0.327
Nutrient $\times$ web	2	0.67	0.542
Error (between subjects)	7		
Time effects			
Time	4	16.42	<0.001
Time $\times$ nutrient	4	26.88	<0.001
Time $\times$ web	8	0.78	0.622
Time $\times$ nutrient $\times$ web	8	0.78	0.626
Error (within subjects)	28		
<b>Simpson's index</b>			
Treatment effects			
Nutrient	1	27.44	0.001
Web	2	3.43	0.091
Nutrient $\times$ web	2	0.18	0.838
Error (between subjects)	7		
Time effects			
Time	4	46.15	<0.001
Time $\times$ nutrient	4	31.31	<0.001
Time $\times$ web	8	0.43	0.894
Time $\times$ nutrient $\times$ web	8	0.45	0.877
Error (within subjects)	28		

when an increase in abundance was observed at the end of the experiment in fish treatments.

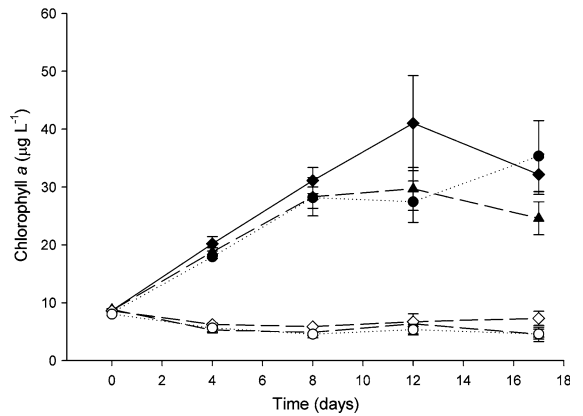
## Discussion

Responses of fresh-water mesocosm experiments to nutrients additions are different. The outcome seems to depend largely on the interactions of the community components and the trophic state of the system (Lynch & Shapiro, 1981). Thus, it has been shown that when nutrients are increased in meso and eutrophic ecosystems: (a) there is no change in phytoplankton biomass, but there are differences in algal composition; (b) there is an increase only in phytoplankton biomass; and (c) both events occur at different seasonal periods based on the timing of the experiments (Lynch & Shapiro, 1981; Drenner et al., 1990; Elser et al., 1990; Faafeng et al., 1990; Persson et al.,

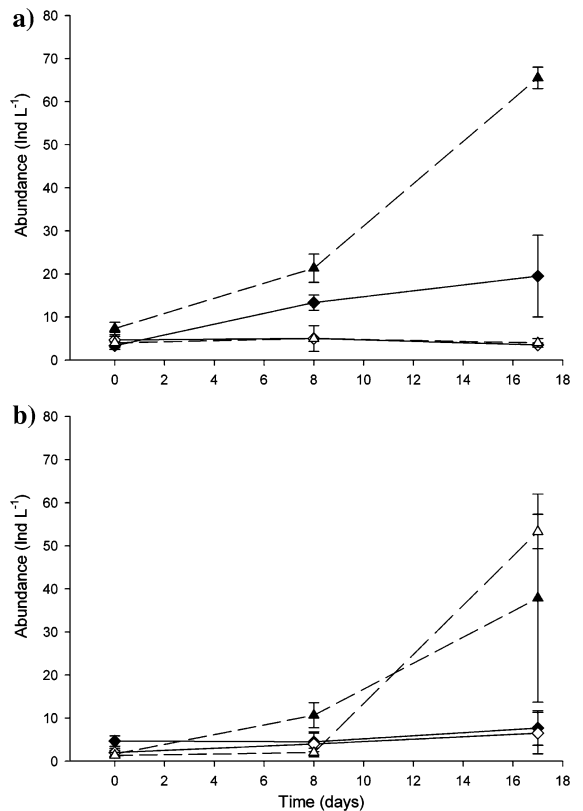


**Fig. 2** Mean ( $\pm 1$  SE) population growth rate of (a) *Scenedesmus quadricauda* (b) *Tetraedron minimum* and (c) *Synedra* sp. in enclosures during the experiment. Nutrient enrichment (black figures), no enrichment (white figures), fish, zooplankton and phytoplankton (diamonds), zooplankton and phytoplankton (triangles) and only phytoplankton (circles)

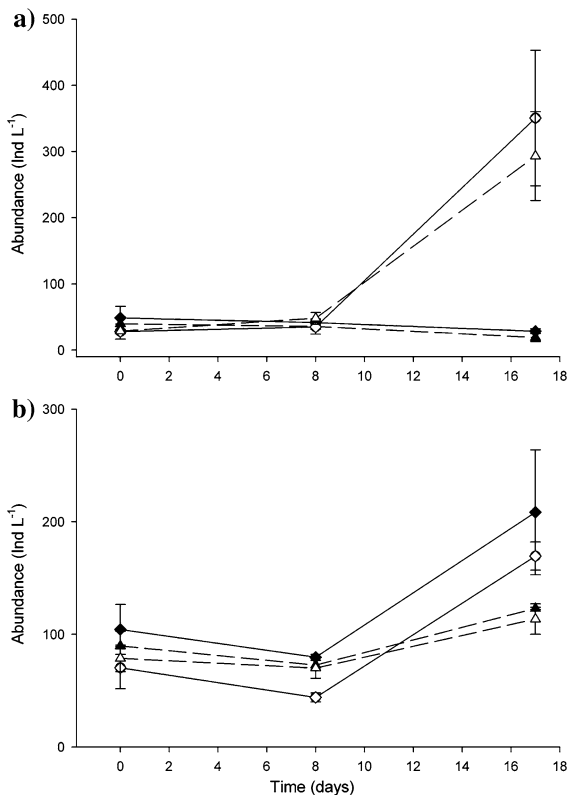
2001; Camacho et al., 2003; Romo et al., 2004). These results have been reported mostly with communities which have evolved in dimictic lakes with long stratification periods and extreme temperature changes seasonally. Mediterranean lakes of the Pacific austral region of South America are monomictic or



**Fig. 3** Mean ( $\pm 1$  SE) chlorophyll *a* in enclosures during the experiment. Nutrient enrichment (black figures), no enrichment (white figures), fish, zooplankton and phytoplankton (diamonds), zooplankton and phytoplankton (triangles) and only phytoplankton (circles)



**Fig. 4** Mean ( $\pm 1$  SE) abundance of (a) *Brachionus calyciflorus* and (b) total cladocerans from enclosures during the experiment. Nutrient enrichment (black figures), no enrichment (white figures), fish, zooplankton and phytoplankton (diamonds), zooplankton and phytoplankton (triangles)



**Fig. 5** Mean ( $\pm 1$  SE) abundance of (a) *Polyarthra* sp. and (b) *Keratella* sp. from enclosures during the experiment. Nutrient enrichment (black figures), no enrichment (white figures), fish, zooplankton and phytoplankton (diamonds), zooplankton and phytoplankton (triangles)

polimictic, do not freeze during winter-time and present a narrower seasonal temperature range (Geller, 1992). These systems in the vicinity of the Pacific Ocean implies daily presence of westerly winds that generate permanent turbulence, a fact that would have structured plankton communities, favoring bigger size diatoms and green algae, (Reynolds et al., 1985) as it occurs in Peñuelas lake.

Our experimental design was devised for a reservoir pelagic community short-term responses, since several works have reported top-down effects at lower periods of experimentation like the one used in this study (Northcote et al., 1990; Vanni et al., 1997; Attayde & Hansson, 1999, 2001a, b; Matveev et al., 2000; Boveri & Quirós, 2002).

Phytoplankton diversity, decreased significantly in nutrient addition treatments, compared to the non-enriched enclosures enhancing the composition in favor of the more common species in the reservoir,

such as *T. minimum*, *Synedra* sp. and *S. quadricauda*. However, fish and zooplankton did not affect algal diversity. At the beginning of the experiment, there was an increase in diversity in all treatments due to the decrease in *S. quadricauda* abundance, the *S. quadricauda* decrease could be due to the enclosures effect for the reduction of turbulence inside them. Later, diversity decreased in the enriched treatments due to the increase of *Synedra* sp., which was dominant during most of the study period. This small diatom ( $<10^3 \mu\text{m}^3$  in volume) is characteristic of nutrient-enriched systems and classified within Reynolds's groups as a D functional taxa, and characterized as a fast growing species according to Reynolds et al. (2002). In nutrient addition treatments, *Synedra* sp. has a fast growth but diminishes its growth rate by decreasing its abundance after 8 days.

Our short time enclosure experiments in Peñuelas reservoir showed that nutrients enrichment significantly increased phytoplankton species population growth rate, on the other hand, fish and zooplankton did not affect phytoplankton abundance or chlorophyll *a* biomass.

Our results showed that consumer effects differed from those found by other authors working on ecosystems with a similar trophic state. For example, in the northern hemisphere, fish has repeatedly been shown to have a positive effect on phytoplankton abundance and biomass (Christoffersen et al., 1993; Romare et al., 1999; Attayde & Hansson, 2001a, b). The same pattern has been described for the southern hemisphere (Northcote et al., 1990; Quirós, 1990; Jeppesen et al., 2000; Boveri & Quirós, 2002; Matveev, 2003). Although our enclosures nutrient range corresponded to meso-eutrophic lakes, the responses differed from the ones reported for eutrophic systems which according to Jeppesen et al. (2003) generally show top-down effects.

The nonsignificant fish effect found on the abundance of phytoplankton at Peñuelas lake may be indicative of the scarce top-down control of herbivorous zooplankton over primary producers. Thus, top fish predators would not provoke a trophic cascading effect. In this aquatic system, the dominant zooplanktonic taxa during the experiment were *B. calyciflorus*, *C. dubia*, and *B. longirostris*, which are small size taxa with low total consumption because of their low abundance (Sommer, 1989; Schmid-Araya & Zúñiga, 1992; Gliwicz, 2003). Consequently, a plausible



explanation for the lack of top-down cascading effects may be that zooplankton is not abundant enough for its overall community filtration rate surpassing the reproductive rates of algal populations. This condition, proposed by Gliwicz (2003) for the phytoplankton standing crop is to be controlled effectively by filter feeding zooplankton.

Top-down results show negative effects on larger size zooplankton, as it is the case of *B. calyciflorus*, *C. dubia*, and *B. longirostris*, and positive effects on the smaller rotifer *Keratella* sp., showing no effects on smaller rotifers such as *Polyarthra* sp. The *Keratella* sp. abundance increases in fish treatments when abundance of larger size zooplankton decreases. Owing to the small size, *Keratella* sp. is not consumed by fish and then this could reduce competition between large zooplankton and *Keratella* sp., increasing their abundance.

The enrichment affects positively the growth rate of *B. calyciflorus* and negatively *Polyarthra* sp. growth rate. *Polyarthra* sp. case could be explained considering that these organisms are sensitive to physical and chemical changes (Hutchinson, 1967; Devetter, 1998; Frost et al., 1998). The phytoplankton species analyzed in non-enriched treatments show that, *T. minimum* had a higher proportion compared to the enriched ones. This species could be the preferred prey of *Polyarthra* sp., therefore, this species increase in non-enriched treatments. In enriched treatments, this proportion was lower, probably affecting the abundance of *Polyarthra* sp.

The bottom-up effects on the zooplankton would be weak since not all zooplanktonic taxa growth rate increased.

Our results agree with the hypothesis of Brett & Goldman (1997), i.e., that nutrient enrichment has a stronger effect than predation, and specifically with the model proposed by McQueen et al. (1986), i.e., the positive effects of nutrients on phytoplankton, and the negative effects of zooplanktivorous fish on zooplankton abundance in meso and eutrophic aquatic systems. However, in short-term experiments in this temperate polymictic reservoir, the effect of fish on zooplankton did not propagate to lower trophic levels as a trophic cascade. Although in the short-term, this could be an indication that these reservoir systems can be chiefly influenced by resource availability and a future interesting step would be to control responses at longer time periods.

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