Environmental Biology of Fishes **68:** 15–24, 2003.

Effects of *Galaxias maculatus* on nutrient dynamics and phytoplankton biomass in a North Patagonian oligotrophic lake

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Received 11 October 2002 Accepted 10 June 2003

Key words: galaxiids, nutrient recycling, fish excretion, phytoplankton uptake, N : P ratio

Synopsis

In this study we analysed the effects of *Galaxias maculatus*, a landlocked small fish species, on nutrient dynamics, and the consequent effects on phytoplankton biomass of an oligotrophic North Patagonian lake. We performed field and laboratory experiments in order to explore nutrient release by *G. maculatus* with increasing fish biomass and body size, and the resulting phytoplankton responses. Our results showed that phytoplankton biomass was strongly enhanced in the presence of fish, and that enhancement was greater with increasing fish biomass. These algal increments were associated with higher nutrient concentrations, due to the excretion/egestion processes of fish. In our two laboratory experiments we did not observe phytoplankton increase, probably due to light conditions, but we did observe significant effects of fish on nutrient concentrations. As was expected, mass-specific nutrient release rates were higher in smaller fish than in larger ones. So, the amount of nutrients supplied to phytoplankton would be influenced by the size structure of fish population. As a consequence of different N and P release rates, an increase in the $N_{NH_4} : P_{TDP}$ ratio was observed in the presence of fish. The fact that *G. maculatus* is a species that moves in schools would determine spatial heterogeneity in nutrient release, with important effects of reducing nutrient limitation and shifting $N_{NH_4} : P_{TDP}$ ratios.

Introduction

Planktivorous fish can increase phytoplankton biomass indirectly by reducing zooplankton grazing (Lynch & Shapiro 1981, Carpenter et al. 1985), and directly through fish excretion and egestion processes, as a direct source of nutrient for phytoplankton, stimulating algal production (Vanni & Findlay 1990, Schindler 1992, Vanni & Layne 1997, Attayde & Hansson 1999, among others). Additionally, Threlkeld (1987) has demonstrated that dead fish can also act as an important source of nutrient for phytoplankton growth.

Fish tissue composition depends on size and species (Davis & Boyd 1978, Sterner & George 2000). Physiological processes maintain an active control of fish nutrient content independent of food elemental ratios (Sterner & George 2000), which greatly differ between food items. Therefore, shifts in diet, with the consequent changes in elemental ratios, may affect nutrient release, by varying the assimilation efficiency in order to maintain their internal stoichiometry (Sterner & George 2000). In addition, it has been demonstrated that the rate of nutrient release varies per unit fish body mass (Schaus et al. 1997), as well as with increasing fish biomass (Vanni et al. 1997). Thus, it is clear that fish nutrient recycling results from a set of complex interactions between fish ecology and physiology (Schindler & Eby 1997).

Phytoplankton productivity in lakes is generally limited by the availability of phosphorus and at times nitrogen. The internal recycling of these limiting nutrients was observed to be important in oligotrophic lakes regarding the great demand of

phytoplankton on nutrients in such poor environments (McQueen et al. 1986). Thus, nutrients supplied by fish through their excretion/egestion processes have significant importance in supplying phytoplankton nutrient demands, and may affect both algal biomass and community structure (Vanni & Layne 1997, Attayde & Hansson 1999).

Galaxias maculatus (Jenyns) (Pisces: Galaxiidae) is a small fish species with a widespread distribution in the Southern Hemisphere, with landlocked forms known in Australia, New Zealand, and South America (Ringuelet et al. 1967, McDowall 1968, 1971). This species was classified as euryphagic carnivore (McDowall 1968, Pollard 1973) and in South America reaches a length of 7 cm (McDowall 1971). In the South Andean lakes of Argentina, this species is an important component of the native fish fauna (Ringuelet et al. 1967, Azpelicueta et al. 1996), and many studies have described different aspects of the biology and ecology of this autochthonous fish (Cussac et al. 1992, Cervellini et al. 1993, Modenutti et al. 1993, Battini 1997, Barriga et al. 2002). Landlocked forms of Australia and Argentina present ontogenetic and seasonal shifts in their diet, beginning their lives as planktivorous, and as they grow, they switch to a diet which combines littoral–benthic prey and zooplankton (Pollard 1973, Cervellini et al. 1993, Battini 1997). In the last decade, it has been demonstrated that *G. maculatus* exerts a strong effect on the zooplankton community, since the early fish stages provoked the failure of the summer cohort of the copepod *Boeckella gracilipes* Daday in a small South Andean lake (Modenutti et al. 1993). On the other hand, South Andean lakes are P and N limited (Díaz & Pedrozo 1996), and zooplankton nutrient recycling has been shown as an important source of nutrients for phytoplankton growth in other South Andean lake (Balseiro et al. 1997, Queimaliños et al. 1998). Recently fish have been recognised as an important source of available nutrients for algal development (Brabrand et al. 1990), so we attempt to elucidate how *G. maculatus* influences phytoplankton growth, through its own nutrient recycling processes, besides its role as top–down controller.

In this study, we focused on the effects of juveniles of *G. maculatus* as nutrient regulators when fed on pelagic prey. We explored their role in the nutrient dynamics of an oligotrophic lake, and their indirect effects on phytoplankton biomass through field and laboratory experiments.

Materials and methods

Study site

Experiments were conducted in Lake Escondido (41°2′S 71°4′W), a small and oligotrophic lake located 38 km West of San Carlos de Bariloche (Patagonia, Argentina), at 764 m above sea level. The lake area is of 8 ha, and its maximum depth fluctuates between 7 and 8 m with a mean depth of 5.5 m. The thermal regime is warm monomictic with a short period of stratification between late October and December (Balseiro & Modenutti 1990). The zooplankton community is characterised by the dominance of rotifers and small crustaceans (<1 mm body length). The dominant cladoceran species is *Bosmina longirostris* (O.F.M.), while copepods are greatly represented by *B. gracilipes* (Balseiro & Modenutti 1990). Furthermore, two native fish species were reported: *G. maculatus* and *Percichthys trucha* (Cuvier & Valenciennes) (Pisces: Percichthyidae) (Balseiro & Modenutti 1990, Semenas 1999).

Experimental design

Field experiment

A mesocosm experiment was run in the lake during late spring with different fish densities in order to evaluate nutrient recycling with increasing fish biomass. The experiment was carried out in 1671 enclosures. We conducted three treatments with five replicates each: (1) *Fishless*: enclosures with natural plankton densities without fish, (2) *Low Fish*: enclosures with natural plankton densities with the addition of four *G. maculatus* (24 fish m^{-3}), 4.21 ± 0.18 cm total length (mean ± standard error), and (3) *High Fish*: enclosures with natural plankton densities with the addition of eight *G. maculatus* (48 fish m^{-3}), of the same size.

Enclosures were made of clear PVC (polycarbonate) closed at both ends, and buoyed at 1.5 m below surface from an iron frame. Each frame was suspended with plastic floats and anchored to the bottom of the lake. Enclosures were raised and opened only for sampling.

The experiment was placed in Lake Escondido on 18 December 2001. Enclosures were filled with lake water filtered through a 55 μm plankton net, using an electric pump. Living zooplankters were collected by vertical trawls from 3 to 0 m with a 40 cm diameter conical plankton net with 55 μm mesh and were placed in each enclosure approximately in natural densities (Table 1).

Table 1. Zooplankton abundances in the lake and different experimental dates (mean ± standard errors). Crustaceans (*B. gracilipes* + *Bosmina longirostris*).

	Crustaceans		Rotifers	
	Initial	Final	Initial	Final
December (field)				
Fishless	4.38 ± 1.81	16.33 ± 9.31	441 ± 125	41 ± 17
Low fish	4.25 ± 1.27	0.40 ± 0.28	279 ± 24	69 ± 49
High fish	3.80 ± 0.70	0.20 ± 0.09	315 ± 46	62 ± 30
Lake	1.00	—	416	—
January (laboratory)				
Fishless	19.13 ± 4.25	14.44 ± 3.38	225 ± 38	134 ± 37
Fish	19.13 ± 4.25	0.20 ± 0.07	217 ± 15	228 ± 26
Lake	12.00	—	191	—
March (laboratory)				
Fishless	3.94 ± 0.63	6.57 ± 0.64	467 ± 20	732 ± 2
Fish	6.12 ± 1.42	0.86 ± 0.65	493 ± 37	496 ± 16
Lake	4.50	—	297	—

Fish were obtained using a seine-net in a shallow area of the lake, were immediately placed in an acclimatisation enclosure, and were added to the experimental units the day after, which was considered the experimental starting day (day 0). To assess the initial conditions, each enclosure was sampled just before fish were added. The enclosures were sampled on days 0, 2, 4, 7, and 9 using a 2 l Ruttner bottle. In all cases, samples were placed in isolated containers to avoid temperature changes, and were carried to the laboratory for nutrient and Chlorophyll *a* (Chl *a*) analyses.

As nutrients could be potentially increased by decaying fish (Threlkeld 1987), fish survival was checked visually in each sampling date. Some fish died during the experiment and they were removed immediately, so, the losses were considered in data analyses.

Laboratory experiments

In order to evaluate allometric variations in nutrient recycling, laboratory experiments with different fish sizes were carried out from 9 to 15 January, and from 20 to 25 March 2002. Experiments were conducted using 35 l containers filled with lake water with natural plankton densities (Table 1). Two treatments with three replicates each were performed: (1) *Fishless*: containers without fish, (2) *Fish*: containers with the addition of three *G. maculatus* (85.7 fish m^{-3}), 4.02 ± 0.31 cm total length in January experiment, and one *G. maculatus* (28.6 fish m^{-3}), 3.62 ± 0.19 cm total length in March experiment.

The containers were filled with fresh epilimnetic water from Lake Escondido. The water was collected from 3 m depth using 12 l Schindler–Patalas trap and was carried to the laboratory without delay in isolated containers to prevent temperature changes. In the laboratory, the lake water was placed in the containers with natural densities of plankton (Table 1). The containers were kept at 17 ± 2°C in a 14 : 10 light : dark cycle during the experiment (6 days in January and 5 days in March), reproducing the light and temperature conditions of the summer season at this latitude.

The same day the water was collected, we also caught the fish in the same way as for the field experiment and fish were carried to the laboratory in isolated tanks. In the laboratory, the fish were placed in an acclimatisation container for 24 h before starting the experiment. Then, they were introduced into the experimental containers. In order to analyse initial conditions, one water sample was taken before introducing fish (day 0). Each day, the containers were sampled with a polypropylene tube. The tube was submerged vertically enough times to obtain a 2 l pooled sample of each container.

One fish died during January experiment and was immediately replaced. No fish died during March experiment.

In the three experiments we worked with fish of small size (juveniles) because they include planktonic prey in their diets (Pollard 1973, Cervellini et al. 1993, Battini 1997). We could not work with larval stages (exclusively planktonic), because they are very fragile and they easily die after handling.

At the end of all experiments (field and laboratory) the fish were collected from the experimental units and preserved for measuring and weighing.

Nutrient and Chl a *analysis*

In all cases, total phosphorus (TP) was determined on 150 ml of unfiltered water (excluding fish). Total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP) and ammonia ($N–NH_4^+$) determinations were made on 300 ml of filtered water through GF/F filters.

The phosphorus fractions (TP, TDP, and SRP) were analysed using the ascorbate-reduced molybdenum blue technique, and $N–NH_4^+$ was determined using the indophenol blue method (APHA 1989). Total particulate phosphorus (TPP) was obtained by the difference between TP and TDP. Nutrient supplied by *G. maculatus* (TDP_{Gm} and $N–NH_{4\,Gm}^+$) was obtained as the difference between fish and fishless treatments.

Mass-specific nutrient release by *G. maculatus* was obtained dividing this difference by the fish biomass per unit volume.

In order to evaluate variations in the relationship between nitrogen and phosphorus, we calculated N : P ratio in all experiments as the ratio between N–NH_4^+ and P–TDP ($N_{NH_4} : P_{TDP}$).

Chl *a* concentration was measured by extraction with 90% ethanol following Nusch (1980) and measured in a Turner AU-10 fluorometer.

Statistical analysis

The effect of fish biomass and incubation time on Chl *a* in the field experiment was examined by multiple regression with Chl *a* as the independent variable.

Pearson correlation was used to test the relationship between Chl *a* concentration and TPP, and between the increase in algal biomass and TDP_{Gm} at time $t - 1$. The increase in algal biomass was calculated as the difference in Chl *a* concentration between t and $t - 1$. One-way ANOVA was applied to test statistical differences between treatments in initial and final zooplankton concentrations. Two-way repeated measures ANOVA was used to determine differences between treatments in nutrient, Chl *a* concentration and $N_{NH_4} : P_{TDP}$ ratio. Differences in mass-specific nutrient release by *G. maculatus* in laboratory experiments were analysed comparing regression slopes through t-test following Zar (1999). Data were log-transformed to meet normality and/or homoscedasticity when necessary. Student–Newman–Keuls test was used for multiple comparisons of means.

Results

Zooplankton

At the start of the experiments (field and laboratory), the zooplankton community was dominated by rotifers (Table 1), while the most abundant crustacean species was the copepod *B. gracilipes.* There were not significant differences between treatments in rotifer and crustacean initial concentrations (one-way ANOVA: all $P > 0.05$). At the end of the experiments, crustacean abundances decreased significantly in fish treatments due to fish predation, but remained approximately constant in fishless treatment (one-way ANOVA: all $P < 0.05$) (Table 1). The field experiment (December) and the first laboratory experiment (January) had no significant differences between treatments in final rotifer concentration (one-way ANOVA: $P > 0.05$), while in the second laboratory experiment (March), rotifers increased in fishless treatment (one-way ANOVA: $P < 0.05$).

Chlorophyll a

Significant positive effect of fish on phytoplankton biomass was found during the field experiment (Table 2, Figure 1a). Fish had remarkable impact on algal biomass, since Chl *a* concentration was greatly

Table 2. Results of two-way repeated measures ANOVA on nutrients and Chl *a* concentrations and $N_{NH_4} : P_{TDP}$ ratio.

	df	P-value											
		Chl *a*		TP		TDP		TPP		NH_4		Atomic $N_{NH_4} : P_{TDP}$	
December (field)													
Treatment	2	<0.001*	NLH	<0.001*	NLH	0.002*	NLH	0.001*	NLH	0.047*	NL H	0.078	NLH
Day	4	<0.001*		<0.001*		<0.001*		<0.001*		<0.001*		<0.001*	
Treatment × Day	8	<0.001*		<0.001*		<0.001*		<0.001*		0.001*		0.004*	
January (Laboratory)													
Treatment	1	0.665		<0.001*		0.006*		0.002*		0.001*		0.004*	
Day	6	<0.001*		<0.001*		<0.001*		<0.001*		<0.001*		<0.001*	
Treatment × Day	6	0.003*		<0.001*		<0.001*		0.002*		<0.001*		<0.001*	
March (Laboratory)													
Treatment	1	0.526		0.004*		0.002*		0.449		0.009*		0.072	
Day	4	<0.001*		<0.001*		<0.001*		0.444		<0.001*		<0.001*	
Treatment × Day	4	0.355		<0.001*		<0.001*		0.244		<0.001*		0.008*	

*$P < 0.05$. N: No fish, L: Low fish, H: High fish. Lines connecting letters indicate treatment means without significant differences

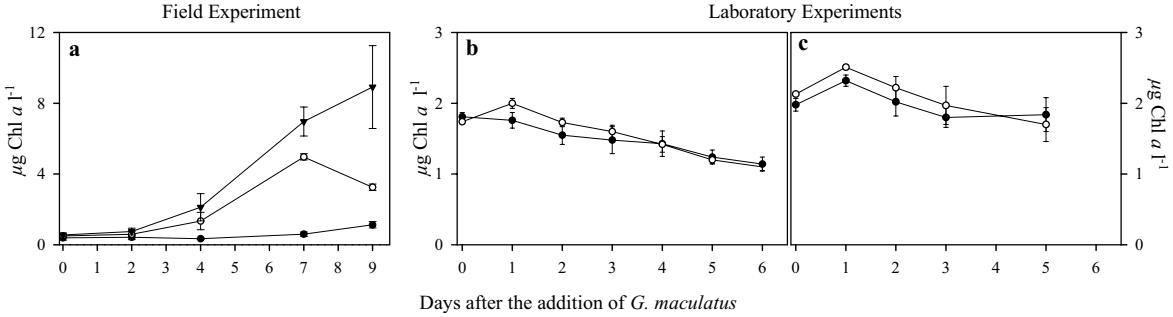

Figure 1. Mean values (± standard errors) of Chl *a* concentrations in fishless and *G. maculatus* treatments during the experiments. (a) Field experiment (black circles: Fishless; white circles: Low fish; triangles: High fish); (b and c) January and March Laboratory experiments (black circles: Fishless; white circles: Fish).

increased in fish enclosures but changed little in the fishless ones (Figure 1a). Positive multiple regression was obtained between Chl *a* concentration, incubation time, and fish biomass ($R^2 = 0.70$, n = 70, $P < 0.0001$). Thus, the treatment with eight fish had a higher effect on algal biomass than that with four fish, and both treatments had a higher algal biomass than the fishless treatment.

On the contrary, laboratory experiments did not show significant differences in Chl *a* concentration (Table 2) with a slight decrease in both fish and fishless treatments (Figure 1b,c). This condition of little or no changes in Chl *a* concentrations allowed us to assume that there were no changes in phytoplankton biomass. Consequently, changes in nutrient concentrations and differences between treatments would reflect nutrient release by fish.

Nutrients

The obtained SRP values were very low in all experimental dates, and their concentrations should be considered undetectable ($<1\ \mu g\ l^{-1}$). Therefore, these values were not included in this study.

In field experiment (December), the average TP and TDP concentrations increased significantly in the presence of *G. maculatus* (Table 2, Figure 2), indicating that fish had a significant effect on the phosphorus dynamics. Low fish treatment had a smaller increase in TP and TDP concentrations than high fish treatment (Figure 2). The average of $N–NH_4^+$ concentration and the $N_{NH_4} : P_{TDP}$ ratio showed no clear trends in this field experiment (Figure 2).

The increase in algal biomass (Chl a_t − Chl a_{t-1}) during the field experiment was positively correlated with TDP_{Gm} at time t − 1, until day 7 (Table 3). Likewise, Chl *a* concentration was positively correlated with TPP in fish treatments (Table 3), indicating that the increase in P uptake due to the increased algal biomass would be responsible for the conversion of released P into particulate phosphorus.

In laboratory experiments, we were able to analyse better the nutrient released by fish. As in the field experiment, we also observed a significant effect of fish on TP and TDP concentrations (Table 2, Figure 3), while no significant variations were observed in fishless treatments. Ammonium showed similar trends as Phosphorus (Table 2, Figure 3); however, a slight increase was observed in fishless treatment in March experiment (Figure 3). Changes in TP, TDP, and NH_4^+ concentrations were significantly greater in January than in March experiment due to the higher fish biomass used in the former (Table 4).

In both laboratory experiments, the $N_{NH_4} : P_{TDP}$ ratio increased significantly in fish treatments compared with fishless ones (Table 2, Figure 3). At the beginning of both laboratory experiments $N_{NH_4} : P_{TDP}$ ratio was around 2, and this value remained constant in fishless treatment of January and increased slightly in March. However, in fish treatments this ratio increased greatly. A 5-fold increase was observed in fish treatment of January ($N_{NH_4} : P_{TDP}$ ratio of 10), while a 2-fold increase was observed in March ($N_{NH_4} : P_{TDP}$ ratio of 4).

Mass-specific nutrient release of *G. maculatus* was tested only in laboratory experiments, because we could assume that most part of nutrients released by fish were mainly accumulated in the water. As expected from body size differences, the smaller fish of March experiment (Table 4) had higher mass-specific nutrient release than larger ones of January (Figure 4), but

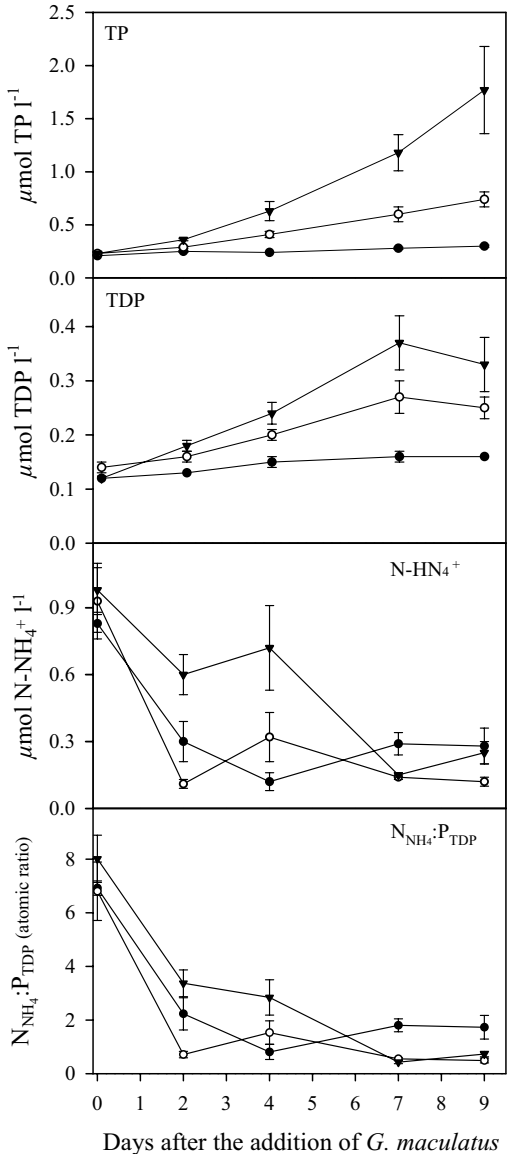

Figure 2. Mean values (± standard errors) of total phosphorus, total dissolved phosphorus, ammonium concentrations and atomic $N_{NH_4} : P_{TDP}$ ratio dynamics during the field experiment with *G. maculatus* (black circles: Fishless; white circles: Low fish; triangles: High fish).

only TDP showed significant differences (comparison of slopes: $t_{0.05,26} = 2.72$, $P < 0.05$). On the contrary, the mass-specific $N_{NH_4} : P_{TDP}$ ratio released by fish was positively related with fish size although no significant differences were observed (comparison of slopes: $t_{0.05,26} = 0.32$, $P > 0.05$) (Figure 4).

Table 3. Pearson correlation coefficients between mean phosphorus fractions and Chl *a* increase in fish treatments of field experiment. Chlorophyll *a* increase was calculated until day 7 between t and t − 1. TDP_{Gm} (TDP supplied by *G. maculatus*, calculated as the TDP difference between fish and fishless treatments), LF (low fish treatment), HF (high fish treatment).

	Treatment	r	P-value	N
Chl *a* increase vs. TDP_{Gm}	LF	0.70	0.003	15
at time t − 1	HF	0.90	<0.001	15
Chl *a* vs. TPP	LF	0.66	< 0.001	25
	HF	0.93	<0.001	25

Discussion

In our field experiment, where the conditions did allow algal growth, phytoplankton biomass was observed to be related directly with fish biomass, as it has been previously documented by Schindler (1992) and Pérez-Fuentetaja et al. (1996), among others. Indeed, in fish treatments, phytoplankton exposed to nutrients released by fish and reduced zooplankton grazing pressure registered an important increase in algal biomass (Figure 1).

Nitrogen released by fish is almost exclusively as ammonium (Brabrand et al. 1990), which is promptly available for phytoplankton uptake (Attayde & Hansson 1999). This fact and the great increase of phytoplankton biomass in our fish treatments suggest that the absence of an increase in the $N–NH_4^+$ concentration in the same treatments (Figure 2) could be due to a great demand of N by growing phytoplankton. A great proportion of phosphorus released by planktivorous and benthivorous fishes is directly available to algae as SRP, but part of the phosphorus is retained in faecal pellets and need microbial activity before it becomes available for algal growth (Brabrand et al. 1990). Our results let us assume that a proportion of phosphorus released by *G. maculatus* was promptly available for algal growth because algal biomass was positively correlated with TDP_{Gm} and TPP in fish treatments (Table 3), which implies that a fraction of phosphorus released by *G. maculatus* was transformed into phytoplankton biomass. However, increase of TDP in fish treatments (Figure 2) would indicate that part of the phosphorus might need further microbial processing before algal uptake. The fact that SRP was not detected does not necessarily imply that *G. maculatus* did not release it, but it could be due to a rapid uptake rate of this fraction by the algae.

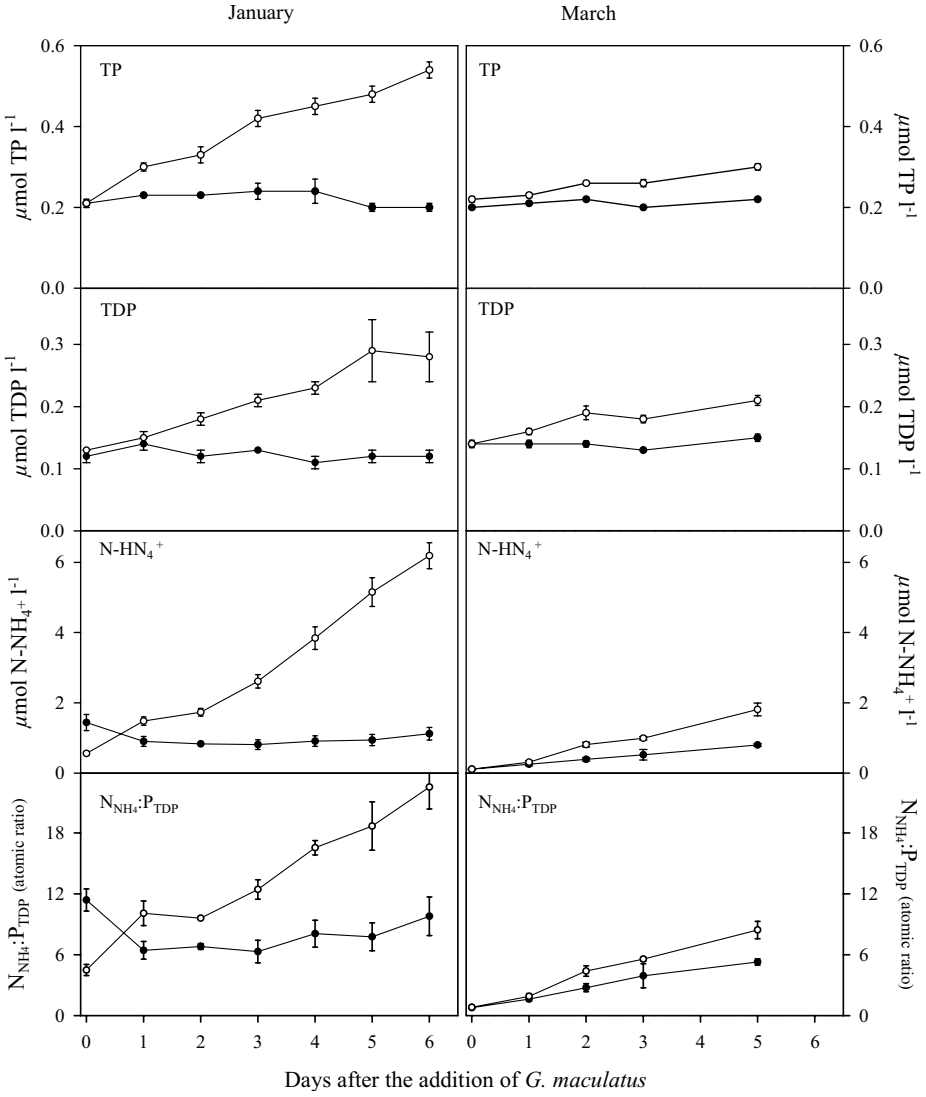

Figure 3. Mean values (± standard errors) of total phosphorus, total dissolved phosphorus, ammonium concentrations and atomic $N_{NH_4} : P_{TDP}$ ratio dynamics during the two laboratory experiments with *G. maculatus* (black circles: Fishless; white circles: Fish).

Table 4. Mean and standard errors of *G. maculatus* wet mass in the experimental unit of each experiment.

Experiment	Individual fish mass (g)		Number of fish	Total mass (g)		g fish l^{-1}	
	Mean	Error		Mean	Error	Mean	Error
December (field)							
Low fish	0.29	0.02	4	1.14	0.07	0.004	0.000
High fish	0.29	0.01	8	2.23	0.05	0.008	0.000
January (laboratory)	0.24	0.00	3	0.71	0.01	0.019	0.000
March (laboratory)	0.15	0.01	1	0.15	0.01	0.004	0.000

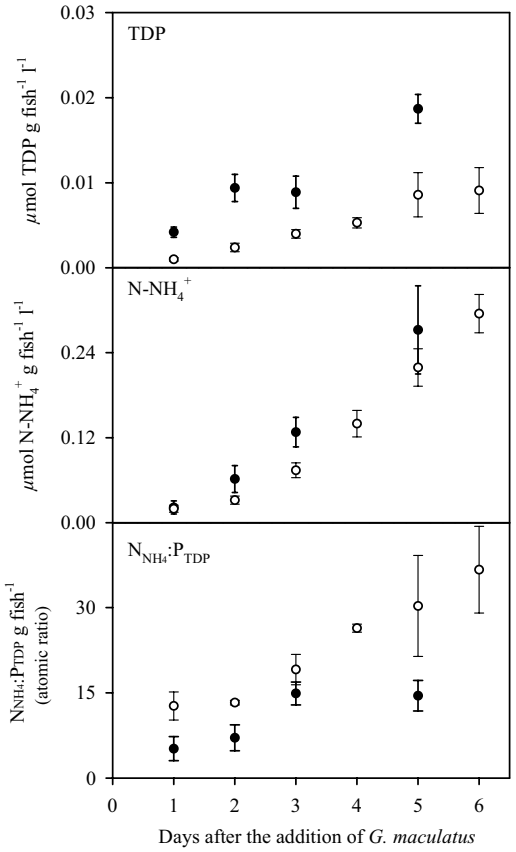

Figure 4. Mass-specific nutrient release by *G. maculatus* (mean values and standard errors) during laboratory experiments (black circles: Smaller fish; white circles: Larger fish).

On the other hand, the laboratory conditions did not allow phytoplankton increase. Consequently, our January and March experiments showed a slight decrease in phytoplankton biomass in both fish and fishless treatments (Figure 1). The difference in nutrient concentrations between fish and fishless containers could be related to nutrient released by fish, despite changes attributable to zooplankton recycling. Thus, the great quantity of nutrient measured in fish treatment in the laboratory, and the great increase in phytoplankton biomass in field experiment show that *G. maculatus* tends to reduce nutrient limitation of phytoplankton growth by providing a source of N and P in available forms. Furthermore, $N_{NH_4} : P_{TDP}$ ratio was significantly increased by fish indicating that *G. maculatus* can strongly influence phytoplankton community by changes in nutrient ratios. These shifts in phytoplankton $N_{NH_4} : P_{TDP}$ ratio can consequently modify the phytoplankton structure (Smith 1982), and also affect herbivores, as they are less flexible to changes in elemental ratios (Sterner & Hessen 1994).

Since our laboratory and field experimental units included neither benthic nor littoral prey, and *G. maculatus* only fed on zooplankton, the TP increment in fish treatments (Table 2) could not have arisen from those zones. Therefore, these increases can only be explained by the loss of P from fish tissue to the water column as was observed by Vanni et al. (1997), whose enclosures were closed to the bottom, so fish had no access to other items than zooplankton. However, the fact that *G. maculatus* juveniles and small adults combine planktonic and littoral prey (Pollard 1973, Cervellini et al. 1993, Battini 1997) indicates that they actually move between pelagic and littoral areas. Consequently, they can also redistribute nutrients retained in littoral and benthic prey, which otherwise would not be available for phytoplankton.

Recent studies showed an inverse allometric relationship between body size and mass-specific nutrient release by fish (Brabrand et al. 1990, Schindler et al. 1993, Schaus et al. 1997). Our results showed that the size structure of fish population may affect the amount of nutrients supplied to phytoplankton, because *G. maculatus* had less mass-specific excretion rate of N and P with increasing size (Figure 4). This increasing mass-specific nutrient release with decreasing body mass in *G. maculatus* could be explained through the higher metabolic rate of smaller fish with the intensification of consumption rates, promoting a higher nutrient allocation to growth, and even promote a higher nutrient release. The higher biomass production of smaller fish would demand a higher protein synthesis, with a high nitrogen requirement. In this context, it may be expected that smaller fish would increase $N_{NH_4} : P_{TDP}$ ratio less than larger ones.

Nutrients released by different zooplankton structures was studied by Balseiro et al. (1997) in one South Andean lake, concluding that changes in zooplankton density and constitution may change the nutrient supply ratio, causing alternative nutrient limitation for algae. The presence of planktivorous fish is associated, in many cases, with changes in zooplankton constitution and density (Lynch & Shapiro 1981, Gliwicz & Pijanowska 1989), and thus, they could be responsible for further alterations in nutrient excretion from zooplankton (Vanni & Findlay 1990, Ramcharan et al. 1996). In this sense, *G. maculatus* reduces crustacean biomass (Table 1) and probably modifies nutrient dynamics in two ways: (1) by their

own nutrient release, and (2) by altering the nutrient release of zooplankton.

Our results showed significant effects of *G. maculatus* on TP and TPP only in presence of high fish densities (Table 2). Although at the moment we do not have precise data on the densities of *G. maculatus* in Lake Escondido, we have a reference value of *G. maculatus* densities of 1–8 ind. m^{-3} for another shallow lake of the same basin (Cussac et al. 1992). In this sense, our experimental fish densities were one order of magnitude higher than presumable lake densities. However, the fact that *G. maculatus* is a species that moves in schools (Barriga et al. 2002) implies that high local densities are common in this species. Direct observations in Lake Escondido schools (Reissig, pers. observ.) and echosounder analysis based on Cussac et al. (1992) data, showed that school densities of this species reach 60–100 ind. m^{-3}; therefore, in our experiments we used similar or even lower densities than that achieved in natural population schools. The great spatial heterogeneity in fish density and our results in TP and TPP release rates under high fish densities, would generate very high spatial heterogeneity in nutrient release. In this sense, the nutrient patches would depend more on the clumping of *G. maculatus* rather than on global fish abundances. Although nutrient heterogeneity can be considered as ephemeral, due to school movements, algal uptake and nutrient diffusion, *G. maculatus* would have an important effect as would generate patches of low nutrient limitation with shifts in $N_{NH_4} : P_{TDP}$ ratios.

Acknowledgements

We are most grateful to B. Modenutti and two reviewers for their valuable comments on the manuscript, to V. Cussac and colleagues for their kindness in providing us the echosounder data, and to M. Battini for assisting us with fish capture. We also thank Gonzalo Pérez, Valeria Labud, and Marcelo Rivas for their kind assistance in the field. This research was financial supported by CONICET PIP 0739/98 and FONCyT PICT 01-06035.

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