

## The role of the predaceous copepod *Parabroteas sarsi* in the pelagic food web of a large deep Andean lake

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**Key words:** *Parabroteas sarsi*, invertebrate predation, visual predation, trophic cascade, *Boeckella*, calanoid copepod

Received 14 July 2003; in revised form 4 December 2003; accepted 9 January 2004

### Abstract

*Parabroteas sarsi* is a predaceous calanoid copepod that inhabits both shallow temporary fishless ponds and deep fish lakes of Patagonia and Antarctica. The aim of this study was to analyse the effect of *P. sarsi* on the plankton structure of a deep Andean lake (>100 m depth) and the zooplankton vertical distribution in order to assess a possible vertical refuge of the predatory copepod against visual fish predation. We tested the extent to which the trophic cascade effect of this predator propagates through the food web. We carried out a vertical sampling in Lake Rivadavia (Patagonia, Argentina) in order to assess zooplankton distribution. *P. sarsi* showed a vertical distribution towards deeper layers of the water column both at midday and at night, indicating that the copepod had an effective refuge against visual predation. Additionally, we carried out both field and laboratory experiments with the presence of *P. sarsi*. The predator was observed to affect significantly the survival of the copepod *Boeckella michaelsoni* both in laboratory and field experiments. On the contrary, rotifers and adults of *Daphnia* cf. *commutata* were not substantially affected by the predator. *B. michaelsoni* mouthparts revealed an omnivorous diet; therefore a broad phytoplanktonic size spectrum could be affected by this copepod. However, no cascade effect was observed due to the presence of *P. sarsi* despite the decrease of *B. michaelsoni* abundance.

### Introduction

The trophic cascade predicts that changes at the top of the food web are connected with the lower levels affecting phytoplankton biomass (Carpenter et al., 1985). In this scenario, predatory fish are considered keystone species (Benndorf, 1995) while invertebrate predators seemed of minor importance, although they are an important source of herbivorous zooplankton mortality (Black & Hairston, 1988; Wojtal et al., 1999; O'Brien, 2001). The potential impact of invertebrate predators in lake food web is difficult to predict since they are both predator and prey

(Luecke et al., 1992). In the Northern Hemisphere, the predaceous cladoceran *Leptodora kindti* can be considered as an effective reducer of herbivorous zooplankton and thus, decreasing filtering rates (Herzig & Auer, 1990; Arndt et al., 1993). However, the phytoplankton biomass control is weak (Gliwicz, 1977). In addition, the predatory copepod *Heterocope septentrionalis* was able to reduce *Daphnia pulex* and *Bosmina longirostris* in arctic ponds (O'Brien, 2001); and, in Lake Kinneret, the cyclopoid copepods *Mesocyclops oregonus* and *Thermocyclops dybowskii* produced a great

predation effect on herbivorous zooplankton (Blumenshine & Hambright, 2003).

In Andean lakes belonging to the Futaleufú basin a particular large zooplankton assemblage was observed (José de Paggi & Paggi, 1985; Pizzolón et al., 1995). The centropagids *Boeckella michaelsoni* (Mrázek) and *Parabroteas sarsi* Day, and the cladoceran *Daphnia* cf. *commutata* Ekman (*Daphnia middendorffiana* Fischer sensu J.C. Paggi) were present. *D.* cf. *commutata* is a large herbivorous species sharing their food resources with other zooplankton species including *B. michaelsoni*. *Parabroteas sarsi* is a predaceous calanoid copepod that inhabits both shallow temporary fishless ponds and deep fish lakes of Patagonia and Antarctica. Studies performed in temporary ponds indicated that this predaceous copepod can access to a great variety of prey including rotifers and cladocerans (Balseiro & Vega, 1994; Vega, 1995; Diéguez & Balseiro, 1998). Although the presence of *P. sarsi* has been reported in large deep lakes with fishes (José de Paggi & Paggi, 1985; Pizzolón et al., 1995), its predation impact and its relationship within the plankton food web remains unknown. The aim of this study was to analyse the effect of *Parabroteas sarsi* on the plankton structure of a deep fish lake with a possible vertical refuge. In addition, we tested the extent to which the trophic cascade effect of the invertebrate predator *P. sarsi* propagates through the food web.

### Study site

Lake Rivadavia (42° 34' S and 71° 39' W) has a surface area of 21.70 km<sup>2</sup> and the maximum depth is of 142 m. The lake has a glacial origin and drains to Lake Verde and then to Lake Futalaufquen conforming the Futalaufquen basin of Pacific watershed. Conductivity is low (24 µS cm<sup>-1</sup>) and lake water belongs to the calcium-bicarbonate type (José de Paggi & Paggi, 1985; Pizzolón et al., 1995). The thermal regime of Lake Rivadavia is warm monomictic, with stratification during spring and summer. Nutrient concentrations were low both in spring and in summer, total phosphorus varied between 5 and 7 µg l<sup>-1</sup> while total dissolved phosphorus was

estimated between 2.5 and 3.5 µg l<sup>-1</sup> (Modenutti et al., 2003).

Lake Rivadavia was reported to have exotic salmonids, *Salmo trutta* L., *Salvelinus fontinalis* (Mitchill) and *Oncorhynchus mykiss* (Walbaum), and autochthonous fishes as *Galaxias platei* Steindachner, *Aplochiton zebra* Jenyns, *Percichthys trucha* (Cuvier & Valenciennes) and *Odontesthes hatcheri* (Eigemann) (Milano et al., 2002; Ruzzante et al., 2003). Crustacean zooplankton was dominated by the calanoid copepod *Boeckella michaelsoni* and the presence of the large cladoceran *Daphnia* cf. *commutata* and the predaceous calanoid copepod *Parabroteas sarsi* was also reported (José de Paggi & Paggi, 1985; Modenutti et al., 2003). Microbial food web was observed to be dominated by phototrophic nanoflagellates and mixotrophic ciliates (Modenutti et al., 2003). Net phytoplankton was dominated by diatoms, chrysophytes, chlorophytes and dinoflagellates (Queimaliños, personal observation). No previous information on seasonal pattern of the plankton community is available.

### Materials and methods

#### Field study

The lake was sampled at a pelagic station (100 m depth) on December 5, 2000 and March 8, 2001. Temperature and light (Photosynthetically Active Radiation, PAR, 400–700 nm) profiles were measured from 0 to 60 m with a PUV 500B submersible radiometer (Biospherical Instruments). Water samples for chlorophyll *a* analyses and phytoplankton quantification were collected from 0 to 50 m each 10 m interval. Zooplankton vertical distribution was studied through a sampling (December 4, 2000) carried out at midday (12 h) and at the night (21 h: 1 h after sunset). In both occasions, vertical tows from 0 to 5 m, 5 to 10 m, 10 to 20 m, 20 to 30 m and 30 to 40 m were performed with two closing conical plankton nets (Bongo). One net was of 48 µm mesh size and the other one was of 202 µm mesh size, and the samples were used for rotifer and crustacean quantification, respectively. Crustaceans were

quantified under stereomicroscope in 5 ml Bogorov chambers, and rotifers in 1 ml Sedgwick–Rafter chamber under direct microscope. Total length (with furcal rami and without setae) of a minimum of 30 individuals of *Parabroteas sarsi* adults (females and males) were measured under a stereomicroscope with a graduate eyepiece. The body size of this predator was compared with other specimens of Laguna Fantasma, a temporary pond near Bariloche (Reissig, personal observation) and data from literature. Statistical analysis was carried out with own measurements of Lake Rivadavia and Laguna Fantasma since the literature data provided only the mean values.

*Boeckella michaelsoni* mandibles were dissected under a stereomicroscope and mounted in polyvinyl alcohol–lactophenol. The slides were observed under a direct microscope Olympus BX50 and images were digitalized with Image Pro Plus Program (Media Cybernetics). Mouthparts were measured using the same computer program. Following Green & Shiel (1999) the Edge Index was calculated. A value <500 indicated an herbivore mode of feeding, within 500 and 1000 an omnivore and >1000 a carnivore.

#### Laboratory experiments

In order to assess *P. sarsi* predatory effect on the copepod *B. michaelsoni* we performed three laboratory experiments (December 2000). In the experiments, 20 or 30 adults of *B. michaelsoni* were exposed to *P. sarsi* in 200 ml of filtered lake water (20  $\mu$ m mesh). The water and the specimens used in the experiments were freshly collected the same day of experimentation at 20 m depth. The experiments lasted 24 h and they were conducted in a growth chamber at 15 °C in darkness. Afterwards, the remaining *B. michaelsoni* were collected and live individuals were counted under a stereomicroscope. The predation experimental series were as follows, P1: 20 adults of *B. michaelsoni* + 6 *P. sarsi* (III and IV copepodits), P2: 30 adults of *B. michaelsoni* + 3 *P. sarsi* (ovigerous females) and P3: 30 adults of *B. michaelsoni* + 3 *P. sarsi* (non-ovigerous females). Each experiment was conducted with three replicates, and at the same time three replicates were con-

ducted without the predator presence and considered as controls.

#### Field experiments

We carried out two series of field incubation experiments: 5–7 December 2000 (late spring, Experiment 1) and 8–11 March 2001 (late summer, Experiment 2). The experimental design consisted of three treatments with three replicates each. Polycarbonate bottles of 2 l were used as experimental units. Lake water was collected at 20 m depth using a Schindler–Patalas trap and filtered through a 55  $\mu$ m mesh net. The filtered water was placed in four isolated tanks. About 1 h before starting the experiments, zooplankton was collected using a conical plankton net with 55  $\mu$ m mesh size. Vertical tows from 20 m to surface were performed for collecting *Boeckella* and rotifers and from 40 to 20 m for collecting *Daphnia* and *Parabroteas*. After sampling, zooplankton was acclimatized in 1 l beakers containing filtered lake water. *Daphnia* and *Parabroteas* were rinsed with filtered lake water in order to avoid other zooplankton, and separated in 500 ml beakers. To initiate the experiment, filtered lake water was poured into the 2 l bottles and the different zooplankton species were added using a wide bore pipette. Three different zooplankton compositions were added (Z, Z + P and Z + D + P). Zooplankton treatment (Z) consisted only in the addition of *B. michaelsoni* and rotifers, Z + P was constituted by *B. michaelsoni* and rotifers with five adults of *P. sarsi*. The treatment Z + D + P consisted in the addition of *B. michaelsoni* and rotifers, five adults of *P. sarsi* and five adults of *Daphnia* cf. *commutata*. The treatments did not reflect precisely natural abundances since those of *Parabroteas* and *Daphnia* have been enhanced.

The Experiment 1 (December) lasted 2 days (48 h), therefore a total of 27 bottles were prepared of which 9 were carried immediately to the lab to quantify the initial conditions. The remaining 18 bottles were incubated in a frame at a depth of 10 m at a pelagic lake station, and after each 24 h of incubation 9 bottles were removed from the frame. The Experiment 2 (March) lasted 3 days (72 h), therefore 36 bottles were used and the same procedure was followed.

### Data analysis

In all cases, the 2 l experimental units were carried to the laboratory in darkness and thermally isolated, within half an hour of removal from the frame. In the laboratory, a volume of 150 ml was used for chlorophyll *a* determinations. The entire volume was filtered through GF/F Whatman filters and chlorophyll *a* concentrations were determined with a fluorometer (Turner AU10) after ethanol 90% extraction following Nusch (1980) procedures. A volume of 100 ml was preserved with acid Lugol solution for phytoplankton quantification. Finally, zooplankton was collected with a plankton net of 55  $\mu\text{m}$  and fixed with 4% formaldehyde.

Phytoplankton enumeration was performed with an inverted microscope following Utermöhl technique at 400 $\times$ . The limit between nano and net phytoplankton was considered as 20  $\mu\text{m}$  GALD (Greatest Axial Linear Dimension). Zooplankton was quantified in Bogorov and Sedgwick–Rafter chambers as above.

Clearance rates were calculated according to Dodson (1984), and analysed through an one-way ANOVA. Phytoplankton growth rates were calculated following Queimaliños et al. (1998). Field experimental data were analysed through repeated measures ANOVA and equal variance and normality were previously tested. When significant differences were obtained, a Tukey Test was applied.

### Results

During our study the lake was thermally stratified. In December, the epilimnion had a temperature of 11.5 °C and reached 30 m depth, whereas in March the mixing layer was at 14.7 °C and was extended up to 32 m depth. The level of 1% of surface PAR irradiance (euphotic zone) was observed to reach the 20 m depth in both occasions. Chlorophyll *a* concentration showed an almost even distribution in the euphotic zone and was similar in both occasions (1.60  $\mu\text{g l}^{-1}$  in December and 1.65  $\mu\text{g l}^{-1}$  in March).

Lake phytoplankton abundance ranged from 489 cell  $\text{ml}^{-1}$  in December to 450 cell  $\text{ml}^{-1}$  in March. The nanoplankton (<20  $\mu\text{m}$ ) was domi-

nated by *Chrysochromulina parva* Lackey and *Rhodomonas lacustris* (Pascher & Ruttner) Javornicky. The net phytoplankton of the lake was mainly composed by the chrysophyceans *Dinobryon sertularia* Ehr. and *D. divergens* Imhof, the dinoflagellate *Gymnodinium paradoxum* Schilling and the chlorophytes *Pandorina morum* Bory and *P. smithii* Chodat. Besides, the diatoms *Synedra ulna* (Nit.) Ehr., *S. actinastroides* Lemm., *Aulacoseira granulata* (Ehr.) and *Asterionella formosa* Hassall were also observed. The nano: net phytoplankton ratio was different in the two sampling occasions being higher in spring than in summer (6 in spring and 0.5 in summer).

Lake zooplankton was dominated by rotifers (*Keratella cochlearis* Gosse and *Synchaeta* spp.) while *B. michaelsoni* dominated the crustacean assemblage. A particular vertical distribution was observed within the zooplankton. Rotifers showed a slight variation in the vertical distribution between midday (12 h) and night (21 h) (Fig. 1). This minor variation in the vertical distribution might indicate that not marked changes in predation impact or food concentration for rotifers occurred. In addition, rotifers migration ability is less significant in comparison to crustaceans, therefore no great changes between day and night may be expected. On the contrary, *D. cf. commutata* and *B. michaelsoni* exhibited the greatest differences in their vertical profiles, with higher abundances at 30–40 m depth during daytime and at 5–10 m depth in the night sampling (Fig. 1). Remarkably, the large predaceous copepod *P. sarsi* did not show differences and was always present in higher abundances in the aphotic zone at 30–40 m depth (Fig. 1).

In Lake Rivadavia, *P. sarsi* total length was observed to average (female and male pooled) 3.078  $\pm$  0.045 mm and cephalothorax length was of 2.361  $\pm$  0.040 mm. No marked changes in body size were observed between December and March specimens. Comparisons of these specimens with others from temporary ponds and other deep lakes showed important differences (Table 1). The specimens from Lake Rivadavia (deep fish lake) are less coloured (almost colourless) and smaller in body size than those of small temporary and fishless ponds (Table 1). A significant statistical difference in body size was observed between specimens from Laguna Fantasma a shallow,

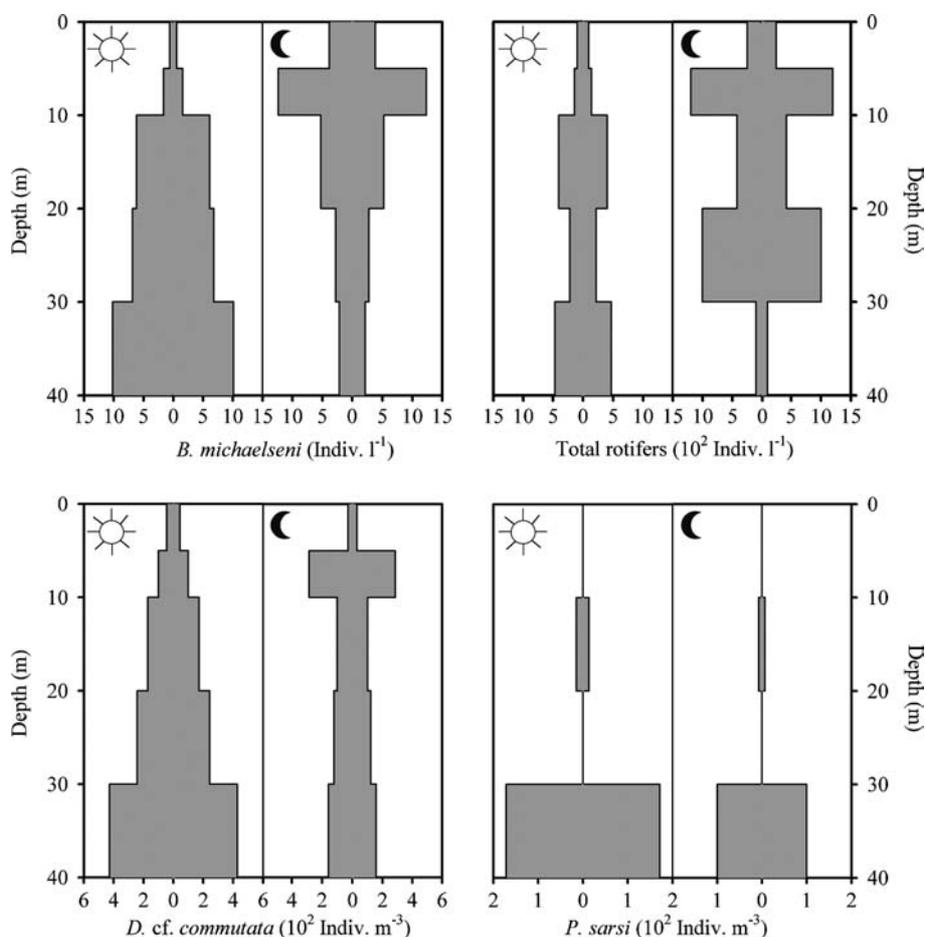


Figure 1. Zooplankton vertical distribution in Lake Rivadavia on December 4, 2000, at midday (☀: 12 h) and at night (☾: 21 h). Abundances of *B. michaelsoni*, *P. sarsi* and *D. cf. commutata* included all instars.

Table 1. Size (total length) and colour of *Parabroteas sarsi* in the different aquatic environments of Antarctica and Patagonia

Site	Type	Presence of fishes	Size (mm)		Colour	Author
			Male	Female		
Lake Situació (43° 05' S 71° 40' W)	DL	F	3.15	3.50	NA	José de Paggi & Paggi (1985)
Temporary pond in Santa Cruz province	SL	NF	NA	7	Red	Brehm (1956)
Signy Island (60° 38' S 45° 20' W)	SL	NF	NA	7.5	NA	Heywood (1970)
Fantasma pond (41° S 72° W)	SL	NF	4.2	4.8	Brilliant red–orange	Vega (1999)
Fantasma pond (41° S 72° W)	SL	NF	4.94 ± 0.03	4.97 ± 0.03	Brilliant red–orange	This study
Lake Rivadavia (42° 34' S 71° 39' W)	DL	F	2.93 ± 0.05	3.08 ± 0.02	Colourless	This study

References: F (fishes), NF (no fishes), DL (deep lake,  $Z_{\max} > 100$  m), SL (shallow lake), NA (not available data). The measurements of this study correspond to mean ± standard error. Literature data reported only mean values.

temporary pond near Bariloche and the deep Lake Rivadavia (ANOVA,  $p < 0.001$ ).

The mouthpart morphology of *Boeckella michaelsoni* was observed to be closely related with *B. gracilipes*, the other sudamerican *Boeckella* that inhabits Patagonian large and deep lakes (Balseiro et al., 2001). The Edge Index was estimated in  $816 \pm 25$  and this value is within the omnivorous range.

Our laboratory feeding experiments revealed that copepodites (III and IV) and adult females of *P. sarsi* were able to access to adults of *B. michaelsoni* (females  $0.928 \pm 0.005$  mm and males  $0.837 \pm 0.004$  mm). *B. michaelsoni* survival in the controls was of 100%. The higher clearance rates were obtained with non-ovigerous females of *P. sarsi* (Table 2). The differences between the observed clearance rates were significant (ANOVA,  $p < 0.05$ ). Our laboratory experiments determined clearance rates at 15 °C and the lake hypolimnion, where *P. sarsi* inhabits, has 7 °C. This difference could alter metabolic rates and might cause a laboratory overestimation of the clearance rates.

During our two field experiments, the survival of *Parabrotteas* was of 100% in the different treatments. The presence of *P. sarsi* decreased *B. michaelsoni* survival. At the end of incuba-

tion in the enclosures where the predaceous copepod was present, *B. michaelsoni* decreased substantially (Fig. 2, Table 3). On the contrary, *D. cf. commutata* was not affected by this predator since after 48 (Experiment 1) or 72 h (Experiment 2) the five adults were recovered. The pattern observed in rotifers differed in our two experiments. In December, total rotifers did not change substantially their abundances in the presence of *P. sarsi* (Table 3). On the contrary in the March experiment, *P. sarsi* enhanced rotifer abundance since *Synchaeta* spp. increased (Fig. 3, Table 3). In this experiment, the presence of *D. cf. commutata* had a negative effect on rotifer survival after 48 and 72 h of incubation although no statistical significant difference was obtained (Fig. 3, Table 3). Probably, the different pattern observed in the December and March experiments was due to the extended incubation time in the latter.

Phytoplankton biomass in term of chlorophyll *a* concentration was observed without remarkable changes in the different treatments of both experiments (Fig. 4, Table 3). These results indicated that the cascade effect of *P. sarsi* is weak. In the first experiment (December) the nanoplanktonic flagellates ( $<20 \mu\text{m}$ ) exhibited negative growth rates in all treatments, whereas in large colonial

Table 2. Clearance rates of *P. sarsi* on *B. michaelsoni* in the laboratory experiments

Copepodites (III and IV)	Ovigerous females	Non-ovigerous females
$0.0435 \pm 0.0068$	$0.0671 \pm 0.0035$	$0.0936 \pm 0.0136$

Values are given as mean  $\pm$  standard error for the different *P. sarsi* instars, and the units are  $1 \text{ predator}^{-1} \text{ day}^{-1}$ .

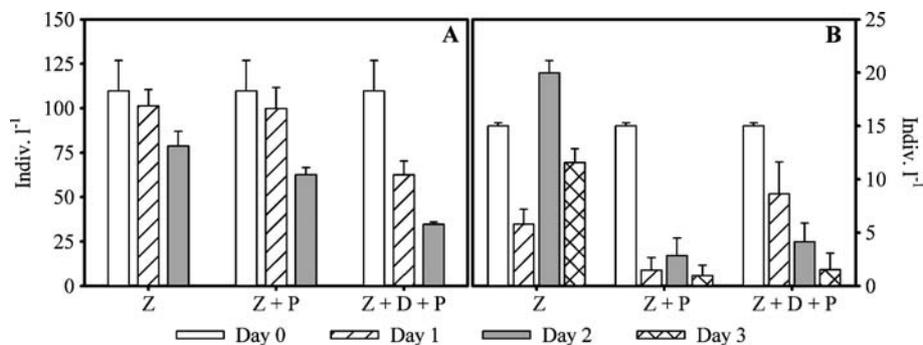


Figure 2. *Boeckella michaelsoni* abundances (mean  $\pm$  standard error) in the field incubations during the first (A) and second (B) experiment. For treatments references (Z, Z + P, Z + D + P), see methods.

Table 3. Result from repeated measures ANOVA of different zooplankton species and chlorophyll *a* concentration in the different treatments during both experiments (December and March)

Factor	Experiment		Z	Z + P	Z + D + P
<i>Boeckella michaelsoni</i>	December	*	A	AB	B
	March	**	A	B	B
Total rotifers	December	*	A	A	B
	March	**	A	B	A
<i>Synchaeta</i> spp.	December	**	A	A	B
	March	**	A	B	A
<i>Keratella cochlearis</i>	December	n.s.	A	A	A
	March	n.s.	A	A	A
Chlorophyll <i>a</i>	December	n.s.	A	A	A
	March	*	A	AB	B

References: Treatments Z, Z + P, Z + D + P see methods. A and B: groups with significant differences between them when assessed with *a posteriori* test (Tukey). AB: belonging to both groups. \*  $p < 0.05$ ; \*\*  $p < 0.001$ . n.s.: non-significant differences.

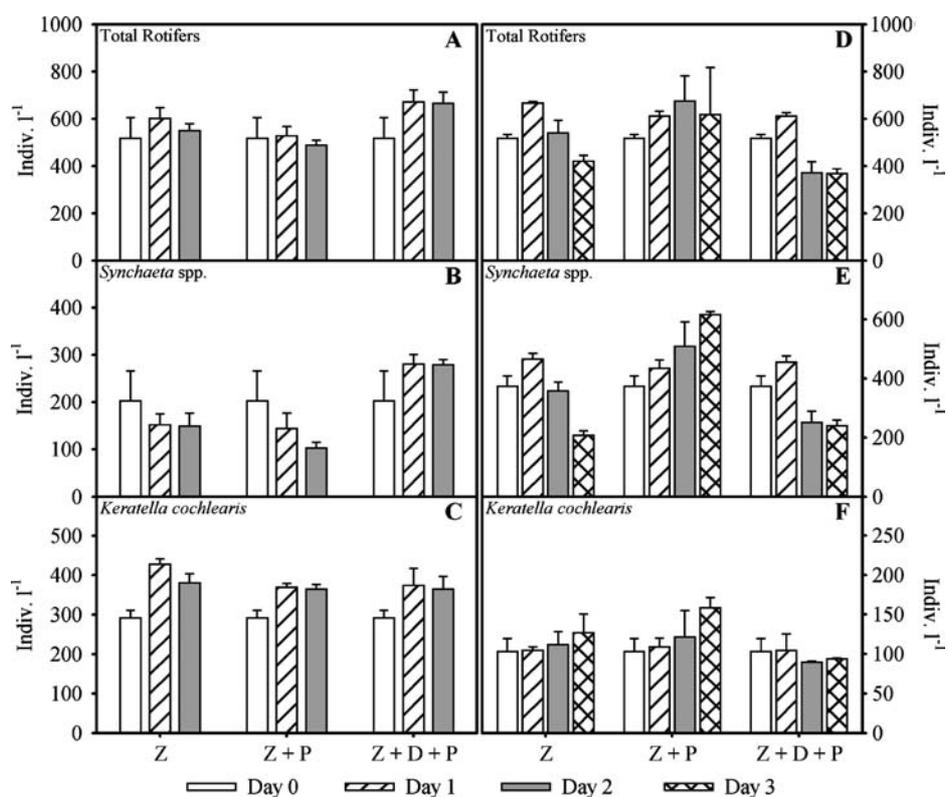


Figure 3. Rotifer abundances (mean  $\pm$  standard error) in the field incubations during the first (A, B and C) and second (D, E and F) experiment. For treatments references (Z, Z + P, Z + D + P), see methods.

flagellates (especially *Dinobryon* spp. and *Pandorina* spp.) a positive response occurred during the

incubations (Fig. 5). A contrasting pattern of phytoplankton growth was observed during the

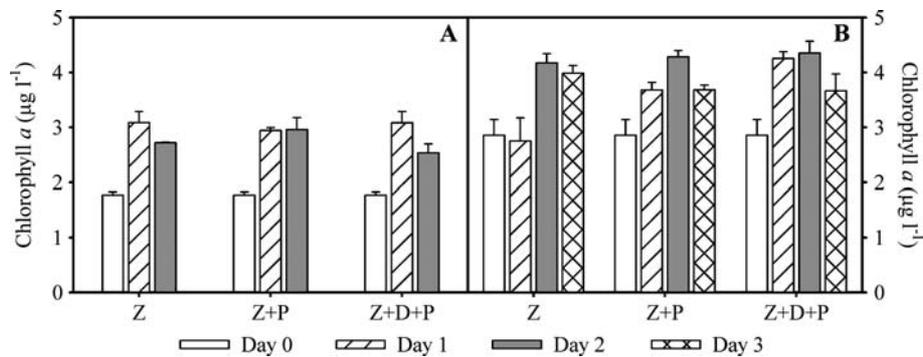


Figure 4. Chlorophyll *a* concentration (mean  $\pm$  standard error) in the field incubations during the first (A) and second (B) experiment. For treatments references (Z, Z + P, Z + D + P), see methods.

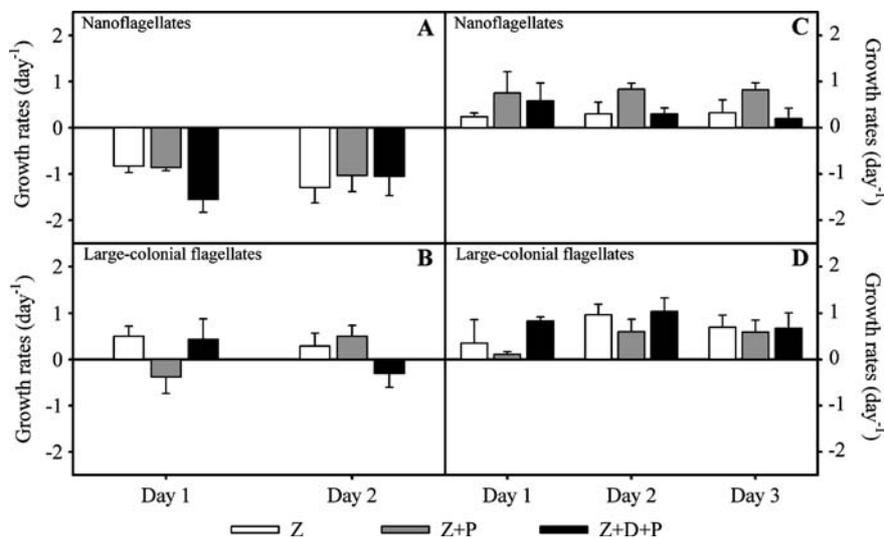


Figure 5. Growth rates (mean  $\pm$  standard error) of nanoflagellates (<20  $\mu\text{m}$ ) and large-colonial flagellates (>20  $\mu\text{m}$ ) in the field incubations during the first (A and B) and second (C and D) experiment. For treatments references (Z, Z + P, Z + D + P), see methods.

second experiment (March). In this case, the nanoflagellate assemblage showed positive growth rates in the treatments except in Z + D + P at 72 h of incubation (Fig. 5). A no clear pattern was detected for large colonial flagellates although at 48 h of incubation a positive effect was observed in the Z + D + P treatment (Fig. 5).

## Discussion

In the deep Lake Rivadavia the predaceous copepod *P. sarsi* was observed to affect significantly *B. michaelsoni* survival both in laboratory and field

experiments. These results indicated that *B. michaelsoni* is the most frequent prey in deep lakes with *P. sarsi*. Besides, a coincident geographic distribution in deep lakes of both copepod species was previously observed (José de Paggi & Paggi, 1985). Although in temporary fishless ponds the predator includes diatoms, rotifers and cladocerans in its diet, from copepodit IV to adult the diet of *P. sarsi* includes other copepod species (Vega, 1999). Therefore, the role of *P. sarsi* in structuring copepod assemblages is of a particular importance in both, deep lakes with fishes and shallow fishless ponds.

Adults of *D. cf. commutata* were not substantially affected by the predator. An increase in prey body size decreases vulnerability to an invertebrate predator (Gliwicz & Pijanowska, 1989). In the case of *D. cf. commutata* the large body size of adults (2.5 mm) would limit the access of the predator as was showed through laboratory experiments by Balseiro & Vega (1994). Adults of *P. sarsi* could easily capture and ingest prey up to 1.6 mm long in the temporary pond Laguna Fantasma. Therefore, this predator can access to *Daphnia* juveniles but the production of a long tail in offspring decreased their mortality rates (Balseiro & Vega, 1994). In the case of Lake Rivadavia, the production of a long tail spine in the juveniles was also observed (Balseiro, personal observation). This defence strategy and the smaller body size of the predator (Table 1) probably contribute to a smaller impact on natural *Daphnia* population.

In our experiments, rotifers were not negatively affected by *P. sarsi*. Vega (1999) reported that during the copepod's development, copepodits included rotifers as an important item in their diet. However, larger prey increases their relative importance in the late copepodit's diet when their maxilliped length increased (Diéguez & Balseiro, 1998). Since our experiments were carried out with *Parabroteas* adults, it can be expected a low impact on rotifers.

There is strong evidence that rotifers cannot become abundant in the presence of large *Daphnia* (>1.2 mm) (Gilbert, 1988). In our late summer experiment (March) when the nanoplankton was diminished (Nano:Net phytoplankton ratio 0.5), *D. cf. commutata* affected negatively rotifer abundances. Under food limited conditions, large bodied *Daphnia* can suppress rotifers by interference and exploitative competition (MacIsaac & Gilbert, 1991). Therefore, both mechanisms may have occurred in our experimental bottles.

The *B. michaelsoni* mouthparts revealed an omnivorous diet, therefore a broad spectrum of phytoplankton sizes could be affected by this copepod. The negative growth rates observed in the field experiment treatments may indicate that this copepod preys on nanoflagellates, as was also observed by Balseiro et al. (2001) for *B. gracilipes* the other calanoid copepod that inhabits large and deep Andean lakes. However, no cascade effect was observed due to the presence of *P.*

*sarsi* despite the decrease of *B. michaelsoni* abundance.

Visual predators (fishes) are highly selective on optically conspicuous prey, therefore they feed preferentially on large-bodied and coloured zooplankton (Brooks & Dodson, 1965). Lake Rivadavia has two large zooplankters (*D. cf. commutata* and *P. sarsi*) that are potential prey for the rich fish assemblage present in the lake. Gut content analysis of fishes revealed that *Daphnia* is a frequent prey item while *P. sarsi* seemed to be not a common prey (Milano et al., 2002; Ruzzante et al., 2003). This result may indicate that the predatory copepod has an effective refuge against visual predation. Poorly illuminated habitats during the day are thought to reduce the probability of attack by visual predators (De Robertis, 2002). Lake Rivadavia presents higher attenuation coefficients ( $K_d = 0.25 \text{ m}^{-1}$ ) than other Andean lakes (Pérez et al., 2002). During our two sampling occasions *P. sarsi* showed a vertical distribution towards deeper layers of the water column (Fig. 1). The relatively turbid waters in a deep lake allowed colourless *Parabroteas* to take advantage of a vertical refuge. On the contrary, *D. cf. commutata* showed an upper distribution during night (Fig. 1) suggesting a diel vertical migration. This behaviour avoids the overlap with visual predators and allows *Daphnia* to graze in food-rich surface waters (Lampert, 1987). The same vertical pattern was observed for *B. michaelsoni* (Fig. 1), allowing *P. sarsi* to prey on *Boeckella* during daytime at the deeper layers below the euphotic zone. Prey capture mechanisms by calanoid copepods were observed to be independent of light since mechanoreception and feeding currents counteract in prey detection (Bundy & Vanderploeg, 2002). This implies that while herbivores need to migrate to upper layers for acquiring food of better quality the predaceous copepod can remain in deep waters avoiding the energetic cost of vertical migration.

The described vertical scenario in Lake Rivadavia highly contrasts with those of shallow temporary ponds, although in both environments the predator is present. Therefore, we conclude that *P. sarsi* can be a major component in zooplankton assemblages both in fishless and in deep fish lakes. In addition, the survival of other calanoid copepods, such as species of *Boeckella*, is significantly influenced by this predator.

## Acknowledgements

This study was supported by FONCyT PICT 01-06035 and CONICET PIP 0739/98 and 02175/01. Mariana Reissig has a CONICET Doctoral fellowship. B. Modenutti, E. Balseiro and C. Queimaliños are CONICET researchers.

## References

- Arndt, H., M. Krockner, B. Nixdorf & A. Köhler, 1993. Long-term annual and seasonal changes of meta and protozooplankton in lake Müggelsee (Berlin): Effects of eutrophication, grazing activities and the impact of predation. *Internationale Revue der gesamten Hydrobiologie* 78: 379–402.
- Balseiro, E. G. & M. Vega, 1994. Vulnerability of *Daphnia middendorffiana* to *Parabroteas sarsi* predation: the role of the tail spine. *Journal of Plankton Research* 16: 783–793.
- Balseiro, E. G., B. E. Modenutti & C. P. Queimaliños, 2001. Feeding of *Boeckella gracilipes* (Copepoda, Calanoida) on ciliates and phytoflagellates in an ultraoligotrophic Andean lake. *Journal of Plankton Research* 23: 849–857.
- Benndorf, J., 1995. Possibilities and limits for controlling eutrophication by biomanipulation. *Internationale Revue der gesamten Hydrobiologie* 80: 519–534.
- Black, R. W. & N. G. Hairston, 1988. Predator driven changes in community structure. *Oecologia* 77: 468–479.
- Blumenshine, S. C. & K. D. Hambright, 2003. Top-down control in pelagic systems: a role for invertebrate predation. *Hydrobiologia* 491: 347–356.
- Brehm, V., 1956. Sobre los copépodos hallados por el Profesor Biraben en la Argentina. *Neotropica* 2: 22–32.
- Brooks, J. L. & S. L. Dodson, 1965. Predation, body size, and composition of plankton. *Science* 150: 28–35.
- Bundy, M. H. & H. A. Vanderploeg, 2002. Detection and capture of inert particles by calanoid copepods: the role of the feeding current. *Journal of Plankton Research* 24: 215–223.
- Carpenter, S. R., J. F. Kitchell & J. R. Hodgson, 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35: 634–638.
- De Robertis, A., 2002. Small-scale spatial distribution of the euphausiid *Euphausia pacifica* and overlap with planktivorous fishes. *Journal of Plankton Research* 24: 1207–1220.
- Diéguez, M. & E. Balseiro, 1998. Colony size in *Conochilus hippocrepis*: defensive adaptation to predator size. *Hydrobiologia* 387: 421–425.
- Dodson, S. I., 1984. Predation of *Heterocope septentrionalis* on two species of *Daphnia*: Morphological defenses and their cost. *Ecology* 65: 1249–1257.
- Gilbert, J. J., 1988. Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. *Limnology and Oceanography* 33: 1286–1303.
- Gliwicz, Z. M., 1977. Food size selection and seasonal succession of filter feeding zooplankton in an eutrophic lake. *Ekologia Polska* 25: 179–226.
- Gliwicz, Z. M. & J. Pijanowska, 1989. The role of predation in zooplankton succession. In Sommer, U. (ed.), *Plankton Ecology: Succession in Plankton Communities*. Springer-Verlag, New York: 253–296.
- Green, J. D. & R. J. Shiel, 1999. Mouthpart morphology of three calanoid copepods from Australian temporary pools: evidence for carnivory. *New Zealand Journal of Marine and Freshwater Research* 33: 385–398.
- Herzig, A. & B. Auer, 1990. The feeding behaviour of *Leptodora kindti* and its impact on the zooplankton community of Neusiedler See (Austria). *Hydrobiologia* 198: 107–117.
- Heywood, R. B., 1970. The mouthparts and feeding habits of *Parabroteas sarsi* (Daday) and *Pseudoboeckella silvestri*, Daday (Copepoda, Calanoida). In Holdgate, M. W. (ed.), *Antarctic Ecology*. Academic Press, London: 637–649.
- José de Paggi, S. & J. C. Paggi, 1985. Zooplankton de los cuerpos de agua preexistentes en el área del Embalse Amutui Quimei (Cuenca del Río Futaleufú). *Neotropica* 31: 119–131.
- Lampert, W., 1987. Vertical migration of freshwater zooplankton: indirect effects of vertebrate predators on algae communities. In Kerfoot, W. C. & A. Sih (eds), *Predation: Direct and Indirect Impacts on Aquatic Communities*. The University Press of New England, Hanover (NH): 291–299.
- Luecke, C., C. C. Lunte, R. A. Wright, D. Robertson & A. S. McLane, 1992. Impacts of variation in planktivorous fish on abundance of Daphnids: a simulation model of the Lake Mendota food web. In Kitchell, J. F. (ed.), *Food Web Management. A Case Study of Lake Mendota*. Springer-Verlag, New York: 408–424.
- Maclsaac, H. J. & J. J. Gilbert, 1991. Discrimination between exploitative and interference competition between cladocera and *Keratella cochlearis*. *Ecology* 72: 924–937.
- Milano, D., V. E. Cussac, P. J. Macchi, D. E. Ruzzante, M. F. Alonso, P. H. Vigliano & M. A. Denegri, 2002. Predator associated morphology in *Galaxias platei* in Patagonian lakes. *Journal of Fish Biology* 61: 138–156.
- Modenutti, B. E., C. P. Queimaliños, E. G. Balseiro & M. Reissig, 2003. Impact of different zooplankton structures on the microbial food web of an Andean oligotrophic lake. *Acta Oecologica* 24 S1: 289–298.
- Nusch, E. A., 1980. Comparison of different methods for chlorophyll and phaeopigment determination. *Archiv für Hydrobiologie Beihrage Ergebnisse der Limnologie* 14: 14–36.
- O'Brien, W. J., 2001. Long-term impact of an invertebrate predator, *Heterocope septentrionalis*, on an arctic pond zooplankton community. *Freshwater Biology* 46: 39–45.
- Pérez, G. L., C. P. Queimaliños & B. E. Modenutti, 2002. Light climate and plankton in the deep chlorophyll maxima in North Patagonian Andean lakes. *Journal of Plankton Research* 24: 591–599.
- Pizzolón, L., N. Santinelli, M. C. Marinone & S. A. Menú Marqué, 1995. Plankton and hydrochemistry of Lake Futaleufú (Patagonia, Argentina) during the growing season. *Hydrobiologia* 316: 63–73.
- Queimaliños, C. P., B. E. Modenutti & E. G. Balseiro, 1998. Phytoplankton responses to experimental enhancement of grazing pressure and nutrient recycling in a small Andean lake. *Freshwater Biology* 40: 41–49.

- Ruzzante, D. E., S. J. Walde, V. E. Cussac, P. J. Macchi, M. F. Alonso & M. Battini, 2003. Resource polymorphism in a Patagonian fish *Percichthys trucha* (Percichthyidae): phenotypic evidence for interlake pattern variation. *Biological Journal of the Linnean Society* 78: 497–515.
- Vega, M., 1995. Morphology and defense structures in the predator-prey interaction: an experimental study of *Parabroteas sarsi* (Copepoda, Calanoida) with different cladoceran preys. *Hydrobiologia* 299: 139–145.
- Vega, P. M., 1999. Life-state differences in the diet of *Parabroteas sarsi* (Daday) (Copepoda, Calanoida): a field study. *Limnologia* 29: 186–190.
- Wojtal, A., P. Frankiewicz & M. Zalewski, 1999. The role of the invertebrate predator *Leptodora kindii* in the trophic cascade of a lowland reservoir. *Hydrobiologia* 416: 215–223.