

DOI: 10.1002/iroh.200711011

CAROLINA TROCHINE*, ESTEBAN G. BALSEIRO and BEATRIZ E. MODENUTTI

Laboratorio de Limnología, CONICET-Centro Regional Universitario Bariloche,
Universidad Nacional del Comahue, Quintral 1250, R8400FRF Bariloche, Argentina,
e-mail: trochine@crub.uncoma.edu.ar

Research Paper

Zooplankton of Fishless Ponds of Northern Patagonia: Insights into Predation Effects of *Mesostoma ehrenbergii*

key words: predator-prey interaction, size spectra, Turbellaria, calanoid copepods, fishless lakes

Abstract

The turbellarian predator *Mesostoma ehrenbergii*, a common inhabitant of fishless ponds of northern Patagonia, can consume prey larger than 1 mm. Because the feeding strategy of *M. ehrenbergii* includes mucus trapping and external digestion, this predator may exploit a broad range of prey sizes. We hypothesize that *M. ehrenbergii* could exert a strong effect on zooplankton composition and body size spectra in Patagonian fishless ponds. We investigated this hypothesis by analyzing the crustacean zooplankton composition and size spectra in five fishless ponds of northern Patagonia, and we carried out experiments to assess predation rates of *M. ehrenbergii* on potential prey species from 0.8 mm to 6 mm. These ponds were colonized by macrophytes, which favored habitat heterogeneity, especially in the smaller ponds that had higher species richness. The surveyed ponds showed distinctive crustacean zooplankton assemblages and sizes, but all were dominated by calanoid copepods of the genus *Boeckella*. Our results indicated that *M. ehrenbergii* consumed the whole size range of offered prey, from ~0.8 mm (*Ceriodaphnia dubia*) to ~6 mm (*Parabroteas sarsi*). Predation rates were higher for intermediate-bodied copepods (~1.5 mm) and *C. dubia* (0.8 mm), but we did not find conclusive evidence that variations in size spectra of crustacean zooplankton are a result of *M. ehrenbergii* predation. We suggest that an interaction between prey body size and its evasion tactic might be important to determine the true effect *Mesostoma* on zooplankters. The structural complexity created by macrophytes in Patagonian fishless ponds may also help account for the lack of a strong predation effect of *Mesostoma* in the field survey.

1. Introduction

Small shallow lakes or ponds covering only few hectares have received little attention despite their numerical prevalence and rich biological diversity (WILLIAMS *et al.*, 1999; BIGGS *et al.*, 2001; OERTLI *et al.*, 2002). In particular, these environments share unique characteristics such as high terrestrial-aquatic interchange as a result of the high ratio of surface area to volume (PALIK *et al.*, 2001) and an extensive littoral zone with different types of aquatic vegetation that may cover the entire water body. Macrophytes play an important role in determining species diversity since they generate more physically complex habitats containing more species (BELL *et al.*, 1991). In addition, a shallow lake morphometry with relatively low water volumes results in a higher exchange between benthic and pelagic zones, and a greater availability of sediments as a source of nutrients in the water column

* Corresponding author

(TESSIER and WOODRUFF, 2002). Further, environmental heterogeneity favours singular species of flora and fauna and, consequently, total biodiversity per unit area may be higher in small lakes or ponds (GEE *et al.*, 1997; OERTLI *et al.*, 2002). Temporary ponds could play an important role in the metapopulation dynamics of many freshwater species because of their high biodiversity (NICOLET *et al.*, 2004). Thus, a region that contains temporary ponds as part of a mosaic of freshwater habitats is likely to contribute to the health of the freshwater environment as a whole (NICOLET *et al.*, 2004).

The northern Patagonian Andean region (around 41°S) has an important hydrographic system that includes several lakes of glacial origin (IRIONDO, 1989). Zooplankton assemblages are characterized by the dominance of endemic calanoid copepods, particularly centropagids of the genus *Boeckella* (MODENUTTI *et al.*, 1998; MENU-MARQUE *et al.*, 2000). Further, fishless lakes represent reservoirs of biodiversity of centropagid copepod assemblages (MENU-MARQUE *et al.*, 2000). Important differences have been documented between the plankton community structure in Patagonian lakes and ponds with and without fish (MODENUTTI and BALSEIRO, 1994; REISSIG *et al.*, 2006). In particular, the genus *Daphnia* is restricted to small fishless lakes (REISSIG *et al.*, 2006) or deep lakes with low C:P ratios (<400) (BALSEIRO *et al.*, 2004). Size-selective predation by fish can reduce the abundance of large taxa (>1 mm), favouring the dominance of small-bodied (<1 mm) zooplankton in the environment (BROOKS and DODSON, 1965; GLIWICZ and PIJANOWSKA, 1989). In particular, non marine centropagid species have a wide size range (~0.7 mm–~3.3 mm), which may be wider (upper limit 6–7 mm) if the predaceous *Parabroteas sarsi* (DADAY) is present (BAYLY, 1992). Recently, REISSIG *et al.* (2006) indicated that this assemblage has been substantially affected by fish predation in lakes of the Patagonian Plateau. However, changes in the zooplankton size spectrum are still possible in fishless environments where other predators are present (*e.g.*, *Chaoborus*, *Mysis*, backswimmers, and dragonflies) (MURDOCH *et al.*, 1984; SWIFT, 1992; SHURIN, 2001; GONZALEZ SAGRARIO and BALSEIRO, 2003; STEINER and ROY, 2003).

Previous studies on fishless Patagonian wetlands showed that the turbellarian predator *Mesostoma ehrenbergii* (FOCKE) is a common inhabitant of these environments, and can consume prey >1 mm (1.5 mm to 2 mm) (TROCHINE *et al.*, 2005, 2006). Because the feeding strategy of *M. ehrenbergii* includes mucus trapping and external digestion, prey size selection does not depend upon the size of the predator's mouthparts, as observed for copepods and insect predators (SWIFT, 1992; DIÉGUEZ and BALSEIRO, 1998). This feeding behaviour might allow *Mesostoma* to consume a broader size range of prey, allowing us to hypothesize that *M. ehrenbergii* exerts an effect on zooplankton species composition and body size in Patagonian fishless ponds. Therefore, our objectives were to characterize zooplankton species assemblages and size spectra of northern Patagonian ponds in the presence and absence of *M. ehrenbergii*. In addition, we conducted laboratory experiments to determine the prey size range of *M. ehrenbergii* among zooplankton species. Thus, we studied whether zooplankton species composition was related to *Mesostoma* and whether *Mesostoma* predation affects the average body size of the zooplankton occurring in the ponds.

2. Methods

2.1. Study Area

We conducted our study in five fishless wetlands in northern Patagonia, located at 41°S, near the city of San Carlos de Bariloche, Río Negro, Argentina (Fig. 1). The study area occurs in Nahuel Huapi National Park, which has an important hydrographic system that includes various lakes of glacial origin (IRIONDO, 1989). The climate is dry and cold, and there is an east-west gradient in precipitation (800–1.400 mm per year).

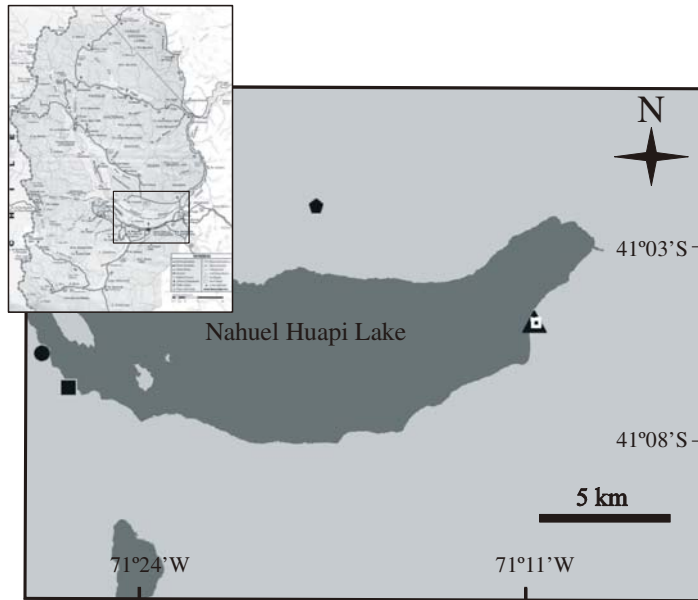


Figure 1. Location of the studied ponds in Nahuel Huapi Lake surrounding: (●) FA, (■) M12, (▲) ÑCh, (◻) ÑGr and (●) CH. Abbreviations: FA, Fantasma; M12, Mallín Km 12; ÑCh, Ñirihuau Chica; ÑGr, Ñirihuau Grande; CH, Del Chancho.

The wetlands were: Fantasma (FA), Mallín Km 12 (M12), Ñirihuau Chica (ÑCh), Ñirihuau Grande (ÑGr), and Del Chancho (CH). These wetlands are in a 300 km² area surrounding the eastern basin of Lake Nahuel Huapi, and are located at 750 and 800 m above sea level (Fig. 1). The depths of the wetlands are between 0.7 m and 2 m. The range in surface area is 4.000–30.000 m² (Table 1). Following the classification of OERTLI *et al.* (2002), these wetlands belong to two different size classes: wetlands between 3.192 m²–10.000 m² and >10.000 m².

Table 1. Features of the northern Patagonian ponds included in this study. Abbreviations: FA, Fantasma; M12, Mallín Km 12; ÑCh, Ñirihuau Chica; ÑGr, Ñirihuau Grande; CH, Del Chancho. Z_{\max} : maximum depth, A_{\max} : maximum surface area during the hydroperiod, Oxygen %: Percentage of oxygen saturation, TDP: Total dissolved phosphorus.

Ponds	Location	Altitude (m a.s.l.)	Z_{\max} (cm)	A_{\max} (m ²)	Conductivity ($\mu\text{S cm}^{-1}$)	Oxygen (%)	TDP ($\mu\text{g L}^{-1}$)
FA	41°05'35" S 71°27'01" W	780	200	10.000	92.8	93.0	6.6
M12	41°06'24" S 71°26'10" W	780	70	20.000	85.3	93.3	6.7
ÑCh	41°05'09" S 71°10'59" W	750	70	4.000	74.4	71.9	6.9
ÑGr	41°05'09" S 71°11'03" W	750	150	6.000	86.9	86.5	5.9
CH	41°02'08" S 71°18'01" W	800	200	30.000	76.7	92.8	2.9

Ponds ÑCh, ÑGr and CH are located in the forest-steppe ecotone where riparian vegetation is dominated by the native deciduous tree *Nothofagus antarctica* (G. FORST.) OERST. and the exotic deciduous shrub *Rosa rubiginosa* L. ponds M12 and FA are located in the forest, and both are surrounded by native trees *Austrocedrus chilensis* (D. DON) PIC. SER. et BIZZ., *Lomatia hirsuta* (LAM.), *Maytenus boaria* MOL., and *N. antarctica*, and the shrub *R. rubiginosa*.

2.2. Data Collection

Fieldwork was carried out during the complete 2004–2005 hydroperiod, and the ponds were sampled monthly at midday. Zooplankton samples were collected with a hand net (200 µm mesh plankton net), by making two or more horizontal tows of 10 m. The samples were preserved with 4% formalin solution. Surface water temperature was measured on each sampling occasion, and air temperature and precipitation data of the sampling days were obtained from the INTA Meteorological Station in San Carlos de Bariloche.

Aquatic vegetation samples were collected during each sampling occasion to determine the species composition in each wetland. All the wetland plants present in the pond were recorded, by surveys conducted by walking the shore and wading into the pond (at least ten transects perpendicular to the shore were included in the survey). Macrophytes were identified to the lowest possible taxonomic category (genus or species).

In the laboratory, zooplankton species were identified and measured. Crustaceans were quantified under a stereomicroscope in a 5 ml Bogorov chamber. At least 60 individuals of each abundant species and all individuals of the rare species were measured under an Olympus SZX9 stereomicroscope at 12–50× magnification. For cladocerans, we measured the linear dimension from the top of the head shield to the base of the caudal spine. For copepods, the total body length from the anterior extremity of cephalothorax to the tips of the furcal rami (without setae) was measured. The proportion of each species or size within species (different instars of copepods) was estimated for each sample.

2.3. Experimental Design

Predation rates of *M. ehrenbergii* were calculated on adult *P. sarsi* and *B. michaelsoni*. These two zooplankters represent the upper and lower limit for centropagid copepods size spectrum in the studied wetlands (6.01 mm and 0.92 mm, respectively). In addition, we calculated predation rates of *M. ehrenbergii* on intermediate-sized copepods: adults of *B. gracilis* (1.48 mm) and *Acanthocyclops robustus* (1.65 mm), and the cladoceran *Ceriodaphnia dubia* (0.81 mm). The sizes that appear in brackets belong to size measurements of at least 40 individuals of each species; these were taken from the same date and pond of those used in the predation trials.

Adults of *M. ehrenbergii* and individuals of the five zooplankton prey species were collected from FA, ÑCh and CH ponds, using a hand net (200 µm size pore). The trials were conducted in 200 ml vessels filled with 175 ml of filtered pond water (55 µm mesh size). The zooplankters were identified, separated, and counted using a stereomicroscope (12×). Five prey abundances (5, 10, 20, 40 and 80) of each species were tested except for *P. sarsi* where four abundances (3, 6, 9 and 12) were tested because of its larger biomass. We used egg-bearing females and adult females without eggs in similar proportions. Males and females of *B. michaelsoni* were used together in the trials because they have no size dimorphism. After placing the prey in each container, four *M. ehrenbergii* adults (~8 mm in length) were added. *M. ehrenbergii* were starved for 24 h prior to the experiments. Each treatment was replicated five times. The experiments were run for 24 h in a temperature-light controlled incubator at 10 °C and a light: dark cycle of 10 : 14 h. After running the experiment, all live individuals were sorted and counted.

Predation rates (P) were calculated by dividing the number of ingested prey by the number of predators per container and the time, t .

2.4. Data Analysis

The correlation coefficient (r) (ROHLF and SOKAL, 1969) was used to estimate associations between wetland area and number of macrophytes. A one-way analysis of variance ANOVA followed by a *post hoc* test was applied to estimate differences among the size distribution of centropagid copepods and daphnids from the studied wetlands, and to estimate differences among abundances in predation rates of *M. ehrenbergii*. Size spectra within ponds were compared by grouping size classes in three categories (<0.8 mm, 0.8–2 mm and >2 mm). The groups were analyzed using an ANOVA comparing dates with and without *M. ehrenbergii*. Data were transformed (\ln or $\arcsin\sqrt{p}$) when needed to meet ANOVA requirements. When these requirements were not fulfilled, a Kruskal-Wallis test was applied. All the statistical analyses were performed with a SigmaStat 3.11.

3. Results

3.1. Features of the Studied Ponds

The hydroperiod of each wetland varied between seven and nine months, except for CH, which is permanent. On the first sampling date (October 2004), all ponds were completely filled by rainfalls. In February, all ponds but CH were dry. By May, two of four temporary ponds (FA and M12) were refilled and in June, abundant precipitation and lower temperatures allowed all wetlands to be fully refilled.

During the sampling period, the range in surface water temperature was 0.5–27 °C. In general, all ponds exhibited similar temperature patterns. We measured the lowest temperatures in June, when all the ponds were ice-covered. Water temperature was strongly influenced by air temperature, because of the shallowness and the small volume of the ponds.

All five wetlands contained macrophytes, and the number of species present in each pond ranged from 1 to 8 (Table 2). On average 87.5% of the plant species recorded in the ponds were emergent, 6.25% submerged and 6.25% floating-leaved species. We detected no

Table 2. Distribution of macrophyte species in northern Patagonian ponds. Abbreviations: FA, Fantasma; M12, Mallín Km 12; ÑCh, Ñirihuau Chica; ÑGr, Ñirihuau Grande; CH, Del Chanco.

Macrophytes/pond Code	FA	M12	ÑCh	ÑGr	CH
<i>Potentilla anserina</i> L.	X		X	X	
<i>Carex aematorrhyncha</i> DESV.	X				
<i>Puccinellia glaucescens</i> (PHIL.) PARODI	X				
<i>Juncus bufonius</i> L.		X		X	
<i>Juncus microcephalus</i> H. B. K.		X	X		
<i>Juncus pallescens</i> LAM.		X	X	X	
<i>Juncus arcticus</i> WILLD		X			
<i>Juncus stipulatus</i> NEES and MEYEN		X			
<i>Schoenoplectus californicus</i> (C. A. MEYER) SOJÁK			X		
<i>Ranunculus trullifolius</i> HOOK. F.			X	X	
<i>Ranunculus spagazzinii</i> LOURTEIG				X	
<i>Myriophyllum quitense</i> KUNTH				X	X
<i>Gunnera magellanica</i> LAM.			X		
<i>Callitriche lechleri</i> (HEGELM) FASSETT				X	
<i>Fonkia uliginosa</i> R. A. PHILIPPI			X		
<i>Hydrocotyle</i> sp.				X	
WETLAND AREA	10.000 m ²	20.000 m ²	4.000 m ²	6.000 m ²	30.000 m ²

correlation between macrophytes species richness and pond area ($r = -0.833$ and $d.f. = 3$; $P = 0.079$). However, the low power of this analysis, and the very high correlation coefficient ($r = -0.833$) obtained suggested a trend in the relationship of these two variables. The smaller wetlands contained higher number of macrophytes, which may have resulted in higher habitat heterogeneity for these environments.

3.2. Composition and Body Size of the Crustacean Zooplankton Community

Crustacean community structure varied among the ponds (Table 3). Calanoid copepods had the highest richness (six species, Table 3), followed by daphnids and cyclopoid copepods with five species each. The most widespread species were *C. dubia* and *A. robustus*, which were recorded at all wetlands (Table 3). Other crustacean groups such as harpacticoid copepods, macrothricids (three species) and chydorids cladocerans were also recorded (Table 3).

Centropagids of the genus *Boeckella* had the highest richness with a total of five species: *B. michaelsoni* (MRÁZEK), *B. gracilis* (DADAY), *B. brasiliensis* (LUBBOCK), *B. brevicaudata* (BRADY), and *B. poppei* (MRÁZEK) (Table 3). Another centropagid, the predator *Parabroteas sarsi* (DADAY), was present in two ponds (Table 3). Centropagid copepods showed a size

Table 3. Distribution of zooplankton species in northern Patagonian ponds. Abbreviations: FA, Fantasma; M12, Mallín Km 12; ÑCh, Ñirihuau Chica; ÑGr, Ñirihuau Grande; CH, Del Chancho.

Species/Ponds	Body Size (mm) (mean \pm S.E)	FA	M12	ÑCh	ÑGr	CH
COPEPODA						
Calanoids						
<i>Parabroteas sarsi</i> (DADAY)	5.00 \pm 0.02	X				X
<i>Boeckella poppei</i> (MRÁZEK)	2.84 \pm 0.04					X
<i>Boeckella brasiliensis</i> (LUBBOCK)	2.60 \pm 0.01					X
<i>Boeckella brevicaudata</i> (BRADY)	1.99 \pm 0.12	X				
<i>Boeckella gracilis</i> (DADAY)	1.17 \pm 0.01	X	X	X	X	
<i>Boeckella michaelsoni</i> (MRÁZEK)	0.92 \pm 0.01					X
Cyclopoids						
<i>Acanthocyclops robustus</i> (SARS)	1.43 \pm 0.03	X	X	X	X	X
<i>Tropocyclops prasinus meridionalis</i> KIEFER	0.52 \pm 0.02	X				
<i>Eucyclops ensifer</i> KIEFER	2.08 \pm 0.04		X			
<i>Mesocyclops araucanus</i> LÖFFLER	1.13 \pm 0.02		X			
<i>Microcyclops anceps</i> (RICHARD)	0.74 \pm 0.02			X	X	
Harpacticoids	0.87 \pm 0.02				X	
CLADOCERA						
Daphnids						
<i>Daphnia</i> sp.	1.91 \pm 0.09					X
<i>Daphnia commutata</i> EKMAN	2.45 \pm 0.41	X				
<i>Simocephalus serrulatus</i> (KOCH)	3.46 \pm 0.16	X				
<i>Simocephalus vetulus</i> (O. F. MÜLLER)	1.53 \pm 0.04		X	X	X	X
<i>Ceriodaphnia dubia</i> RICHARD	0.78 \pm 0.01	X	X	X	X	X
Macrothricids						
<i>Macrothrix</i> sp.	0.70 \pm 0.00					X
<i>Pseudomoina</i> sp.	1.06 \pm 0.02			X		
Chydorids						
Chydoridae	0.38 \pm 0.01	X	X	X	X	X

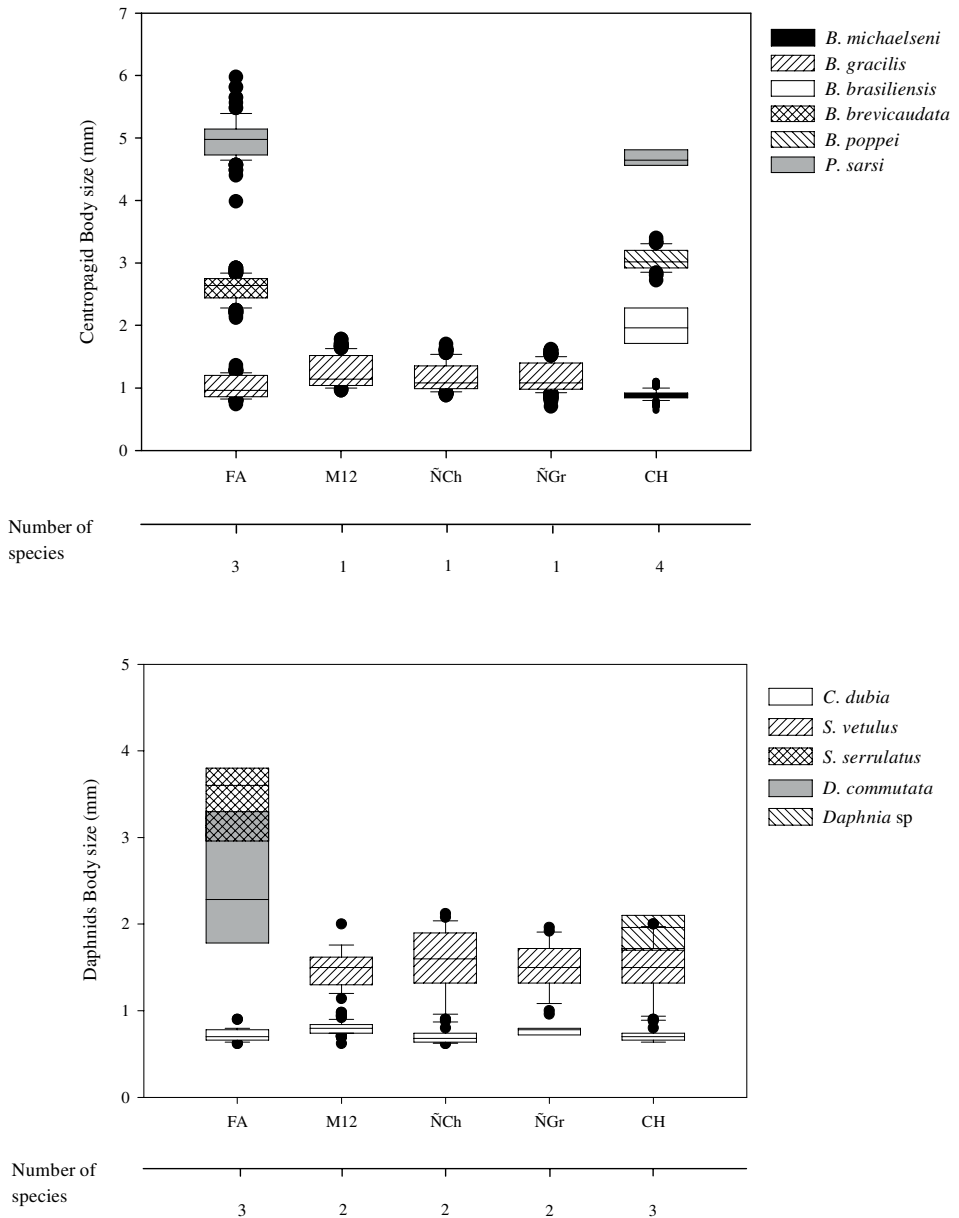


Figure 2. Zooplankton assemblages of fishless ponds of northern Patagonia: Body size (mm) of Centropagids (a) and Daphnids (b). Median, quartiles and data outside the 10th and 90th percentiles are indicated. Abbreviations: FA, Fantasma; M12, Mallín Km 12; ÑCh, Ñirihuau Chica; ÑGr, Ñirihuau Grande; CH, Del Chanco.

gradient from <0.9 to >6 mm (Fig. 2). There were 1–4 centropagid copepod species in a single pond (Table 3; Fig. 2). *B. gracilis* was the most common species and was recorded in four of the five ponds (Table 3). We observed significant differences for centropagid sizes among wetlands (Kruskal-Wallis $P < 0.001$). Dunn's *post hoc* test showed four different groups of size spectra (CH, FA, M12 and ÑCh – ÑGr) ($P < 0.05$).

Two species of *Daphnia* were recorded [*D. cf. commutata* EKMAN (*D. middendorffiana* FISCHER, *sensu* PAGGI (1973)) and *Daphnia* sp.], with body sizes averaging <3 mm (Table 3; Fig. 2). There was no significant difference in body sizes between these species (Kruskal-Wallis $P = 0.368$). *Simocephalus serrulatus* (KOCH) reached a body size of ~3.5 mm in pond FA while *S. vetulus* (O. F. MÜLLER) had a size of ~2 mm (Table 3). *Ceriodaphnia dubia* (~0.8 mm) was recorded in all ponds (Table 3; Fig. 2). Differences in daphnid body size

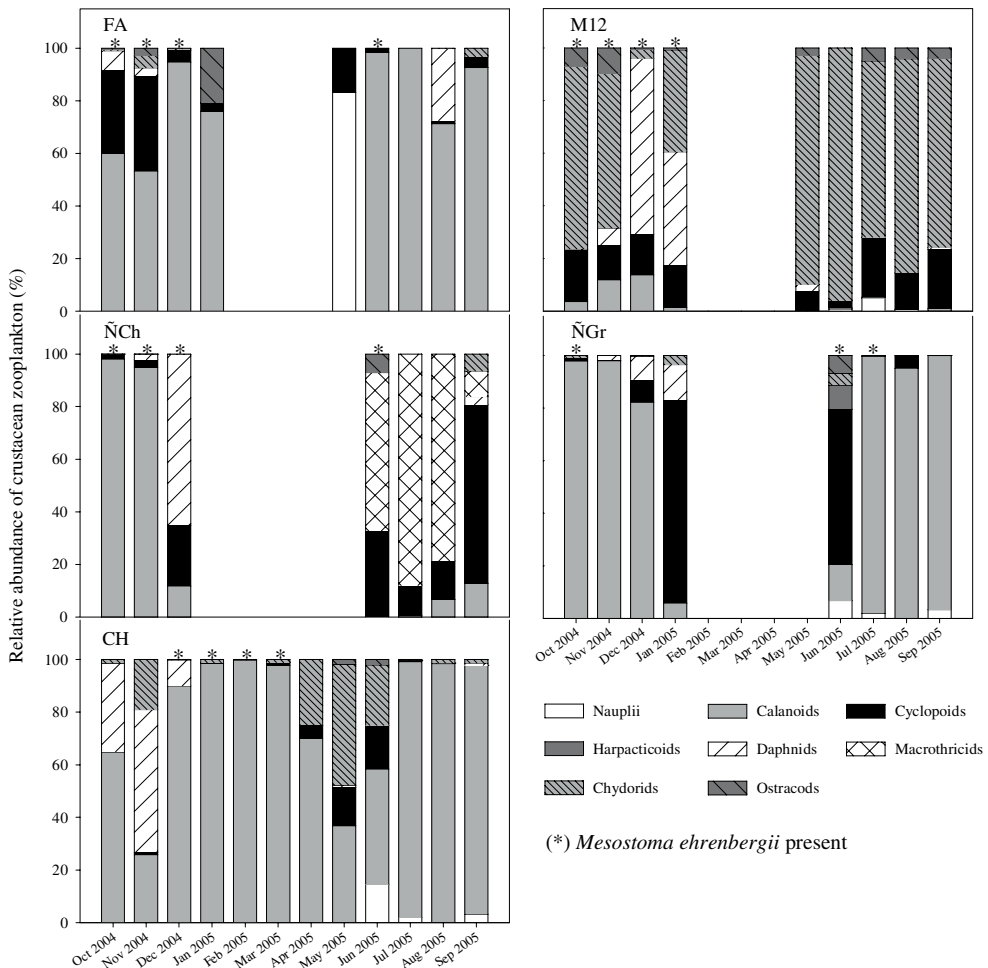


Figure 3. Relative abundance of zooplankton groups in northern Patagonian ponds. The taxa included in these graphs represented >1% of the zooplankton abundance during at least one sample period during the study. Abbreviations: FA, Fantasma; M12, Mallín Km 12; ÑCh, Ñirihuaú Chica; ÑGr, Ñirihuaú Grande; CH, Del Chancho.

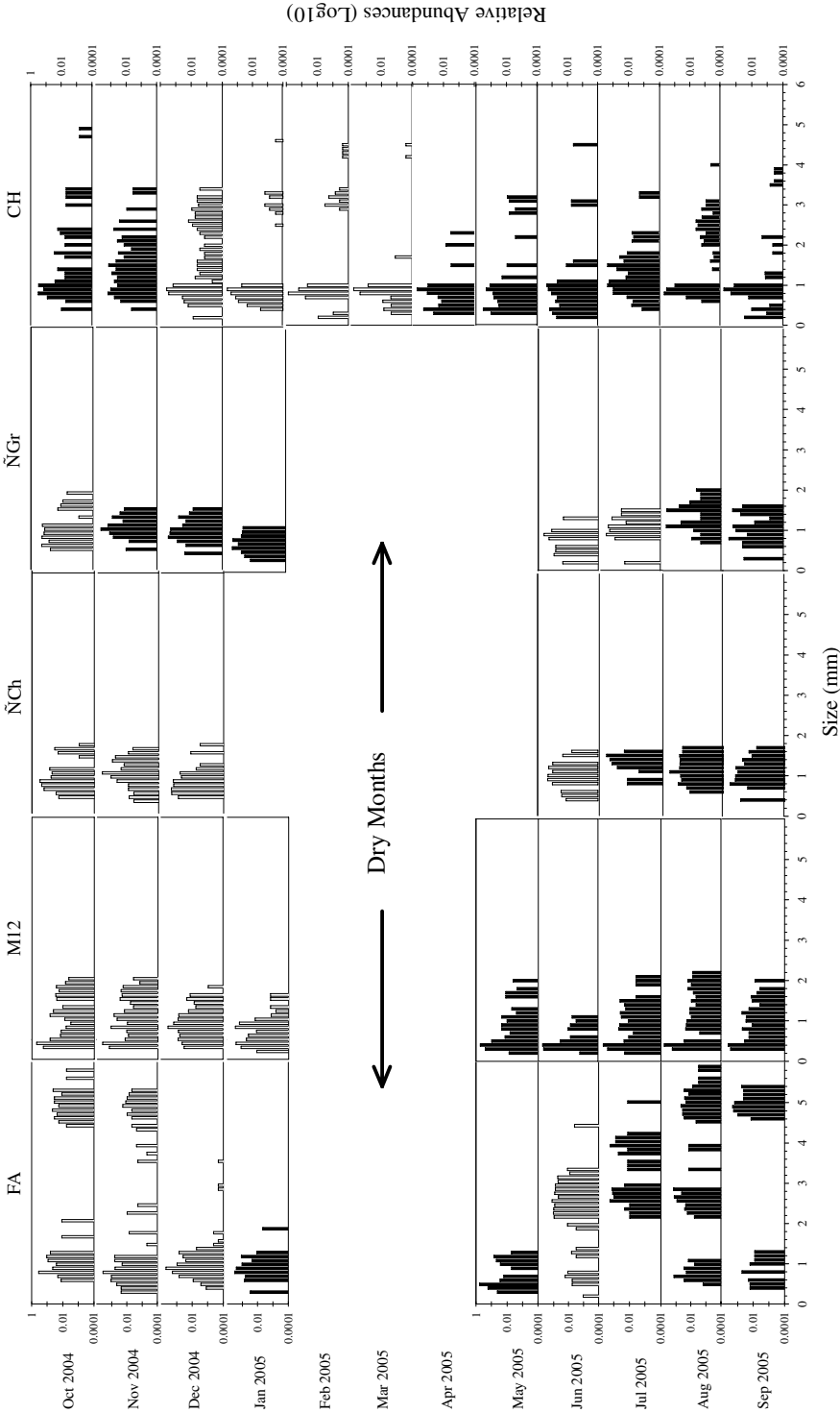


Figure 4. Zooplankton size spectrum obtained for ponds FA, M12, NCh, NGr and CH. White bars indicate the presence of *Mesostoma ehrenbergii* in the pond; black bars indicate that *M. ehrenbergii* is absent. Abbreviations: FA, Fantasma; M12, Mallin Km 12; NCh, Nirihuau Chica; NGr, Nirihuau Grande; CH, Del Chancho.

among ponds were significant (Fig. 2; Kruskal-Wallis $P < 0.001$). The a posteriori all pairwise multiple comparison showed that daphnids size spectra of FA and CH differed from those of ponds M12 and ÑCh, while ÑGr daphnid sizes did not differ from any of the others ponds (Kruskal-Wallis $P = 0.001$; Dunn's *post hoc* test $P < 0.05$).

Calanoid copepods clearly dominated zooplankton community structure in ponds FA, ÑGr and CH (Fig. 3), whereas chydorids were the most abundant group in M12 (Fig. 3), and calanoids, cyclopoids and macrothricids were the main taxa in ÑCh during the hydroperiod (Fig. 3). Daphnids were more abundant during the spring and early summer except in FA, where the highest abundance was observed in August (~30%) (Fig. 3). Cyclopoids were present in all five wetlands during most of the hydroperiod, in abundances that fluctuated between <1% and 80% of the total zooplankton abundance (Fig. 3).

Crustacean zooplankton sizes ranged from 0.1 mm for copepod nauplii, to 6 mm for the adults of the copepod *P. sarsi*. This range was observed in ponds FA and CH (Fig. 4). Ponds

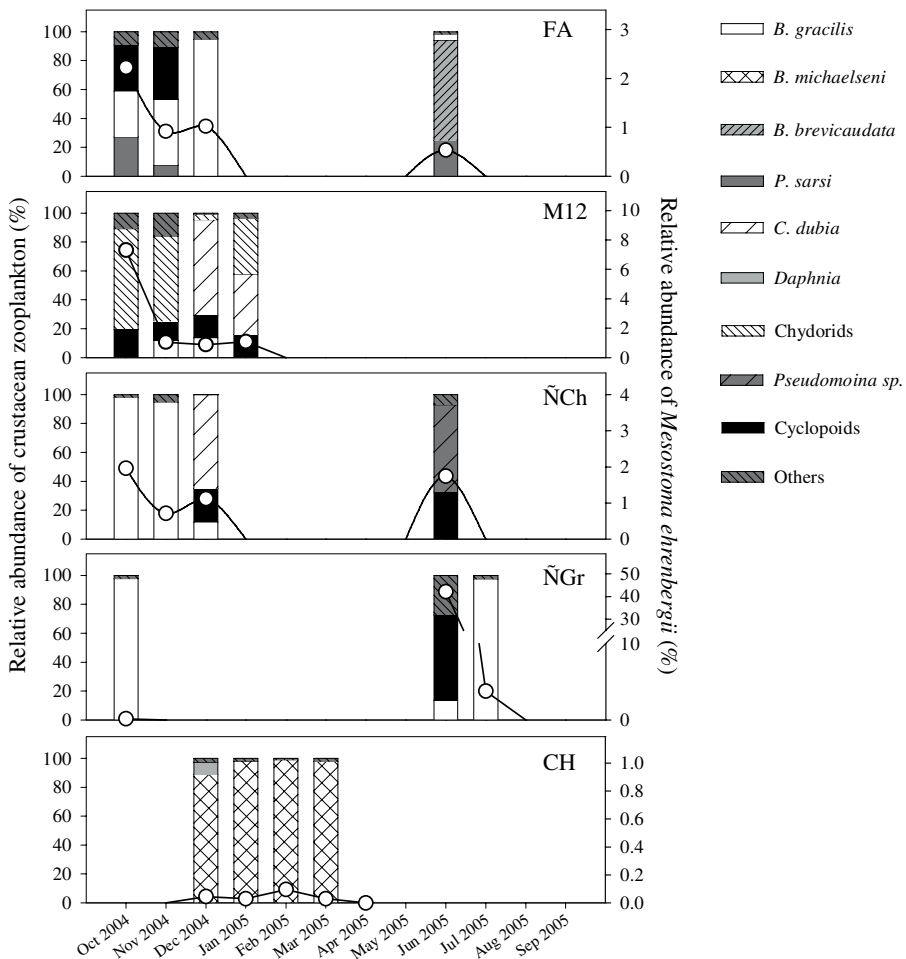


Figure 5. Bar plot: Relative abundance of zooplankton taxa when *Mesostoma ehrenbergii* is present (left axis). Line and scatter plot: Relative abundances of *M. ehrenbergii* (right axes). Abbreviations: FA, Fantasma; M12, Mallin Km 12; ÑCh, Ñirihuau Chica; ÑGr, Ñirihuau Grande; CH, Del Chancho.

M12, ÑCh and ÑGr showed a narrower size distribution, with a dominance of intermediate-sized zooplankton (around 1 mm) (Fig. 4). In particular, FA and CH showed a marked variability of zooplankton sizes during the hydroperiod (Fig. 4).

3.3. Abundance of *Mesostoma* and Its Association with Crustacea

We found the turbellarian predator *Mesostoma ehrenbergii* between October and January in low abundance (<3% of total zooplankton abundance) (Fig. 5). However, high abundance

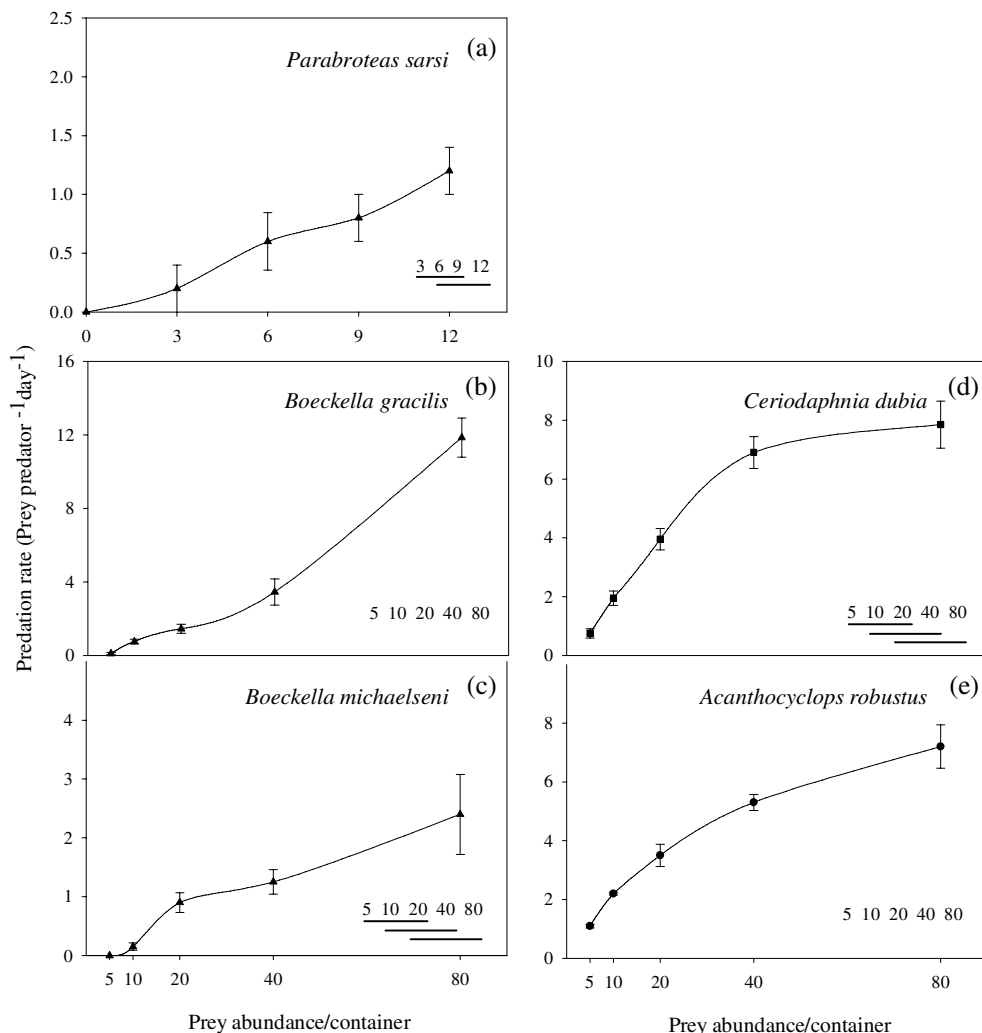


Figure 6. Predation rates of *Mesostoma ehrenbergii* on prey species of different body size: (a) *Parabroteas sarsi*, ~6 mm, (b) *Boeckella gracilis*, ~1.5 mm, (c) *Boeckella michaelsoni*, ~0.9 mm, (d) *Ceriodaphnia dubia*, ~0.8 mm and (e) *Acanthocyclops robustus*, ~1.6 mm. Lines connecting abundances in the right corner of the graphs indicate means without significant differences (ANOVA $P < 0.001$; *post hoc* test $P < 0.05$).

of juvenile *M. ehrenbergii* was recorded in October in M12 and in June in ÑGr (Fig. 5). The statistical analysis (ANOVA), performed to elucidate if the presence of *M. ehrenbergii* affects the crustacean zooplankton size structure, through the grouping of zooplankters in size classes (small, medium and large), did not show an effect of this predator (FA, ANOVA $F_{1,21} = 0.010$, $P > 0.05$; M12, ANOVA $F_{1,21} = 0.036$, $P > 0.05$; ÑCh, ANOVA $F_{1,15} = 10^{-4}$, $P > 0.05$; ÑGr, ANOVA $F_{1,12} = 10^{-4}$, $P > 0.05$; CH, ANOVA $F_{1,27} = 0.013$, $P > 0.05$).

3.4. Predation Rates of *M. ehrenbergii* on Its Prey

Our experiments demonstrated that *M. ehrenbergii* consumed prey of a broad size spectrum, ranging from 0.8 mm to 6 mm. Predation rates were lower for *Parabroteas sarsi* (6 mm) and *B. michaelsoni* (0.9 mm) (Fig. 6a, c) than for *B. gracilis* (1.5 mm), *A. robustus* (1.65 mm) and *C. dubia* (0.8 mm) (Fig. 6b, d, e). The functional response obtained for the rates of predation of *M. ehrenbergii* on the studied prey species differed greatly (Fig. 6). Predation rates of *M. ehrenbergii* on calanoid copepods increased with prey abundance without reaching a saturation level (Fig. 6a, b, c). Contrary, predation rates of *M. ehrenbergii* on *A. robustus* and *C. dubia* increased curvilinearly with prey abundance reaching saturation level at ~8 prey per day (Fig. 6d, e).

4. Discussion

The studied Patagonian fishless ponds showed distinctive crustacean zooplankton assemblages and sizes along the hydroperiod. Our initial hypothesis indicating that the turbellarian predator *M. ehrenbergii* could exert an effect on the zooplankton composition and body size spectrum in Patagonian fishless ponds was not supported by our field data. However, our experimental investigation revealed a strong predation effect of *M. ehrenbergii* on intermediate-bodied copepods (1.5–1.6 mm) and cladocerans (0.8 mm). The effect of the flatworm *M. ehrenbergii* in nature may depend on the interaction between the evasion tactic of the prey and its body size, along with other factors (e.g., macrophyte composition of the ponds).

Zooplankton composition of these wetlands was observed to be dominated by centropagid copepods of the genus *Boeckella*. Both historical (e.g., colonization, vicariance) and ecological processes (e.g., competition, predation) could have been important in structuring the species assemblages in our temporary habitats (KING *et al.*, 1996; HOLLAND and JENKINS, 1998). The most common species in large deep lakes of the northern Patagonian region, *B. gracilipes* DADAY (MODENUTTI *et al.*, 1998; BALSEIRO *et al.*, 2001), was not recorded in any of our ponds. Other species such as *P. sarsi*, *B. gracilis* and *B. michaelsoni* have been recorded in other larger lakes of Patagonia but not in the Nahuel Huapi area (MODENUTTI *et al.*, 2003; REISSIG *et al.*, 2004). Thus, ponds surrounding Lake Nahuel Huapi area might represent a species reservoir of calanoid copepods. A total of 3 to 4 centropagids of different sizes occurred in the same environment (Fig. 2), and were likely able to coexist via exploitation of different food niches (REISSIG *et al.*, 2006). In addition, the coexistence of *Daphnia* species with centropagid copepods is consistent with low resource competition. In particular, MODENUTTI *et al.* (2003) observed that *Daphnia cf. commutata* and *B. michaelsoni* had a low niche overlap. Cladocerans usually feed most efficiently on bacteria and picophytoplankton and show reduced feeding rates for longer filaments, whereas copepods tend to focus foraging more on larger food particles (DEMOTT, 1989; BALSEIRO *et al.*, 2001). The presence of *C. dubia* in all of our studied wetlands is consistent with the finding that it is the most widespread daphnid in lakes with and without fish of the

northern Patagonia (BALSEIRO *et al.*, 1992; BALSEIRO *et al.*, 1997; REISSIG *et al.*, 2006). Other cladoceran species that are commonly found in littoral zone of lakes (*e.g.* chydorids, macrothricids and *Simocephalus*; BALSEIRO and MODENUTTI, 1990) occurred in our pond samples. None of our five ponds showed a zooplankton size structure smaller than 1 mm, a finding consistent with the absence of fishes in these ponds (GLIWICZ and PIJANOWSKA, 1989). REISSIG *et al.* (2006) showed that, in the presence of fish, the range of zooplankton sizes tended to be narrower because of the disappearance of *Daphnia* and large centropagid copepods.

Our laboratory predation experiments indicate that *M. ehrenbergii* feeds on a broad range of prey sizes, the range of which was 0.8 mm (*C. dubia*) to 6 mm (*P. sarsi*) for northern Patagonian environments. Different predation strategies (ambush and active swimming, both associated with a mucus trapping tactic) (SCHWARTZ and HEBERT, 1982; TROCHINE *et al.*, 2005; 2006) and external digestion allowed *Mesostoma* to feed on a broad range of prey sizes. Our experiments demonstrated that *M. ehrenbergii* has a high consumption rate on medium-sized copepods, such as *B. gracilis* and *A. robustus*, and cladocerans, such as *C. dubia*. The wide range sizes of preferred prey (0.8–1.65 mm) might be related to the swimming behavior of the taxa. Cladocerans generally have limited locomotory abilities, while copepods are able to accelerate rapidly, sustain great speeds, and maneuver quickly (KERFOOT, 1978). When attacked by a predator, cladocerans often play tortoise, relying on secondary defenses (spines, hard coats, gelatinous coverings) to deter the predator. Instead, copepods respond escaping with a burst of speed (KERFOOT *et al.*, 1980). Thus, the high consumption rates obtained in our study on prey species that differed in sizes and swimming abilities suggested an interaction between these two factors that modulates the predator-prey relationship of *Mesostoma* and zooplankton. *Mesostoma* might be able to prey upon *C. dubia* because its 'dead man' strategy is not effective against this predator. On the other hand, *Mesostoma* had low consumption rates on the copepod *B. michaelsoni*, which is about the same size as *C. dubia*. We did not use smaller cladocerans, such as chydorids, in our experiments because previous studies indicated that these small prey (<0.5 mm) are ignored by *Mesostoma* (SCHWARTZ and HEBERT, 1982; BLAUSTEIN and DUMONT, 1990).

The fact that copepods were readily consumed by *Mesostoma* differs from previous studies on lakes of the Northern Hemisphere, where cladocerans were more consumed than copepods (MALY *et al.*, 1980; SCHWARTZ and HEBERT, 1982; ROCHA *et al.*, 1990; BLAUSTEIN and DUMONT, 1990). SCHWARTZ and HEBERT (1982, 1986) suggested a large impact of *Mesostoma* on intermediate-sized cladocerans (~1.2 mm) in the arctic, and hence a shift from a cladoceran-dominated to a copepod-dominated community structure. Other studies done in Botswana (BRENDONCK *et al.*, 2002), USA (MALY *et al.*, 1980), and Brazil (ROCHA *et al.*, 1990) have shown that *M. ehrenbergii* is a voracious predator of zooplankton in freshwater fishless environments though no clear effects on zooplankton assemblages have been indicated by these authors. Nonetheless, DE ROECK *et al.* (2005) indicated that *Mesostoma* has a potentially strong influence on the population dynamics and life history characteristics (*e.g.*, hatching of resting eggs) of the anostracan species *Branchipodopsis wolffi* DADAY. In our study, the low rates of predation on *B. michaelsoni* suggest that this small copepod might not be a preferred prey for *M. ehrenbergii*. In CH pond *B. michaelsoni* co-occurred with *M. ehrenbergii*; therefore we suggest that other prey species present in the pond (such as *C. dubia* and *Daphnia* neonates) might be its main food source, as was observed for lakes of the Northern Hemisphere (SCHWARTZ and HEBERT, 1982, 1986).

Interestingly, the predaceous calanoid *P. sarsi* coexists with *M. ehrenbergii*, suggesting that resource competition between predators may occur in the absence of fish predation. Nevertheless, *M. ehrenbergii* was able to consume *P. sarsi* adults (~6 mm), at very low rates. In natural habitats, copepodites I of *P. sarsi* might be more susceptible to predation by this turbellarian because their size lies within the preferred prey range of *M. ehrenbergii* (1.36 mm–1.5 mm). Thus, the effect of *M. ehrenbergii* predation on *P. sarsi* populations in

northern Patagonian fishless ponds might be larger than expected. Unfortunately, we did not carry out experiments with copepodites of *P. sarsi*.

Finally, the structural complexity given by macrophytes in Patagonian fishless ponds may also accomplish for the lack of a strong predation effect of *Mesostoma* in the field survey. In a previous study we indicated that macrophyte habitat heterogeneity provide a bottleneck for *M. ehrenbergii* predation on the calanoid *B. gracilis* (TROCHINE *et al.*, 2006). Thus, the difference in macrophyte assemblages observed among the studied ponds may be also crucial for determining the true effect of *M. ehrenbergii* on its prey in a natural habitat. Particularly, our present investigation suggested that smaller ponds had higher numbers of macrophyte species, which may result in higher habitat heterogeneity in these environments, and, hence, complex predation effects. Additionally, we observed that *M. ehrenbergii* consumes prey from different trophic levels (*e.g.*, predators, herbivores) making the net predation effect difficult to predict in northern Patagonian fishless ponds.

5. Acknowledgements

Special thanks to M. GUERRIERI for his invaluable help in the field. We also thank ING. C. BRION, DRA. C. EZCURRA and Dr. J. PUNTIERI for macrophyte identifications. We are grateful to two anonymous reviewers for valuable suggestions that improved this manuscript.

This work was supported by FONCyT PICT 01-13395, CONICET PIP 6507 and UNC B119. C. TROCHINE, B. MODENUTTI and E. BALSEIRO are CONICET researchers.

6. References

- BALSEIRO, E. G. and B. E. MODENUTTI, 1990: Zooplankton Dynamics of Lake Escondido (Río Negro, Argentina) with special reference to a population of *Boeckella gracilipes* (Copepoda, Calanoida). – *Inter. Revue der ges. Hydrobiol.* **75**: 475–491.
- BALSEIRO, E. G., B. E. MODENUTTI and C. P. QUEIMALIÑOS, 1992: The coexistence of *Bosmina* and *Ceriodaphnia* in a South Andes lake: an analysis of demographic responses. – *Freshw. Biol.* **28**: 93–101.
- BALSEIRO, E. G., B. E. MODENUTTI and C. P. QUEIMALIÑOS, 1997: Nutrient recycling and shifts in N:P ratio by different zooplankton structures in a South Andes lake. – *J. Plankton Res.* **19**: 805–817.
- BALSEIRO, E. G., B. E. MODENUTTI and C. P. QUEIMALIÑOS, 2001: Feeding of *Boeckella gracilipes* (Copepoda, Calanoida) on ciliates and phytoflagellates in an ultraoligotrophic Andean lake. – *J. Plankton Res.* **23**: 849–857.
- BALSEIRO, E. G., B. E. MODENUTTI and C. P. QUEIMALIÑOS, 2004: Grazing impact on autotrophic picoplankton in two south andean lakes (Patagonia, Argentina) with different light: nutrient ratios. – *Rev. Chil. Hist. Nat.* **77**: 73–85.
- BAYLY, I. A. E., 1992: The non-marine Centropagidae: (Copepoda: Calanoida) of the world. SPB Academic Publishing, The Hague, The Netherlands, 34 pp.
- BEISNER, B. E., E. MCCAULEY and F. J. WRONA, 1996: Temperature-mediated dynamics of planktonic food chains: the effect of an invertebrate carnivore. – *Freshw. Biol.* **35**: 219–232.
- BELL, S. S., E. D. MCCOY and H. R. MUSHINSKY, 1991: Habitat Structure: the Physical Arrangement of Objects in Space. Chapman and Hall, London.
- BIGGS, J., G. FOX, P. NICOLET and M. WHITFIELD, 2001: Dangers and opportunities in managing temporary ponds. – Special topic, European Temporary Ponds: A Threatened Habitat, *Freshw. Forum* **17**: 71–80.
- BLAUSTEIN, L. and H. J. DUMONT, 1990: Typhloplanid flatworms (*Mesostoma* and related genera): Mechanisms of predation and evidence that they structure aquatic invertebrate communities. – *Hydrobiologia* **198**: 61–77.
- BRENDONCK, L., E. MICHELS, L. DE MEESTER and B. RIDDOCH, 2002: Temporary pools are not ‘enemy-free’. – *Hydrobiologia* **486**: 147–159.

- BROOKS, J. L. and S. L. DODSON, 1965: Predation, body size, and composition of plankton. – *Science* **150**: 28–35.
- DEMOTT, W. R., 1989: The role of competition in zooplankton succession. pp. 195–252. – *In*: SOMMER, U. (ed), *Plankton Ecology: Succession in Plankton Communities*. Springer-Verlag, New York, USA.
- DE ROECK, E., T. ARTOIS and L. BRENDONCK, 2005: Consumptive and non-consumptive effects of turbellarian (*Mesostoma* sp.) predation on anostracans. – *Hydrobiologia* **542**: 103–111.
- DIÉGUEZ, M. and E. BALSEIRO, 1998: Colony size in *Conochilus hippocrepis*: defensive adaptation to predator size. – *Hydrobiologia* **387**: 421–425.
- GEE, J. H. R., B. D. SMITH, K. M. LEE and S. W. GRIFFITHS, 1997: The ecological basis of freshwater pond management for biodiversity. – *Aquatic Conserv.: Mar. Freshw. Ecosyst.* **7**: 91–104.
- GLIWICZ, Z. and J. PIJANOWSKA, 1989: The role of predation in zooplankton succession. pp. 253–296. – *In*: SOMMER, U. (ed.), *Plankton Ecology*. Springer Verlag, Heidelberg.
- GONZALEZ SAGRARIO, M. A. and E. BALSEIRO, 2003: Indirect enhancement of large zooplankton by consumption of predacious macroinvertebrates by littoral fish. – *Arch. Hydrobiol.* **158**: 551–574.
- HOLLAND, T. A. and D. G. JENKINS, 1998: Comparison of processes regulating zooplankton assemblages in new freshwater pools. – *Hydrobiologia* **387/388**: 207–214.
- IRIONDO, M., 1989: Quaternary lakes of Argentina. – *Paleogeogr., Paleoclim.*, **70**: 81–88.
- KERFOOT, W. C., 1978: Combat between predatory copepods and their prey: *Cyclops*, *Epischura*, and *Bosmina*. – *Limnol. Oceanogr.* **23**: 1089–1102.
- KERFOOT, W. C., D. L. KELLOG and J. R. STRICKLER, 1980: Visual observations of live zooplankters: evasion, escape, and chemical defenses. pp. 11–27. – *In*: KERFOOT, W. C. (ed.), *Evolution and Ecology of Zooplankton Communities*, University Press New England, Hannover, Germany.
- KING, J. L., M. A. SIMOVICH and R. C. BRUSCA, 1996: Species richness, endemism and ecology of crustacean assemblages in northern California vernal pools. – *Hydrobiologia* **328**: 85–116.
- MALY, M. J., S. SHOENHOLTZ and M. T. ARTS, 1980: The influence of flatworm predation on zooplankton inhabiting small ponds. – *Hydrobiologia* **76**: 233–240.
- MENU-MARQUE, S., J. J. MORRONE and C. LOCASCIO DE MITROVICH, 2000: Distributional patterns of the South American species of *Boeckella* (Copepoda: Centropagidae): A track analysis. – *J. Crust. Biol.* **20**: 262–272.
- MODENUTTI, B. E. and E. G. BALSEIRO, 1994: Zooplankton size spectrum in four lakes of the Patagonian Plateau. – *Limnologia* **24**: 51–56.
- MODENUTTI, B. E., E. G. BALSEIRO, C. P. QUEIMALIÑOS, D. AÑON SUAREZ, M. C. DIÉGUEZ and R. J. ALBARIÑO, 1998: Structure and dynamics of food web in Andean lakes. – *Lakes Reserv.: Res. Manag.* **3**: 17–186.
- MODENUTTI, B. E., C. P. QUEIMALIÑOS, E. G. BALSEIRO and M. REISSIG, 2003: Impact of different zooplankton structures on the microbial food web of an Andean oligotrophic lake. – *Acta Oecol.* **24** S1: 289–298.
- MURDOCH, W. W., M. A. SCOTT and P. EBSWORTH, 1984: Effects of the general predator *Notonecta* (Hemiptera) upon a freshwater community. – *J. Anim. Ecol.* **53**: 791–808.
- NICOLET, P., J. BIGGS, G. FOX, M. J. HODSON, C. REYNOLDS, M. WHITFIELD and P. WILLIAMS, 2004: The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. – *Biol. Conserv.* **120**: 261–278.
- OERTLI, B., D. A. JOYER, E. CATELLA, R. JUGE, D. CAMBIN and J. B. LACHAVANNE, 2002: Does size matter? The relationship between pond area and biodiversity. – *Biol. Conserv.* **104**: 59–70.
- PALIK, P. B., D. P. BATZER, R. BUECH, D. NICHOLS, K. CEASE, L. EGELAND and D. E. STREBLOW, 2001: Seasonal pond characteristics across a chronosequence of adjacent forest ages in northern Minnesota, USA. – *Wetlands* **21**: 532–542.
- REISSIG, M., C. P. QUEIMALIÑOS and E. G. BALSEIRO, 2004: The role of the predaceous copepod *Parabroteas sarsi* in the pelagic food web of a large deep Andean lake. – *Hydrobiologia* **524**: 67–77.
- REISSIG, M., C. TROCHINE, C. P. QUEIMALIÑOS, E. G. BALSEIRO and B. E. MODENUTTI, 2006: Impact of fish introduction on planktonic food webs in lakes of the Patagonian Plateau. – *Biol. Conserv.* **132**: 437–447.
- ROCHA, O., T. MATSUMURA-TUNDISI, J. G. TUNDISI and C. PADOVESI-FONSECA, 1990: Predation on and by the pelagic Turbellaria in some lakes in Brazil. – *Hydrobiologia* **198**: 91–101.
- ROHLF, F. J. and R. R. SOKAL, 1969: *Statistical tables*. W. H. Freeman and Co. San Francisco, USA.
- SCHWARTZ, S. S. and P. D. N. HEBERT, 1982: A laboratory study of the feeding behavior of the rhabdocoel *Mesostoma ehrenbergii* on pond Cladocera. – *Can. J. Zool.* **60**: 1305–1307.

- SCHWARTZ, S. S. and P. D. N. HEBERT, 1986: Prey preference and utilization by *Mesostoma lingua* (Turbellaria, Rhabdocoela) at a low arctic site. – *Hydrobiologia* **135**: 251–257.
- SHURIN, J. B., 2001: Interactive effects of predation and dispersal on zooplankton communities. – *Ecology* **82**: 3404–3416.
- STEINER, C. F. and A. H. ROY, 2003: Seasonal succession in fishless ponds: effects of enrichment and invertebrate predators on zooplankton community structure. – *Hydrobiologia* **490**: 125–134.
- SWIFT, M. C., 1992: Prey capture by the four instars of *Chaoborus crystallinus*. – *Limnol. Oceanogr.* **37**: 14–24.
- TESSIER, A. J. and P. WOODRUFF, 2002: Cryptic trophic cascade along a gradient of lake size. – *Ecology* **83**: 1263–1270.
- TROCHINE, C., B. MODENUTTI and E. BALSEIRO, 2005: When mating increases predation risk: the relationship between the flatworm *Mesostoma ehrenbergii* and the copepod *Boeckella gracilis*. – *Arch. Hydrobiol.* **163**: 555–569.
- TROCHINE, C., B. MODENUTTI and E. BALSEIRO, 2006: Influence of spatial heterogeneity on the predation of *Mesostoma ehrenbergii* (Focke) on calanoid and cyclopoid copepods. – *J. Plankton Res.* **28**: 267–274.
- WILLIAMS, P., J. BIGGS, M. WHITFIELD, A. THORNE, S. BRYANT, G. FOX and P. NICOLET, 1999: *The Pond Book: A Guide to the Management and Creation of Ponds*. Ponds Conservation Trust, Oxford.

Manuscript received July 18th, 2007; revised December 18th, 2007; accepted December 19th, 2007