

# High predation is of key importance for dominance of small-bodied zooplankton in warm shallow lakes: evidence from lakes, fish exclosures and surface sediments

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**Abstract** The mean body size of limnetic cladocerans decreases from cold temperate to tropical regions, in both the northern and the southern hemisphere. This size shift has been attributed to both direct (e.g. physiological) or indirect (especially increased predation) impacts. To provide further information on the role of predation, we compiled results from several studies of subtropical Uruguayan lakes using three different approaches: (i) field

observations from two lakes with contrasting fish abundance, Lakes Rivera and Rodó, (ii) fish exclusion experiments conducted in in-lake mesocosms in three lakes, and (iii) analyses of the *Daphnia* egg bank in the surface sediment of eighteen lakes. When fish predation pressure was low due to fish kills in Lake Rivera, large-bodied *Daphnia* appeared. In contrast, small-sized cladocerans were abundant in Lake Rodó, which exhibited a typical high abundance of fish. Likewise, relatively large cladocerans (e.g. *Daphnia* and *Simocephalus*) appeared in fishless

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mesocosms after only 2 weeks, most likely hatched from resting egg banks stored in the surface sediment, but their abundance declined again after fish stocking. Moreover, field studies showed that 9 out of 18 Uruguayan shallow lakes had resting eggs of *Daphnia* in their surface sediment despite that this genus was only recorded in three of the lakes in summer water samples, indicating that *Daphnia* might be able to build up populations at low risk of predation. Our results show that medium and large-sized zooplankton can occur in subtropical lakes when fish predation is removed. The evidence provided here collectively confirms the hypothesis that predation, rather than high-temperature induced physiological constraints, is the key factor determining the dominance of small-sized zooplankton in warm lakes.

**Keywords** Zooplankton community structure · Fish predation · Subtropical shallow lakes

## Introduction

Cladocerans are typically the most important planktonic herbivores in freshwater lakes (Brooks & Dodson, 1965) and are occasionally capable of consuming as much as 80–100% of the phytoplankton biomass (Lampert, 1988; Jeppesen et al., 1997; Shurin et al., 2006). Thus, zooplankton may potentially exert strong control of algal standing crops when large-bodied cladocerans (like *Daphnia* spp) dominate, even at high nutrient concentrations (Jeppesen et al., 1998). However, in nutrient-enriched north temperate lakes, small-bodied zooplankters often dominate (e.g. *Diaphanosoma* and *Bosmina*) (Jeppesen et al., 2000) due to high fish predation (Brooks & Dodson, 1965; Gliwicz, 2003).

In subtropical and tropical lakes, small zooplankters are particularly dominant, even at low nutrient concentrations (Fernando et al., 1987; Dumont, 1994; Meerhoff et al., 2007a; Havens et al., 2009). In accordance with this, Gillooly & Dodson (2000) showed that the mean body length of planktonic cladocerans decreases from cold temperate to tropical regions, in both the northern and the southern hemisphere. In their study, no large-bodied species were observed in the subtropical and tropical waters, a latitudinal pattern that could not be attributed to spatial variation in primary production, nutrient

regeneration or oxygen availability. Lacerot (2010) found a similar latitudinal pattern in cladoceran body size in a study of shallow lakes in South America, covering a wide latitudinal gradient from Natal in Brazil to Tierra del Fuego in Argentina (5°–55°S).

The reasons behind declining size with increasing temperature have been debated, yet, so far, answers are inconclusive. Gillooly & Dodson (2000) noted that the strong correlation of body size with lake temperature might reflect both direct (e.g. physiological) and indirect (e.g. increased predation) temperature effects. They concluded, however, that differences in water temperature were the major driver behind this pattern and argued that the upper thermal tolerance of large, typically temperate, cladocerans (ca. 30°C) is often exceeded in subtropical and tropical lakes (Gillooly & Dodson, 2000), whereas some species (e.g. *Diaphanosoma*) may undergo evolutionary adaptation allowing them to dominate under warmer conditions (Han et al., 2010). Growth, reproduction and respiration of zooplankton, as well as size at maturity, are also influenced by temperature (Moore et al., 1996; Weetman & Atkinson, 2004), whereas food requirements of cladocerans increase more steeply with body size at elevated temperatures (Hardy & Duncan, 1994). However, increased temperature may also have several indirect effects, such as changes in food quality and increased size-selective predation, by allowing an earlier onset of fish reproduction (Moore et al., 1996). Recently, several authors have argued that higher fish predation, rather than temperature, is responsible for the reduction in average body size observed in the zooplankton community towards the tropics (Sarma et al., 2005; Jeppesen et al., 2007; Meerhoff et al., 2007b; Havens et al., 2009; Havens & Beaver, 2010; Lacerot, 2010; Sosnovsky et al., 2010). Tropical and subtropical fish assemblages are usually dominated by small omnivorous fish and often show replacement among predatory fish from large-bodied to smaller forms that are less efficient at controlling large, coarse fish (Lazzaro, 1997; Kruk et al., 2009; Jeppesen et al., 2010). *Daphnia* and other large-bodied cladocerans may, therefore, be subjected to high predation by fish all year-round or at least in the warmer (i.e. reproductive) seasons, this being reinforced also by earlier reproduction and more cohorts of fish than observed in the temperate zone (Lazzaro, 1997; Pinel-Alloul et al., 1998; Jeppesen et al., 2010). Moreover, in contrast to

north temperate lakes (Burks et al., 2002), submerged macrophytes are apparently not an efficient daytime refuge for zooplankton in subtropical lakes (Meerhoff et al., 2006), as fish abundance, and thus predation among the plants, is high (Meerhoff et al., 2007a), which enhances the predation risk for large-bodied zooplankton. Plant-associated macroinvertebrates can also predate and control zooplankton in subtropical shallow lakes, contributing further to a weakening of the refuge effect promoted by vegetation in the subtropics (González-Sagrario et al., 2009; González-Sagrario & Balseiro, 2010). Recent evidence for the role of predation was provided by experimental studies conducted in summer in subtropical Uruguay; despite high temperatures stocked *Daphnia* became the dominant zooplankton when small omnivorous–planktivorous fish were absent or controlled by piscivores, causing strong cascading effects on phytoplankton and water clarity (Iglesias et al., 2008; Mazzeo et al., 2010).

The aim of this study was to present further evidence for the hypothesis that fish predation, rather than temperature, is the key factor determining the typically small size range of cladocerans in the subtropics. We combine results obtained by three different approaches: (i) field observations from two subtropical lakes with contrasting fish abundance, (ii) fish exclusion experiments conducted in mesocosms in three subtropical lakes in summer, and (iii) analyses of the *Daphnia* egg bank stored in the surface sediment of 18 subtropical shallow lakes.

## Materials and methods

### Field studies—comparison of two urban hypertrophic, subtropical lakes

Lake Rivera and Lake Rodó are small (5 and 1.5 ha, respectively), shallow lakes (mean depths 0.8 and 1.7 m, respectively) located in two city parks of Montevideo in Uruguay (34°55'S, 56°10'W). Both lakes are mainly used for recreational and cultural activities, but are eutrophic as a result of high input of nutrients from urban areas [mean annual total phosphorus (TP): 2.4 and 0.2 mg l<sup>-1</sup> and total nitrogen (TN): 11.5 and 2.8 mg l<sup>-1</sup> in Rivera and Rodó, respectively]. Lake Rivera has received a substantial amount of sewage and shows great inter-annual

variation in the occurrence of free-floating plants (mainly *Eichhornia crassipes* and *Spirodela intermedia*). Lake Rivera usually exhibits high fish densities (mainly of the dominant species *Cnesterodon decemmaculatus*). However, in 1999 an extensive fish kill (likely due to elevated ammonia concentrations) led to a severe decrease in the fish density from summer to autumn, resulting in almost fishless conditions (Mazzeo et al., 2000). Lake Rodó, in contrast, typically has a high density of fish (Scasso et al., 2001). Here, we compare the fish and zooplankton structures of the two lakes during 1999 when Lake Rivera was almost fishless, while Lake Rodó had a diverse fish community dominated by omnivore–planktivores and high fish densities (Table 1).

We applied the same sampling strategy in both systems. We assessed fish communities by point sample electro-fishing (Perrow et al., 1996) in spring and summer, at around 100 points along transects covering the whole lake (one electric burst per point).

Phytoplankton and zooplankton were seasonally collected with a 5-L Patalas sampler at three random points (triplicate) in the pelagic area, covering the whole water column. We estimated the phytoplankton biomass as chlorophyll a (Chl-a, hot ethanol method, Nusch, 1980). We calculated mean body size of zooplankton after measuring at least 20 individuals of each species in each lake, and particularly for cladocerans we also measured total body length of adult females. Calculation of biomass was conducted using the length-weight regressions of Bottrell et al. (1976) and Ruttner-Kolisko (1977). We applied analysis of variance (ANOVA) to test statistical differences, either considering one factor (lakes) or two factors (lakes and seasons). We transformed data (ln  $x + 1$  or square root) and checked the homogeneity of variances (Cochran's test) and normal distribution of the residuals (by visual inspection). We compared body size of cladocerans (defined as the body length of *Daphnia obtusa*) between lakes with Student's *t* test. The relationship between phytoplankton and zooplankton biomass was explored with linear and non-linear regressions, considering all the replicates in each lake.

### Fish enclosure-mesocosm experiments

The experiments were carried out in summer 2008 in three subtropical shallow lakes in Uruguay, Lakes

**Table 1** Body size (mean standard length (SL) and range) and feeding preferences (as described in published literature) of fish and shrimps in Lake Rodó, indicating the publications used

	<i>Cnesterodon decemmaculatus</i> 1.4 cm SL 0.8–3.5 cm	<i>Jenynsia multidentata</i> 2.4 cm SL 1.0–6.1 cm	<i>Australoheros facetus</i> 3.1 cm SL 1.0–13.0 cm	<i>Gymnogeophagus rhabdotus</i> 2.7 cm SL 0.9–7.0 cm	<i>Chrenicichla scottii</i> 7.9 cm SL 2.4–14.5 cm	<i>Sybranchus marmoratus</i>	<i>Macrobrachium borellii</i>	<i>Palaemonetes argentinus</i>
Detritus	✓		✓	✓			✓	✓
Phytoplankton	✓						✓	✓
Periphyton		✓	✓	✓			✓	✓
Zooplankton	✓	✓	✓	✓	✓		✓	✓
Macroinvertebrates	✓	✓	✓	✓	✓	✓	✓	✓
Shrimps		✓	✓	✓	✓	✓	✓	✓
Fish		✓	✓	✓	✓	✓	✓	✓
References	1, 2, 3, 4	1, 2, 3, 4	1, 5, 6, 7	5	8	9–10	11	12

The item ‘macroinvertebrates’ includes all groups except *M. borellii* and *P. argentinus*, which were included as a separate category (i.e. shrimps)

1, Ringuelet (1975); 2, Escalante (1983); 3, Hartz et al. (1996); 4, Quintans et al. (2009); 5, Yafe et al. (2002); 6, Escalante (1984); 7, Ruiz et al. (1992); 8, Lobón-Cervía et al. (1993); 9, Meschiatti & Arcifa (2002); 10, Mériçoux & Ponton (1998); 11, Collins & Paggi (1998); 12, Collins (1999)

Diario (34°54’S, 55°00’W), Blanca (34°53’S, 54°50’W) and Nutrias (34°40’S, 54°17’W), covering a wide range of turbidity and submerged plant coverage (Table 2). Previous work on these lakes has shown that the zooplankton community of all three lakes consisted mainly of rotifers and nauplii, whereas large-sized cladocerans (like *Daphnia* or *Simocephalus*) showed low abundance (or even absence), particularly so during summer (Iglesias et al., 2007; Kruk et al., 2009). In each lake, we introduced eight 1000-L 1.50-m high plastic bags that were kept open to the atmosphere and fixed into the bottom in order to ensure isolation from outside water and allow full contact between water and sediment. The plastic bags were placed at 1-m depth. Fish were prevented from entering the mesocosms by adding a fine mesh (size: 1 mm) to the bottom during the set-up.

In each mesocosm we introduced an artificial plant bed (120 1-m long plants) mimicking submerged *Myriophyllum* or *Cabomba* spp (as in Meerhoff et al., 2007a), and half of the mesocosms were stocked with fish (four randomly assigned replicates). We added a combination of two of the commonest omnivorous–planktivorous species in the region, *C. decemmaculatus* (50 individuals) and *Jenynsia multidentata* (40 individuals), according to reported average natural densities of these species in vegetated habitats (Teixeira de Mello et al., 2009). The mesocosms were left undisturbed for 2 weeks prior to fish addition and the first sampling event ( $T_0$ ) to allow the zooplankton community to develop from the contemporary pool and from resting stages in the sediment. Two months later we carried out a second sampling ( $T_F$ ) to determine the effects of fish on zooplankton assemblages. The experiment was part of a larger study of the effects of fish and macroinvertebrates on trophic dynamics in subtropical and temperate macrophytes rich lakes (Iglesias, 2010).

Zooplankton was collected for quantitative analysis with a pump that integrated different depths and zones inside each mesocosm (without prior mixing of water). Besides, we took one sample outside the mesocosms (“reference lake sample”). Eight litres of water were filtered through a 50-µm mesh size net and subsequently fixed with acid Lugol. Sample counting followed Paggi & José de Paggi (1974). Copepods were identified and grouped as calanoids and cyclopoids, and cladocerans as ‘free-swimming’

**Table 2** Main limnological characteristics of the 18 Uruguayan lakes (in alphabetical order) sampled for *Daphnia* ephippia

Lake	DapW	DapEphi	Ephi DL	Dap L	Area	Z <sub>max</sub>	SD	TP	TN	K	PVI	Fish species
Aguada	2	0		0.5	3.95	0.4	43.0	975	63	100		Chei, Aust, Cnes, Hepta, Hyph, Phal, Rham
Barro	0	10.1	≥0.71 <sup>b</sup>	≥1.44	4.90	0.3	32.8	884	187	0		Gymno, Jen, Pime
Blanca <sup>a</sup>	0	10.6	≥0.71 <sup>b</sup>	≥1.44	3.43	0.7	51.9	1017	223	13		Cnes, Jen, Austra, Rham, Pime
Chaparral	0	0		2.5	8.73	0.7	47.2	598	40	74.5		Chei, Jen
Chica	0	4.8	0.71	1.44	46.48	0.1	90.5	1164	68	0		Cnes, Cory, Jen, Phal, Symb
Cisne	0.11	0		127	4.17	0.1	413.0	1048	327	0		Ast, Char, Chei, Aust, Cory, Cypho, Diap, Gymno, Hop, Hypo, Hyso, Oligo, Parap, Rham
Clotilde	0.001	7.4	0.65	1.34	4.11	1.8	27.7	451	70	28.5		Ast, Aust, Char, Rach, Cnes, Cory, Hop, Hyph, Hypo, Jen, Mima, Oligo, Phal, Pime, Rham, Symb
Diario <sup>a</sup>	0	0		101	1.32	0.6	75.8	825	272	34		Bryco, Rach, Cren, Cichla, Cnes, Cory, Diap, Gymno, Hyph, Jen, Odon, Oligo, Plata, Rham
Escondida	0.14	1.5	–	14	1.12	1.1	24.2	489	215	16		Aust, Cnes, Hop, Jen, Symb
Garcia	3.89	0		13.5	0.00	1.6	29.8	332	129	5		Aust, Ast, Cnes, Cypho, Hepta, Hyph, Jen, Oligo, Phal, Rham, Symb
Mansa	0	2.8	0.67	5	4.51	1.0	184.2	1534	135	68.5		Rach, Cnes, Cory, Cypho, Hop, Jen, Oligo, Phal
Moros	0	0		2.5	13.98	1.0	28.7	437	180	14		Cichla, Cnes, Cypho, Hepta, Hyph, Symb
Nueva	0	0		0.5	6.96	0.6	60.9	1160	67	90		No fish was found
Nutrias <sup>a</sup>	0.15	6.3	0.65	24	3.34	0.5	99.8	1136	30	0		Ast, Chei, Cnes, Cory, Jen, Oligo, Rham
Ponderosa	0	0		0.5	9.37	0.9	86.5	888	60	65		Chei, Jen, Rham, Symb
Redonda	0	56.6	–	6	1.55	2.0	23.9	514	73	58		Cal, Rach, Cnes, Jen, Phal, Symb
Techera	0	8.2	0.68	3	13.67	0.7	37.9	1681	134	96		Cypho, Jen, Phal
Pajarera	0	0		0.5	13.81	0.3	179.8	2691	150	0		Ast, Rach, Chei, Cnes, Hop, Hyph, Phal, Rham, Symb

Dap W (ind l<sup>-1</sup>), *Daphnia* abundance in water; DapEphi (numb g DW<sup>-1</sup>), *Daphnia* ephippia in sediment sample; Ephi DL (mm), measured ephippia dorsal length; Dap L (mm), estimated *Daphnia* body size (as measured from the centre of the eye to the base of the tail spine); Z<sub>max</sub> (m), maximum depth; SD (m), Secchi depth; TP (µg l<sup>-1</sup>), total phosphorus; TN (µg l<sup>-1</sup>), total nitrogen, and K (µS cm<sup>-1</sup>), conductivity; PVI (%), plant volume infested. Fish species: Ast, *Aspianax* sp; Bry, *Bryconamericus theringi*; Cal, *Callichthys callichthys*; Char, *Charax stenopterus*; Rach, *Characidium rachovii*; Chei, *Cheirodon* sp; Cren, *Chrenichthys scottii*; Aust, *Australoheros facetus*; Cnes, *Chesterodon decemmaculatus*; Cory, *Corydoras paleatus*; Cyph, *Cyphocharax voga*; Diap, *Diapomaterofalli*; Gymno, *Gymnogeophagus* sp; Hepta, *Heptapterus* sp; Hypo, *Hyphessobrycon* sp; Hypo, *Hypostomus commersoni*; Jen, *Jenynsia multidentata*; Mima, *Mimagoniatis inaequalis*; Odo, *Odontesthes bonariensis*; Oligo, *Oligosarcus jenynsii*; Para, *Parapimelodus valenciennis*; Phallo, *Phalloceros caudimaculatus*; Pime, *Pimelodella australis*; Plata, *Platanichthys platana*; Pseudo, *Pseudocorynopoma doriaei*; Rham, *Rhamdia quelen*; Syn, *Synbranchius marmoratus*. Environmental data were published in Kruk et al. (2006) and Kruk et al. (2009)

<sup>a</sup> The three lakes where the fish exclusion experiment took place

<sup>b</sup> Large *Ctenodaphnia* ephippia were present but not fully intact, preventing measurement

and ‘plant-associated’. Mean body size of crustacean zooplankton was estimated after measuring 20 individuals of each species present in each sample. We analysed the data in each lake using Student’s *t* test, with fish presence or absence as factor.

#### Surface sediment samples of subtropical lakes

We analysed the surface sediments in 18 shallow lakes located along the Uruguayan coast, which varied markedly in trophic status, fish densities and other limnological characteristics (values provided in Table 2; for methodological details see Kruk et al., 2009). We took the surface sediment samples (three replicates per lake) from the deepest point of each lake by free diving (top 5 cm, likely representing the last 2–10 years; García-Rodríguez et al., 2004; Vandekerkhove et al., 2005a).

We heated approximately 5 g (wet weight) homogenised surface sediment in 50 ml 10% KOH for 20 min. The samples were kept cold (4°C) for a maximum of 2 weeks until counting. We identified (based on Vandekerkhove et al., 2004) and quantified the resting eggs of *Daphnia* retained on a 140- $\mu$ m mesh sieve using a binocular microscope.

We estimated the body size of *Daphnia* using the existing relationship between the dorsal length of ephippia (Ephi DL) and the size of the ephippia-bearing *Daphnia* female (as measured from the centre of the eye to the base of the tail spine, Dap L): Dap L (mm) = 0.33 ( $\pm$ 0.02) + 1.55 ( $\pm$ 0.03) \* Ephi DL (mm); ( $r^2 = 0.91$ ,  $P < 0.001$ ,  $n = 230$ ; Jeppesen et al., 2002). We measured all intact *Daphnia* ephippia collected, however, the numbers were low as the edge of many ephippia were partly damaged.

## Results

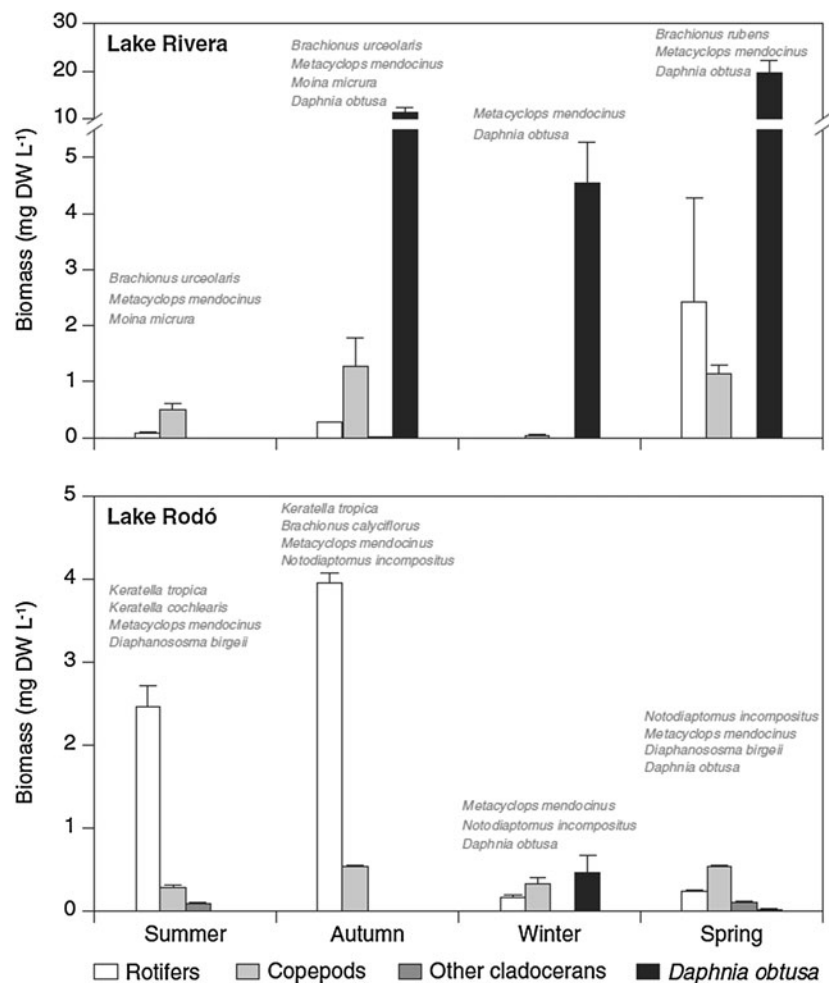
#### Field studies—comparison of two urban hypertrophic, subtropical lakes

The structure of the zooplankton community differed markedly between the two lakes. The almost fishless Lake Rivera showed lower taxonomic richness, 10 species of rotifers, 1 of copepods (only cyclopoids) and 2 of cladocerans, while lake Rodó presented 20 species of rotifers, 3 of copepods (2 cyclopoids and 1 calanoid)

and 4 of cladocerans. All the species occurring in Lake Rivera, except for two rotifers (*Brachionus urceolaris* and *B. rubens*), were found also in Lake Rodó. The cladocerans *Moina micrura* and *Daphnia obtusa* were found in both lakes, while *Diaphanosoma birgei* and *Alona* sp only occurred in Lake Rodó. Zooplankton biomass differed significantly between the two lakes for total rotifers (Rodó > Rivera), *D. obtusa* (Rivera > Rodó) and other cladocerans (Rodó > Rivera) (ANOVA, interaction between lakes and seasons:  $F_{3,16} = 17.7$ ,  $P < 0.001$ ;  $F_{3,16} = 34.1$ ,  $P < 0.001$ ;  $F_{3,16} = 18.1$ ,  $P < 0.001$ , respectively). In Lake Rivera, cladocerans dominated the zooplankton community in terms of biomass, except in summer when copepod biomass was higher (Fig. 1). *Daphnia obtusa* had the highest contribution to total zooplankton biomass. The highest abundance of *D. obtusa* occurred from autumn to spring, and males were observed in winter and spring. In contrast, in Lake Rodó small and medium-sized cladocerans dominated the biomass in winter (due to *D. obtusa*), while copepods dominated in spring, but total biomass was tenfold higher in Lake Rivera (Fig. 1). The mean, minimum and maximum body sizes of cladocerans in Lake Rivera were 1.85, 0.23, 3.74 mm and 0.55, 0.29, 0.81 mm in Lake Rodó. Moreover, *D. obtusa* was significantly larger in Lake Rivera than in Lake Rodó (mean 1.85 and 0.60 mm, respectively, *t* test  $t_{196} = 25.9$ ,  $P < 0.01$ ; Fig. 2). In Lake Rivera, the mean size of cladocerans, represented almost exclusively by *D. obtusa*, exceeded the mean size expected for the 35° latitude (Gillooly & Dodson, 2000). In contrast, in Lake Rodó cladoceran mean size was smaller than expected (Gillooly & Dodson, 2000; Fig. 2).

We found only three fish species in Lake Rivera: *C. decemmaculatus*, *Gymnogeophagus rhabdotus* and *Synbranchus marmoratus*, the latter two being represented by only one individual each. Total biomass was extremely low (<1.0 kg ha<sup>-1</sup>). *Cnesterodon decemmaculatus* reached a density of 1,170 ind ha<sup>-1</sup> in January (summer) and only 78 ind ha<sup>-1</sup> in September (spring). Lake Rodó, in contrast, exhibited higher species richness (eight species), a total biomass of 20.0 kg ha<sup>-1</sup> and dominance by small-bodied fish. The total estimated density of ca. 100,200 ind ha<sup>-1</sup> was 100 times higher than in Lake Rivera. The most important species were *C. decemmaculatus* (96% of total abundance, 32% of total biomass) and *Australoheros facetus* (37% of total

**Fig. 1** Field evidence from two urban subtropical Uruguayan lakes. Biomass of main zooplankton groups in Lake Rivera (fishless) and Lake Rodó, indicating the species with the highest contribution to the biomass of each group (mean  $\pm$  1 SE). Note the different scales in each lake



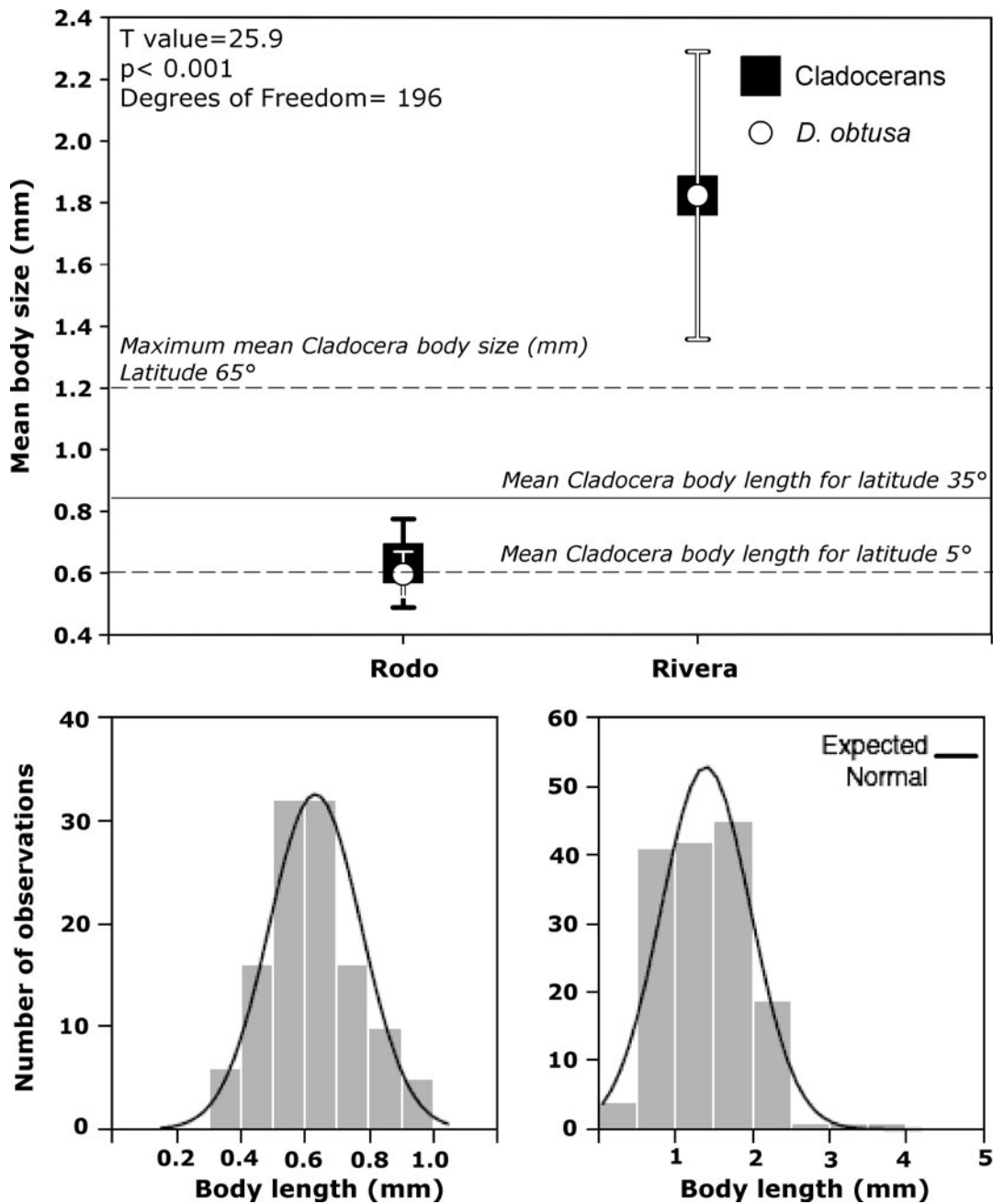
biomass). The piscivorous *Chrenicichla lacustris* accounted for 11% of total biomass. In addition, shrimps (*Palaemonetes argentinus* and *Macrobrachium borelli*) occurred in high densities only in Lake Rodó, maximum total biomass and density being 8 kg ha<sup>-1</sup> and 145,0 ind ha<sup>-1</sup>, respectively. All the fish species found in Lake Rodó, except for adult *C. lacustris*, were omnivore-zooplanktivores (Table 1), and so were the shrimps (Collins, 1999; Collins & Paggi, 1998).

Phytoplankton biomass (Chl-a) was typically higher in Lake Rivera than in Lake Rodó, except during winter (ANOVA, interaction between lakes and seasons,  $F_{3,16} = 188.2$ ,  $P < 0.001$ ). The tenfold decrease in algal biomass during winter in Lake Rivera coincided with the highest proportion of cladocerans in terms of both abundance and biomass (Fig. 1). We found a negative relationship between

cladoceran abundance and Chl-a ( $r^2 = 0.79$ ,  $P < 0.001$ ).

#### Fish enclosure-mesocosm experiments

Following the 2 weeks' incubation (but prior to fish addition) cladocerans were in all cases more diverse and abundant inside the mesocosms than in the "reference" lake samples outside, both considering plant-associated and free-swimming species (Fig. 3). It was noteworthy that under fish-free conditions large-sized cladocerans (*Daphnia*) suddenly became part of the zooplankton community in Lake Nutrias and occurred in high densities in clear Lake Diario. In Lake Blanca large-sized *Simocephalus* sp appeared for the first time (despite quite extensive previous sampling campaigns since 2000) (Fig. 3). Two months after fish introduction, the zooplankton



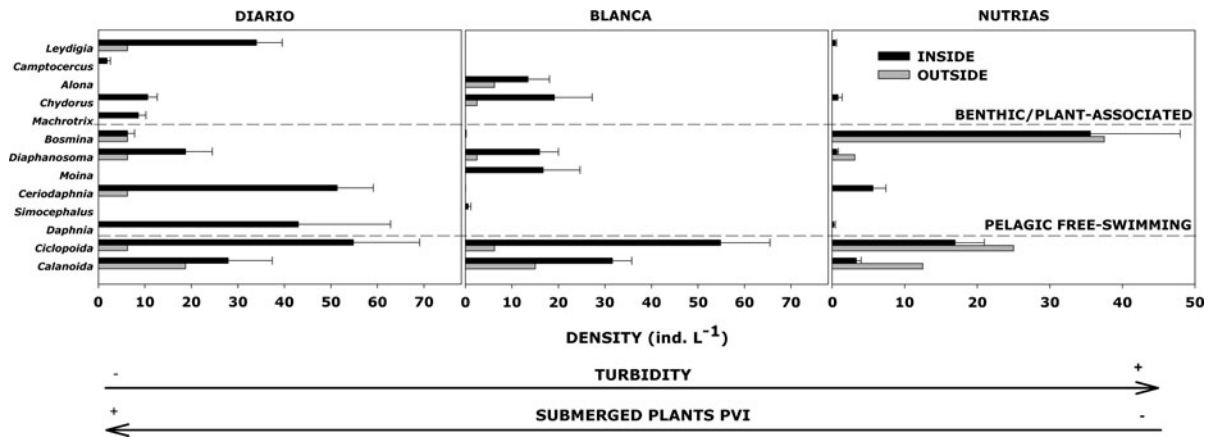
**Fig. 2** Field evidence from two urban subtropical Uruguayan lakes. Comparison of mean body length of cladocerans and *Daphnia obtusa* in Lake Rivera and Lake Rodó, showing also

the body length expected from the latitudinal gradient study of Gillooly & Dodson (2000). Above: mean values ( $\pm 1$  SD). Below: distribution of frequency of *Daphnia* body sizes

composition had reverted to the earlier dominance of small-sized individuals inside the mesocosms with fish. Cladocerans were again rare, while in the fishless mesocosms they were still abundant (together with calanoid copepods). The effect of fish on these

two zooplankton groups was significant in the three lakes (Fig. 4). The size structure of the zooplankton assemblages also differed remarkably with the presence of fish; the mesozooplankton (i.e. cladocerans + calanoid copepods) to microzooplankton (i.e.





**Fig. 3** Experimental evidence from mesocosms in three subtropical Uruguayan lakes. Mean density ( $\pm 1$  SE) of free-swimming and plant-associated cladocerans and copepods

(calanoid and cyclopoid) inside fish enclosures (black) and from lake (outside) samples (grey) at initial conditions

rotifers + nauplii) density ratio was much higher in the fishless mesocosms in the three lakes, being: 0.25 and 0.70 (Lake Diario,  $t$  test  $t_6 = 3.2$ ,  $P < 0.01$ ); 0.30 and 1.12 (Lake Blanca,  $t$  test  $t_6 = 3.7$ ,  $P < 0.01$ ), and 0.43 and 2.58 (Lake Nutrias,  $t$  test  $t_6 = 2.4$ ,  $P < 0.05$ ) in mesocosms with and without fish, respectively.

Pelagic cladocerans were particularly sensitive to fish, occasionally totally disappearing (Fig. 4), or alternatively, becoming significantly smaller in the fish treatments (Fig. 5). Also, the occurrence or mean body size of large plant-associated species (e.g. individuals from the *Simocephalus* genus) were affected. Contrarily, small plant-associated cladocerans (e.g. *Chydorus* spp) and copepods (both calanoids and cyclopoids) appeared to be less affected by fish. We only found differences in body size for copepods in the clearest lake, Lake Diario ( $t$  test  $t_6 = 2.9$ ,  $P < 0.01$ ;  $t_6 = 2.6$ ,  $P < 0.05$ , for cyclopoids and calanoids, respectively).

#### Surface sediment samples

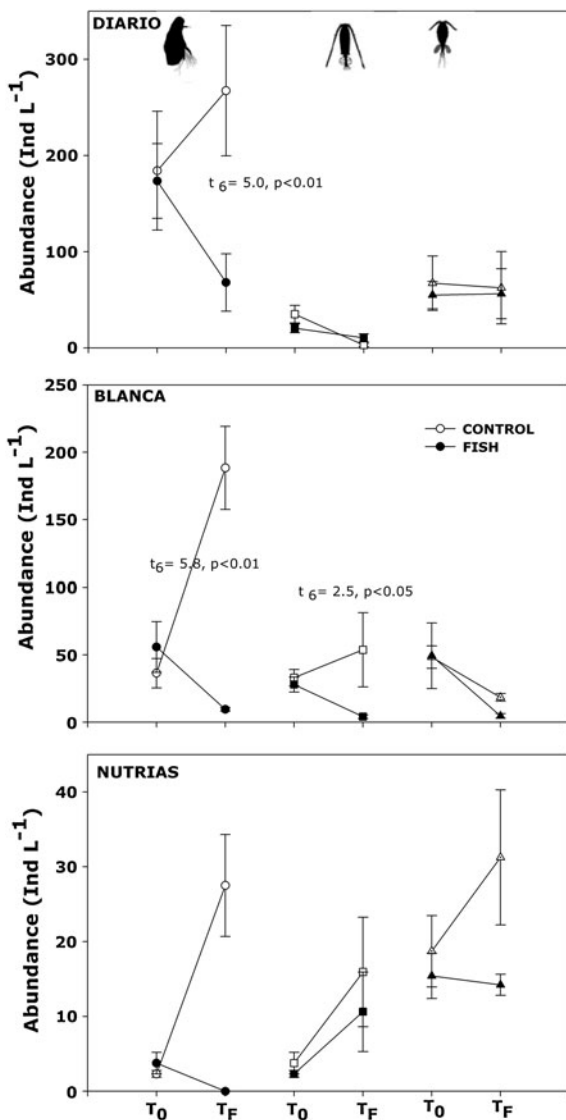
Many limnological features and the fish community structure varied among the 18 studied systems (Table 2). *Daphnia* spp ephippia were found in the surface sediment of nine of the lakes, average density being 6.0 individuals (g DW)<sup>-1</sup> (Table 2). Remarkably, *Daphnia* was found in both the sediment and the water in only four of these nine lakes, appearing in very low numbers in the summer water samples

(<5 ind l<sup>-1</sup>, Table 2; Kruk et al., 2009). In contrast, *Daphnia* spp was observed in water samples in two of the lakes where ephippia were not found in the sediments. Moreover, *Daphnia* also occurred in our fish-free mesocosms in Lake Diario, even though they were not found in sediments or water samples taken using our snap-shot approach. In summary, *Daphnia* was found in contemporary samples only in 33% of the lakes, the percentage increasing to 72% when including evidence of their presence from ephippia data or the fish enclosure experiments.

Calculated size of *Daphnia* based on dorsal length of ephippia ranged from 1.3 to 1.4 mm in most of the lakes, being much larger though in Lake Barro and Lake Blanca, as large *Ctenodaphnia* contributed substantially to the pool of *Daphnia* resting eggs in these lakes (but we were unable to measure the size of eggs from this group, as they were too damaged) (Table 2).

#### Discussion

Our results, obtained from different approaches, support the hypothesis that fish predation is the key structuring factor for the dominance of small zooplankton in subtropical lakes. When the predation pressure was extremely low in almost fishless Lake Rivera, large-bodied *Daphnia* appeared abundantly and phytoplankton biomass was low. In contrast, small-sized cladocerans were constantly abundant in Lake Rodó which had a typical high abundance of



**Fig. 4** Experimental evidence from mesocosms in three subtropical Uruguayan lakes. Initial ( $T_0$ ) and final ( $T_F$ ) abundances of the main zooplankton groups found in each lake (from top to bottom: Blanca, Diario and Nutrias), in mesocosms with (black symbols) and without fish (white symbols). From right to left results for cladocerans, calanoid and cyclopoid copepods are presented. Statistics correspond to Student's  $t$  test analyses. Note the different scales

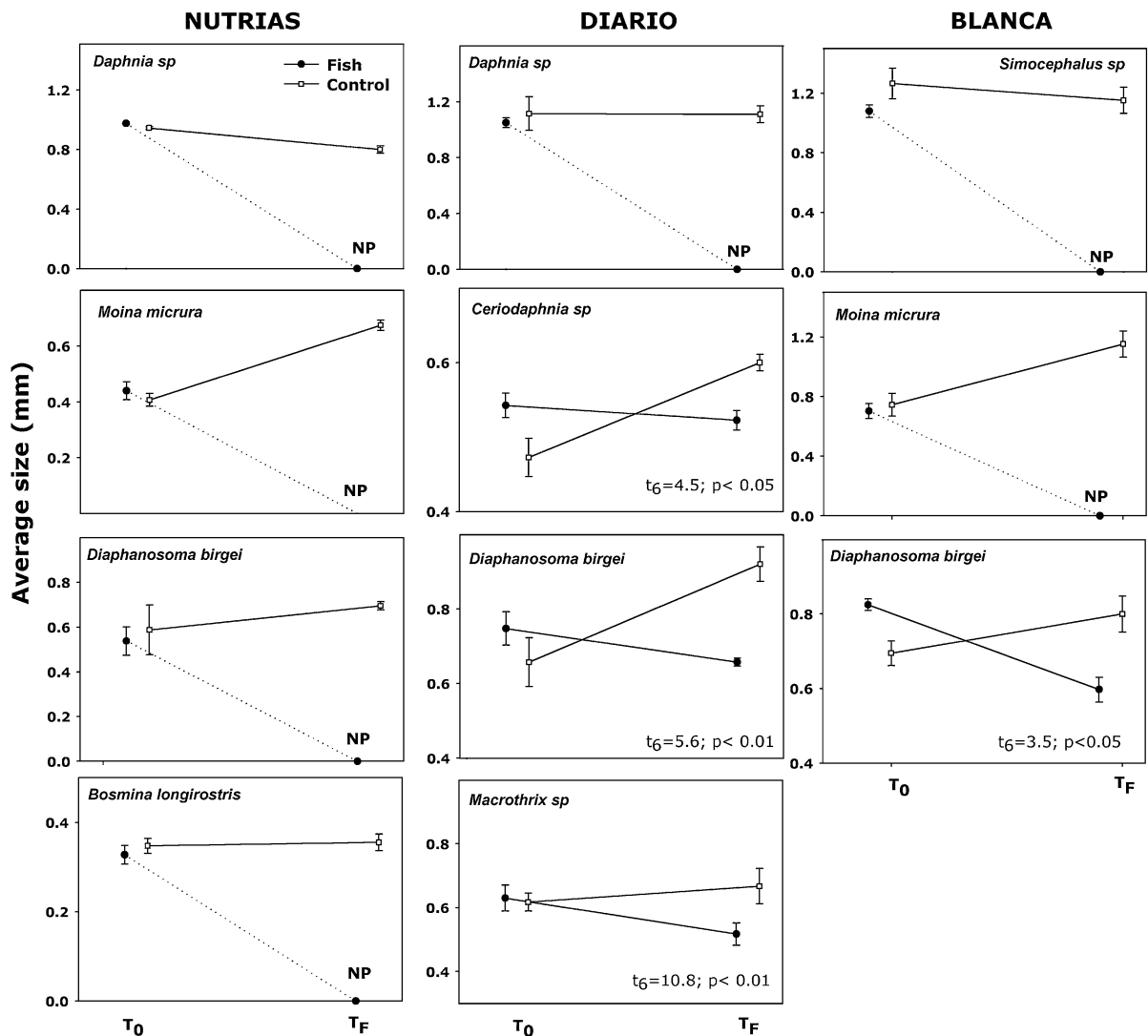
small fish. Likewise, relatively large cladocerans (e.g. *Daphnia* and *Simocephalus*) appeared in the mesocosms after only 2 weeks in a fish-free environment, most likely hatched from resting eggs in the surface sediment. Accordingly, nine of the 18 surveyed subtropical shallow lakes had *Daphnia* resting eggs in the surface sediment despite that *Daphnia* was

found in just four of the water column samples collected in summer (Table 2).

The seasonal dynamics of cladocerans in Lake Rodó followed a pattern often seen in lakes and reservoirs in Uruguay. Medium (and seldom large-sized) cladocerans are only found in moderately high densities by the end of winter and spring, and sometimes in autumn, coinciding with periods of low abundance or activity of fish (Fabian, 1993; Scasso et al., 2001; Mazzeo et al., 2003; Iglesias et al., 2007). Dominance of small forms has also been observed in warm lakes in subtropical US, Florida (Havens & Beaver, 2010) and in the Mediterranean region (Romo et al., 2005). In the latter study, the authors identified a short window for *Daphnia* in early spring in Spanish Lake Albufera, followed by dominance of small forms during all other seasons. While the shift to small-bodied zooplankton in spring and summer in Lake Rodó and other warm lakes could potentially be a physiological response to increased temperatures, it also coincides with the time when small omnivorous-planktivorous fish reproduce and shrimps start hatching and reach their highest densities (Iglesias et al., 2007). Both shrimps and the dominant fish species have multiple reproductive events starting in spring and recruit high numbers of potentially zooplanktivorous individuals in spring to early summer (Boschi, 1981; Lorier & Berois, 1995; Garcia et al., 2004; Ituarte et al., 2007). Supporting this view *Daphnia* dominated in Lake Rivera during all seasons except the summer before the fish kills.

Predation effects were not only evidenced by the lower biomass of large-bodied zooplankton in Lake Rodó, but also by their lower mean body sizes. In addition, *Daphnia* mean size in almost fishless Lake Rivera was also significantly larger than in Lake Rodó, and in Lake Rivera cladoceran (principally *Daphnia*) mean size exceeded that expected for the 35° latitude and the average water temperature (18.7°C) (according to Gillooly & Dodson, 2000). It even exceeded the mean size expected at the highest latitude (65°) (Fig. 2), while the mean size in Lake Rodó was as expected.

Effects of fish predation were also clear in our experimental study, particularly considering the abundance (Fig. 4) and body size of the pelagic or free-swimming species of cladocerans (i.e. *Daphnia*, *Simocephalus*, *Ceriodaphnia*, *Diaphanosoma*, *Bosmina* and *Moina*, Fig. 5). Copepods and small



**Fig. 5** Experimental evidence from mesocosms in three subtropical Uruguayan lakes. Initial ( $T_0$ ) and final ( $T_F$ ) average body size (mm) of the main cladoceran genera found in each lake, in mesocosms with and without fish. Statistics correspond

to Student's  $t$  test analyses. Note the different scales and that some species disappeared in fish mesocosms at  $T_F$  (shown as not present: NP); their mean size was set to 0 in the figure

plant-associated cladocerans (e.g. *Chydorus* spp) appeared to be less sensitive to fish predation, with fish effects being notable only in the most clear-water lake (Lake Diario). However, we also found effects (smaller individuals) on medium to large-sized plant-associated taxa, such as *Macrothrix* sp, even in the more turbid lakes, Lake Blanca and Lake Nutrias. These findings agree with the hypothesis of a direct fish effect rather than an indirect temperature effect. The average size of cladocerans in the fish-containing mesocosms lay within the range reported for South

American shallow lakes with fish (Lacerot, 2010) and the expectations for the region (according to Gillooly & Dodson, 2000), while the average cladoceran size found in the fishless mesocosms exceeded these levels. The observations obtained in a “natural experiment” in tropical Lake Naini Tal (India) by Nagdali & Gupta (2002) are in line with these results. These authors recorded a shift to large-bodied zooplankton and a higher zooplankton:phytoplankton biomass ratio following a massive (>80%) kill, due to fungal infection, of the most abundant planktivorous

mosquito fish (*Gambusia affinis*). However, 4 months later the abundance of mosquito fish and also those of plankton and nutrients had returned to the levels recorded in the previous year, indicating that fish played a key role for the dominance of small-bodied zooplankton and the low grazing pressure on phytoplankton in this tropical lake. Similar evidence is provided from shallow Argentinean Pampean lakes, where large-bodied zooplankton including *Daphnia* were abundant during the cold season in a year with few fish, while small-sized zooplankton dominated when fish were abundant (Sosnovsky et al., 2010).

Further evidence for the role of predation is derived from contemporary and paleoecological studies of reservoirs, lakes and ponds in tropical Africa. Here, Mergeay et al. (2004) found a clear relationship between changes in *Daphnia* species composition (identified from ephippia in the sediment) and historical information on fish abundance and stockings in shallow Lake Naivasha (Kenya). Moreover, contemporary and surface sediment analyses of 40 standing water bodies in the highlands of Kenya, covering small ephemeral pools to large permanent lakes, showed presence of *Daphnia* in 70% of the lakes (Mergeay et al., 2006). In the Uruguayan lakes, *Daphnia* appeared in the surface sediment in half of the lakes, but only in 1/3 of the water samples. Similar findings were obtained in a set of 32 Ethiopian highland reservoirs (Mergeay et al., 2006), with *Daphnia* appearing in the sediments of 62% of the water bodies, but only in 40% of the water samples. Higher occurrence of *Daphnia* in the sediments may be expected as sediments integrate several years and all seasons, while the snap-shot samples represent a summer situation when *Daphnia* densities are typically low. Surface sediment samples therefore add valuable additional spatio-temporal integrated information about the cladocerans in lakes (Vandekerckhove et al., 2005b; Davidson et al., 2007). The relatively high percentage of *Daphnia* occurrence in the combined sediment-contemporary samples in our study suggests that large-bodied zooplankton may, indeed, be present in many (if not all) warm lakes despite the high mean water temperatures. Moreover, the size of *Daphnia*, calculated from ephippia mean size, suggests that the *Daphnia* (if hatched) would be 1.3–1.4 mm (eye to tail spine) and even higher in two lakes (Lake Blanca and Lake Barro, Table 2), which reach the maximum level or even more than would be expected for this latitude

region according to Gillooly & Dodson (2000) (Fig. 2). The typically high densities of fish seem, however, to be able to reduce the density substantially or totally eliminate large-bodied zooplankton from the lake water, not least in summer, but sometimes allowing a window during winter or spring.

For water bodies with a similar high predation risk and nutrient state, it is likely that zooplankton might be somewhat smaller in warm lakes than in their colder counterparts due to the direct effect of temperature on metabolism and physiological constraints (particularly on *Daphnia*) (Moore et al., 1996). However, our results add strong evidence to the hypothesis that higher predation (Jeppesen et al., 2005), mostly from fish (Meerhoff et al., 2007b; Iglesias et al., 2008; Mazzeo et al., 2010), but potentially also from some macroinvertebrates (Trochine et al., 2006; Iglesias et al., 2007; González-Sagrario et al., 2009), rather than physiological constraints, is the key factor for the dominance of particularly small-sized zooplankton in warm lakes.

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