Field and experimental evidence of the effect of *Jenynsia multidentata*, a small omnivorous–planktivorous fish, on the size distribution of zooplankton in subtropical lakes

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SUMMARY

1. Small cladocerans, copepod nauplii and rotifers often dominate the zooplankton community in tropical and subtropical lakes. This is probably because of high predation pressure by small omnivorous–planktivorous fish, but experimental evidence is scarce.
2. This study used two approaches to test the effect of the small omnivorous–planktivorous fish species *Jenynsia multidentata*, which is frequently abundant in (sub)tropical eutrophic lakes in South America, on the size distribution of zooplankton. In Lake Blanca (Uruguay), which lacks any piscivores, we sampled seasonally for both fish and zooplankton. We also conducted an outdoor mesocosm experiment with treatments containing or lacking *J. multidentata*.
3. Together, the empirical and experimental data suggest that *J. multidentata* predation plays an important role in modulating the size structure of the zooplankton community in subtropical lakes. In the absence of *J. multidentata*, stocked large-sized zooplankters like *Daphnia obtusa* were abundant in the experiments, while small-sized zooplankton dominated in the presence of fish, as they did in the lake itself from spring to the end of the season.

Keywords: *Jenynsia multidentata*, predatory, subtropical shallow lake, zooplankton structure

Introduction

The importance of fish predation for structuring the freshwater zooplankton community is well documented, particularly in temperate lakes in Europe and North America, and the presence or absence of planktivorous fish is known to induce major shifts in the size distribution of zooplankton (Hrbacek *et al.*, 1961; Brooks & Dodson, 1965) or behavioural shifts (Timms & Moss, 1984; Schriver *et al.*, 1995; Kairesalo, Tátrai & Luokkanen, 1998; Burks *et al.*, 2002; Romare & Hansson, 2003). Far less is known about lakes in warmer climatic regions. A recent study has shown the impact of *Odontesthes bonariensis* (Valenciennes, 1835) predation on subtropical zooplankton community structure (Boveri & Quirós, 2007), and other studies have focused on zooplankton behavioural shifts related to predation risk (Meerhoff *et al.*, 2006, 2007a,b; Trochine, Modenutti & Balseiro, 2006; Iglesias

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et al., 2007). The zooplankton communities of tropical and subtropical shallow lakes are most often dominated by small cladocerans, copepod nauplii and rotifers (Crisman & Beaver, 1990; Dumont, 1994; Branco *et al.*, 2002; Garcia *et al.*, 2002; Havens, East & Beaver, 2007), probably due to high predation pressure by small omnivorous–planktivorous fish (Fernando, 1994; Lazzaro, 1997; Pinel-Alloul *et al.*, 1998) and by large invertebrate predators (Boschi, 1981; Collins & Paggi, 1998; Collins, 1999; Iglesias *et al.*, 2007). However, experimental evidence is scarce.

Variations in abundance or foraging activity of planktivorous fish also influence seasonal patterns in the size distribution of herbivorous zooplankton in (sub)tropical lakes. Mazzeo *et al.* (2003) found that a shift to dominance of small sized specimens (rotifers) in the zooplankton in summer in Lake Blanca coincided with an increase in abundance of *Jenynsia multidentata* (Jenyns, 1842). Likewise, in Lake Rodó (Montevideo, Uruguay), a hypereutrophic urban shallow lake, Scasso *et al.* (2001) found the summer decline in mesozooplankton abundance to be related to fish activity, in this case principally represented by *Cnesterodon decemmaculatus* (Jenyns, 1842) and *J. multidentata*. Also in a Spanish warm temperate lake (Lake Albufera), Romo *et al.* (2005) attributed the lower abundance or absence of larger-bodied zooplankton from late spring to autumn to high fish predation. Others have argued that low abundance or absence of *Daphnia* in warmer regions may relate to a lower upper thermal tolerance of these organisms (Moore, Folt & Stemberger, 1996). Daily physical and chemical fluctuations and sudden environmental shifts (e.g. due to heavy precipitation leading to large variations in water level) may also favour dominance of small forms (for a review see Jeppesen *et al.*, 2005a).

Among the many small fish species in subtropical lakes in the south eastern region of South America, the 'one-sided livebearer' *J. multidentata*, is one of the most common omnivorous–planktivorous fish (Ringuelet, 1975), often occurring in high densities in (hyper)eutrophic shallow lakes (Scasso *et al.*, 2001; Mazzeo *et al.*, 2003; Garcia *et al.*, 2006). *Jenynsia multidentata* can feed on zooplankton, phytoplankton, periphyton, invertebrates and also on detritus (Escalante, 1987; Koblitz & Andreata, 1996; Marti *et al.*, 2006). Its distribution ranges from Rio de Janeiro (Brazil: 43°15′W, 22°15′S) to Uruguay and Argentina

(67°20′W, 39°47′S) (Ghedotti, 1998). It exhibits a wide tolerance of several environmental variables (being euryhaline, eurythermic, euryoic) (Thormahlen de Gil, 1940; Gómez, 1993; Menni, Gómez & López Armengol, 1996; Betito, 2006), allowing the species to inhabit many aquatic systems (Bistoni *et al.*, 1999; Kruk *et al.*, 2006). In shallow lakes that lack piscivores *J. multidentata* may reach extremely high abundances (Mazzeo *et al.*, 2003), often associated with aquatic plants (Mazzeo *et al.*, 2003; Iglesias *et al.*, 2007; Meerhoff *et al.*, 2007a,b). It is viviparous (Siccardi, 1940), reproducing throughout the year in the tropics (Novaes & Andreata, 1996) and in spring and summer in subtropical and temperate regions (Turner, 1957; Garcia *et al.*, 2004).

The aim of the present study was to assess the impact of an omnivorous–planktivorous fish on zooplankton size distribution in a subtropical shallow eutrophic lake, using both an empirical and an experimental approach. We hypothesized that the zooplankton community would be dominated by medium to large sized herbivorous individuals (cladocerans and calanoid copepods) only in the absence or at low abundance or activity of predatory fish.

Methods

Field survey

The field data were collected four times from winter 2003 to autumn 2004. Both fish and zooplankton communities were sampled in a shallow lake that lacks piscivorous fish. Lake Blanca (Maldonado, Uruguay, 34°54′S; 54°50′W) is a shallow (total area = 69.1 ha, Z_{max} = 3.6 m), warm polymictic (temperature range: 11.3–26.3 °C) and eutrophic lake (in-lake annual mean total phosphorus (TP), total nitrogen (TN) and chlorophyll *a* concentrations: 94, 1010 and 31.9 μg L^{-1}, respectively). Since a dramatic reduction in lake volume during 1997–98 (Mazzeo *et al.*, 2003), eliminating most of the native species, the fish community has been dominated by small (13 mm < SL < 86 mm) *J. multidentata*.

For each sampling season, the plant volume infested (PVI, *sensu* Canfield *et al.*, 1984) of submerged and emergent vegetation coverage was mapped. Five sampling points within each of three microhabitats were randomly selected: emergent plants (EP), submerged plants (SP = PVI ≥25%), and open water

without plants (OW). Water samples for zooplankton quantification were collected with a vertical tube enclosing the whole water column at midday and midnight and averaged before analyses. In each habitat 20 L of water were filtered through a 50 μm mesh size net and subsequently preserved in 4% formaldehyde.

Zooplankton were classified to species level and counts were made according to Paggi & de Paggi (1974). For each habitat the abundances of microzooplankton (nauplii + rotifers) and mesozooplankton (small cladocerans + calanoid copepodites + adults) were determined and the mesozooplankton/microzooplankton (meso/microzooplankton) ratio calculated.

Quantitative sampling of the fish community was performed using two unbaited minnow traps (double cone, 60×80 cm, 5 cm opening, mesh 0.5 mm, volume = 40 L) per station, one placed close to the surface and one close to the sediment. The catches integrated the periods between sunrise and sunset (day) and sunset and sunrise (night), respectively. Fish were classified to species level and capture per unit effort was calculated (CPUE = total number of individuals collected over the period in two traps, per hour).

Use of trap samples for dietary analyses is not advisable due to abnormal feeding conditions inside the traps and post-catch digestion (Windell & Bowen, 1978). For diet analyses, point-sample electric fishing (Perrow, Jowitt & González, 1996) was undertaken using Sachs Elektrofischfanggerate GmbH D-88299 Leutkirch equipment. In each considered habitat (submerged plants, emergent plants and open waters), five samples were taken at noon and midnight. Each sample integrated catches of nine pulses of 5 s taken in random transects (mesh seine 0.5 mm). Fish were fixed in 10% formaldehyde. This technique prevents regurgitation; digestion stops quickly and the stomach content is well preserved (Bowen, 1983; APHA, 1998).

Length–age relationship was established for each sex of *J. multidentata* from the apparent shift of the modes in a time series of length–frequency samples (modal progression analysis) using the FiSAT II software based on the results of Bhattacharya's method ($n = 8574$ fishes, s.i. > 2; Gayanilo *et al.*, 2005). It was assumed that the length of the fish of a certain age is normally distributed. (Sparre & Venema, 1997).

Gut content analysis of 151 randomly chosen *J. multidentata* belonging to all sampled seasons were performed under dissecting microscope. To test differences in the use of trophic resources, three age (by length) groups were considered: group 0 (0–9 months), group 1 (12–21 months) and group 2 (≥24 months). Presence/absence data were registered and frequency of occurrence of each item was calculated (Hyslop, 1980). Trophic level, defined as position in the food chain assessed by the number of energy-transfer steps to reach that level (Begon, Townsend & Harper, 2006), was estimated from the percent contribution of each item (SIMPER; Clarke, 1993; Clarke & Warwick, 1994) using the approach of TrophLab (Pauly *et al.*, 2000). The same methodology was followed for *C. decemmaculatus*.

Mesocosm experiment

An experiment in six outdoor 3800 L mesocosms ($3 \times 2 \times 0.60$ m) was conducted from 9 April to 11 May 2005 to test the effect of *J. multidentata* on the zooplankton community. The bottoms of the mesocosms were covered with washed river sand and they were filled with groundwater. Thirty per cent of the total surface area was covered with *Eichhornia crassipes* (Mart) Solms. The experimental units were allowed to settle for 2 months prior to initiation of the experiment to allow phytoplankton and zooplankton to develop. High nitrogen and phosphorous inputs were maintained, to prevent any confounding effects of nutrient limitation, by weekly additions of 5 mg N and 5 mg P to each unit, as commercial fertilizer NPK (15-15-15) ISUSA, TN, P_2O_5 and K_2O, respectively.

To evaluate the predation effect on medium and large-sized cladocerans, *Daphnia obtusa* Kurz specimens were cultured and added 2 months before the initiation of the experiment. To ensure uniform initial conditions in the experimental units, up to 2000 L from each mesocosm were distributed among the other five mesocosms (400 L to each). This homogenization procedure was done using a special pump allowing interchange of water, phytoplankton and zooplankton.

Initial samples were taken at T_0 after homogenization and just before randomly assigning two different treatments to the experimental units: no-fish: zooplankton + phytoplankton ($n = 3$) and fish: *Jenynsia*

multidentata (9 ind m^{-2} collected from Lake Blanca) + zooplankton + phytoplankton (*n* = 3). To prevent predation of fish by birds, the mesocosms were covered by a plastic net.

Water samples for analysis of zooplankton and nutrients (TN and TP; Valderrama, 1981) were collected throughout the water column with a tube at midday, integrating eight sites per mesocosm without previous mixing of water. For zooplankton quantitative analysis, 15 L of water were filtered through a 50 μm net and the specimens fixed with acid Lugol. Counts were made according to Paggi & de Paggi (1974) and abundances were expressed as ind L^{-1}. Animals were grouped as microzooplankton (nauplii + rotifers) and mesozooplankton (cladocerans + calanoid copepodites and adults) and the mesozooplankton/microzooplankton ratio was calculated. Dissolved oxygen, conductivity and pH were recorded *in situ* in the central part of the mesocosm using Horiba sensors.

Statistical analyses

Field data were analysed using ANOVA with season as factor (four levels: winter, spring, summer and autumn), and considering each habitat (submerged plants, emergent plants and open waters) separately, Tukey *post hoc* tests were used. We thus assumed the four seasons to be independent datasets, which is likely for organisms with fast turnover, such as zooplankton. To test for ontogenetic difference in use of food resources, analysis of similarity (ANOSIM, Clarke, 1993; Clarke & Warwick, 1994) test (999 permutations; $P_{global} < 0.05$) over Raup-Crick similarity matrix for presence/absence data (Raup & Crick, 1979) was performed considering the age groups defined *a priori*. Student *t*-test in each sampling date was performed for physical, chemical and biological mesocosm data to investigate statistical differences between fish and no-fish treatments. Assumptions of the statistical tests were verified, Cochran *C*-tests were used to check variance homocedasticity, while normality was tested using Kolmogorov–Smirnov test and by visual inspection of residuals. When violations were detected, square root transformations (*x* or *x* + 1) were performed. The correlation between the seasonal variation of mesozooplankton abundance and fish CPUE was analysed using non-parametric Spearman (rs).

Results

Field survey

The zooplankton community was dominated by microzooplankton, except in winter when mesozooplankton was important as well. Microzooplankton abundance peaked in autumn (1691 ind L^{-1}), while minimum numbers occurred in winter (191 ind L^{-1}). Nauplii dominated the microzooplankton in winter, while rotifers were most abundant during the other seasons. *Keratella cochlearis* Gosse was the most abundant rotifer in the system year round, but *Fillinia longiseta* Ehrenberg and *Polyarthra* sp. Ehrenberg were also common, principally in summer and autumn. Among the mesozooplankton, the most abundant cladoceran species were *Bosmina longirostris* Müller and *Diaphanosoma birgei* Korinec. Cladocerans were homogeneously distributed in spring (n.s., OW = PE = PS) while they in winter and summer occurred in higher abundances in the open waters followed by the emergent plants ($F_{2,12}$ = 19.1, $P < 0.001$ and $F_{2,12}$ = 15.3, $P < 0.001$, respectively, OW > PE > PS, Fig. 1a). In autumn they were more abundant in the submerged plants ($F_{2,12}$ = 6.1, $P < 0.05$. PS > PE = OW, Fig. 1a). The calanoid copepod *Notodiaptomus incompositus* Brian was also common and was homogeneously distributed all year round among the three habitats (Fig. 1b).

The meso/microzooplankton ratio varied strongly among seasons in all three habitats. Statistical differences among habitats were found in winter and autumn when highest values occurred in open water ($F_{2,12}$ = 13.0, $P < 0.001$ and $F_{2,12}$ = 7.0, $P < 0.01$, respectively. OW > PS = PE, Fig. 1c), while no statistical differences were detected in spring and summer. Considering the seasonal variation of the ratio, winter values were an order of magnitude higher than the other seasons ($F_{3,36}$ = 86.8, $P < 0.0001$. Winter > spring = summer = autumn, Fig. 1c).

The fish community was dominated by *J. multidentata*. The highest and lowest catches occurred in summer and winter, while intermediate catches occurred in spring and autumn (2-way ANOVA $F_{3,36}$ = 40.3, $P < 0.001$; Fig. 1d). In winter, CPUE was higher in the submerged plants ($F_{(2,12)}$ = 17.5, $P < 0.001$; SP > EP > OW), while in spring fish were collected primarily in the emergent plant sites ($F_{(2,12)}$ = 18.1, $P < 0.001$; EP > SP = OW for spring
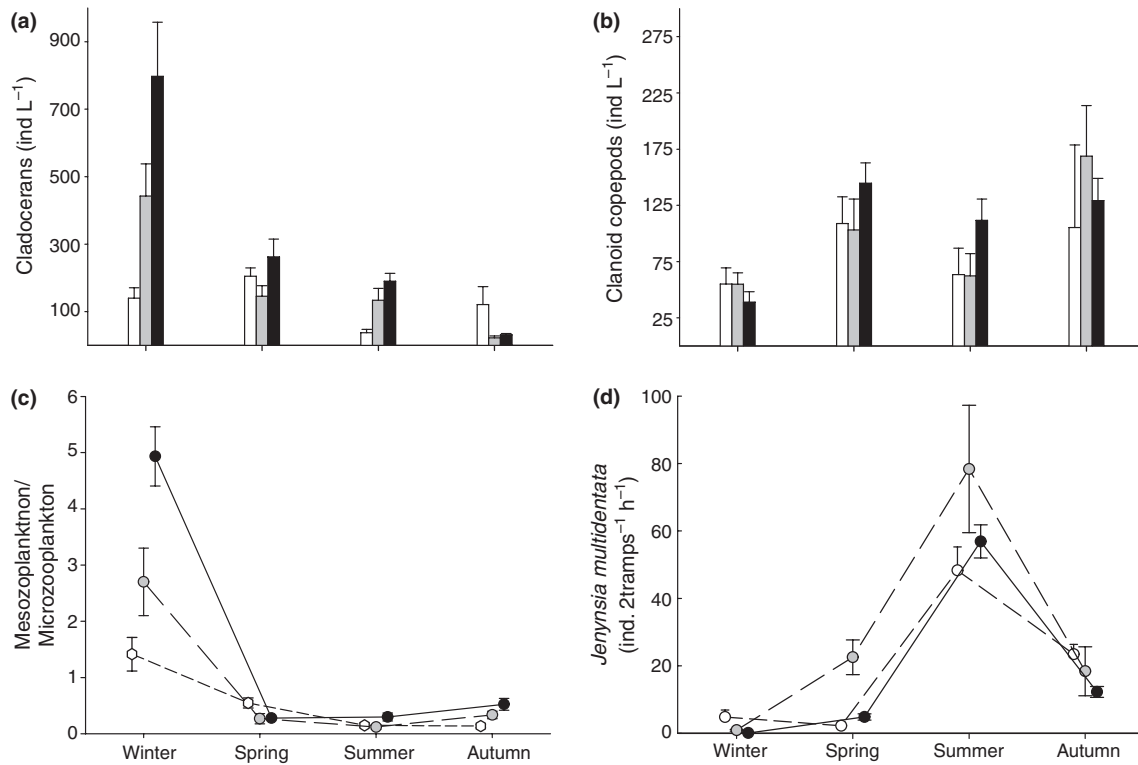
Fig. 1 Seasonal variation in: (a) cladoceran abundance; (b) calanoid copepod abundance (adults + copepodites), (c) herbivorous mesozooplankton/microzooplankton abundance ratio and (d) the CPUE of the omnivorous planktivorous fish *Jenynsia multidentata*; in submerged plants (open), emergent plants (grey) and open waters (black). Error bars represent ±1SE. Mesozooplankton = cladocerans + calanoid copepodites and adults, microzooplankton = rotifers + nauplii.

and summer respectively). In summer and autumn no differences among habitats were detected.

Young of the year (YOY) individuals of *J. multidentata* were absent in winter samples, recruitment started in spring and continued until autumn. The other fish species captured, the small omnivorous *Cnesterodon decemmaculatus* (Jenyns, 1842; Poeciliidae), occurred at low abundance (<1.5% of total fish density and biomass).

Mesozooplankton abundances were correlated negatively with the CPUE of *J. multidentata* in all the considered habitats (rs = −0.69, $P < 0.0001$; rs = −0.58, $P < 0.0001$; rs = −0.63, $P < 0.0001$ for PS, PE and OW, respectively).

Gut content analysis confirmed the previously reported omnivorous–planktivorous diet habits of *J. multidentata*. Mesozooplankton constituted the most frequent item ($F_o = 0.81$). The diet also included insects (mainly Diptera, *Chaoborus* sp. and chironomids) and basal items of trophic level 1 (e.g. periphyton, phytoplankton, plant remains, sediments and/or

detritus) (Table 1). Shrimps and fish were infrequent items. The trophic level was 3.0 ± 0.4 (mean ± SE).

All comparisons of food choices between age groups showed significant differences (Table 2). *J. multidentata* exhibit a clear ontogenetic diet shift, mesozooplankton contributed c. 90% of gut content of age group 0, while it represented c. 70% for group 1

Table 1 Items found in the stomach contents of *Jenynsia multidentata* from Lake Blanca. Frequency of occurrence (F_0 *sensu* Hyslop, 1980) and percent contribution of each item by age group (SIMPER *sensu* Clarke, 1993)

Item	F_0	% contribution		
		Group 0	Group 1	Group 2
Mesozooplancton	0.811	87.0	69.2	40.3
Diptera	0.336	9.0	22.6	36.4
Periphyton	0.315	3.9	7.9	18.2
Shrimp	0.098	0.1	0.3	5.1
Fish	0.014	0.0	0.0	0.0*

*Very close to 0.

Table 2 ANOSIM comparison of food choices among three different age groups of *Jenynsia multidentata* from Lake Blanca

Comparison	R	P
Global analysis	0.139	0.01
0 versus 1	0.088	0.02
1 versus 2	0.268	0.02
0 versus 2	0.388	0.02

Group 0: 0–9 month, group 1: 12–21 month, and group 2: >24 month old fish, respectively.
The *R* statistic generated by ANOSIM is 0 when there is no difference between groups.
Increasing positive values mean greater differences between groups.

declining to less than 40% in group 2 (Table 1). Almost the entire *C. decemmaculatus* catches were obtained in SP (79%), and its gut contents consisted only of basal items (i.e. trophic level = 2; *n* = 15).

Mesocosm experiment

No fish kill occurred during the experiment as all fish stocked were recovered from the mesocosms at the end of the experiment. A major decline in *D. obtusa* abundance occurred shortly after the mesocosms were stocked with *J. multidentata* (Fig. 2a), significant differences being observed from day 11, when *Daphnia* disappeared from one of the fish tanks and abundances of 3.3 and 20.0 ind L^{-1} were registered in the other two. On day 32 *Daphnia* was absent in two of the three tanks, while it reached 196 ind L^{-1} in the last replicate. In the no-fish treatment we found abundances of 198.0 ± 107.6 and 275.0 ± 119.0 ind L^{-1} (mean $\pm$ SE) on days 11 and 32, respectively (n.s., $t_4 = 4.6$, $P < 0.05$, $t_4 = 4.2$, $P < 0.05$, on day 0, 11 and 32, respectively (Fig. 2a,b). Concomitantly, in the fish treatment, microzooplankton (particularly rotifers) rose in abundance from 10 ± 2 to 299 ± 96 ind L^{-1} (mean $\pm$ SE), being higher than in the no-fish treatment from day 11 until the end of the experiment ($t_4 = -5.5$, $P < 0.01$, $t_4 = -2.8$, $P < 0.05$, at time 11 and 32, respectively). From initially similar meso/microzooplankton ratios, the ratio dropped in the fish treatments, but increased in the no-fish treatments, resulting in significant differences among treatments from day 11 until the end of the experiment (n.s.,
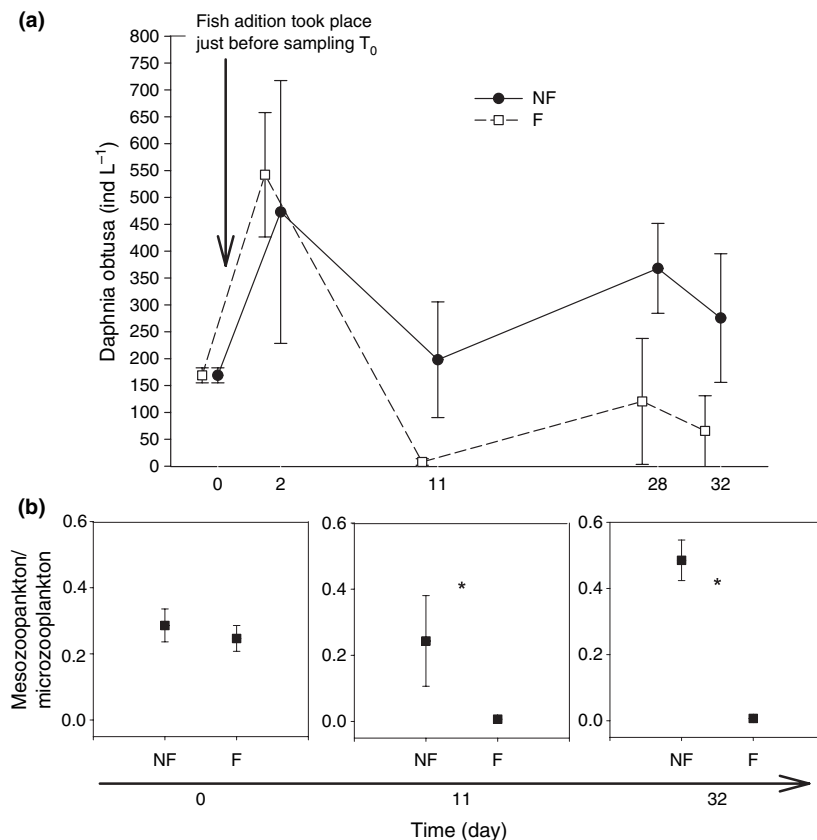

Fig. 2 (a) Changes in *Daphnia obtusa* abundance (top graph) during the experiment. NF = no-fish treatment, F = 9 ind m^{-2} fish treatment, error bars represent 1 SE. Sampling was conducted on the same dates in the two treatments, but NF has been shifted in the figure to clarify patterns. (b) Experimental variation in the herbivorous mesozooplankton/microzooplankton ratio is shown at start-up (day 0) and day 11 and 32. *significant differences between treatments. Mesozooplankton = cladocerans + calanoid copepodites and adults, microzooplankton = rotifers + nauplii. Mean (three replicates average), ± 1 SE.

$t_4 = 3.2$, $P < 0.05$, $t_4 = 6.4$, $P < 0.01$, at time 0, 11 and 32, respectively, Fig. 2b).

No significant differences were detected for physical and chemical variables among treatments during the experiment. The temperature varied from 13.1 to 19.7 °C, dissolved oxygen from 8.2 to 12.9, pH values were always around 9, while conductivity was near 500 μS cm^{-1}. The supply of TP and TN ensured no bottom-up limitation during the experiment and no statistical differences were detected among treatments: TP rose from 2.6 ± 0.1 to 7.2 ± 0.5 mg L^{-1}, while TN varied from 2.1 ± 0.3 to 22.6 ± 0.9 mg L^{-1} on day 0 and 32, respectively.

Discussion

Both field and experimental data suggest a strong effect of *J. multidentata* on the size distribution of zooplankton. The zooplankton community in Lake Blanca was dominated by microzooplankters, particularly rotifers, and this is consistent with previously reported results for eutrophic-hypereutrophic (sub)tropical lakes (Crisman & Beaver, 1990; Dumont, 1994; Branco *et al.*, 2002; Garcia *et al.*, 2002; Jeppesen *et al.*, 2005a; Havens *et al.*, 2007). The small size of the cladocerans (mainly *B. longirostris* and *D. birgei*), the absence of large bodied specimens (e.g. *Daphnia* spp.) and the dominance of rotifers are consistent with what would be expected due to size selective predation on larger zooplankton by abundant zooplanktivorous fish.

A clear seasonal variation in meso/microzooplankton ratios was found in the lake in all three habitats considered. In winter, when fish catches were low (2.3 fish in 2 traps h^{-1}) higher ratios were found, reflecting the highest mesozooplankton and the lowest microzooplankton abundances observed. The ratio was an order of magnitude lower during spring when catches of *J. multidentata* started to increase and YOY fish appeared in the lake, and during the rest of the seasons when catches were high (up to 40 times winter catches). Zooplankton constitutes *c.* 90% of gut content of YOY fish, which was more than twice as high frequency as in 2-year-old specimens (Table 1), High abundances of YOY fish in spring (G. Goyenola, unpubl. data) and likely also a higher fish metabolism may therefore explain the strong effect on zooplankton in spring despite relatively minor changes in fish CPUE from winter to spring. The seasonal variation in

herbivorous zooplankton size fractions accords with previous findings from subtropical and warm temperate lakes, such as those for Lake Blanca (Mazzeo *et al.*, 2003) and Lake Rodó in Uruguay (Scasso *et al.*, 2001), and in Lake Albufera in Spain (Romo *et al.*, 2005). The omnivorous habit of *J. multidentata*, shown by the gut content analyses, may be responsible for a high carrying capacity of this species. Therefore, it is to be expected that top-down control of *J. multidentata* on mesozooplankton will be high. Furthermore, *J. multidentata* was abundant not only in the open water, but also among plants, leaving little opportunity for cladocerans to seek refuge from predators among vegetation as otherwise reported from temperate shallow lakes (Burks *et al.*, 2002; Meerhoff *et al.*, 2007b).

The role of fish for structuring the zooplankton community and size structure is confirmed by the experimental results. *Jenynsia multidentata* exerted a strong predation pressure on cladocerans, particularly *D. obtusa*. Following a decrease in *Daphnia* abundance, rotifers became significantly more abundant in the fish treatments and accordingly the meso/microzooplankton ratio decreased substantially, while the ratio remained high in the no-fish treatments (Fig. 2). The ratios estimated were higher in the experiment (fish treatments) than in the lake, and also that *D. obtusa* occurred in one of the fish mesocosm but not in the lake. These differences probably reflect a higher abundance of fish in the lake. We used 9 fish m^{-2}, the density previously reported in Laguna Blanca (Mazzeo *et al.*, 2003), but recent studies have reported higher densities, around 25–42 fish m^{-2} (Meerhoff *et al.*, 2007a,b).

Our field and experimental results show that at reduced fish (in our study *J. multidentata*) abundance or activity, large-sized zooplankton, including *D. obtusa*, are able to reach high abundances. In accordance with these results, Mazzeo *et al.* (2000) observed an extremely high abundance of *D. obtusa* in Lake Rivera (hypertrophic system located in Montevideo, Uruguay), and short-term clear-water conditions after an extensive fish kill caused by high ammonia levels.

Considering the habitat preferences of *J. multidentata*, its often high abundance and its ability to persist at low oxygen levels and in turbid water conditions, it is likely that this species (together with other small fish species) reinforces the eutrophication process in nutrient enriched subtropical lakes in South America.

Control of the abundance of small omnivorous–planktivorous fish is therefore a key issue in the rehabilitation of such lakes. Experience from temperate lakes suggests that reductions in nutrient loading may lead to lower abundances of planktivorous–benthivorous fish and a higher proportion of piscivorous fish (Jeppesen *et al.*, 2005b). To reinforce recovery, fish manipulations have been used in temperate lakes (Meijer *et al.*, 1994; Benndorf, 1995; Hansson *et al.*, 1998; Mehner *et al.*, 2002). Previous studies have shown, however, that in contrast to temperate lakes active removal may have only a short term effect in warmer climates, mainly because a viviparous fish population (e.g. *Jenynsia multidentata* or *Cnesterodon decemmaculatus*) recovers fast even after extensive fish removal (Jeppesen *et al.*, 2005a, 2007). In (sub) tropical lakes, fish reproduce several times a year (Fernando, 1994; Lazzaro, 1997; Pinel-Alloul *et al.*, 1998), whereas temperate fishes typically reproduce only once a year. Piscivorous fish stocking may be an alternative biomanipulation strategy in subtropical systems, not least when predatory fish are missing or their abundance is low. However, this remains to be tested.

Acknowledgments

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