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Effects of fish manipulation on the plankton community in small hypertrophic lakes from the Pampa Plain (Argentina)

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Abstract

Trophic cascade hypotheses predict that fish will affect the structure and biomass of pelagic plankton communities. In order to investigate trophic cascade effects from fish down to phytoplankton, whole-lake studies were performed in five hypertrophic (mean total phosphorus (TP) concentrations higher than $1000\,mg\,m^{-3}$) shallow lakes located in the Pampa Plain. The main climatic characteristic of this region is the alternation between periods of drought and flood, with corresponding changes of lake depth and conductivity of lake water. All lakes were studied from April to December 2000. Samples were taken of their physical and chemical characteristics and biotic communities, focusing on the zooplankton community. Fish were manipulated in four lakes (Capurro, Longinotti, Vedia 1, Vedia 2), while the fifth (Lake Vedia 3) was left undisturbed as a reference system. High abundance of planktivorous minnows (*Jenynsia multidentata* and *Cheirodon interruptus*) dominated the fish community in the reference lake. In the manipulated lakes, fish stocks were largely reduced in late autumn (May). During winter, Capurro, Longinotti and Vedia 1 were stocked with a visual planktivore, the pampean silverside (*Odontesthes bonariensis*, Atherinidae). Fish stocking was 24, 33 and $19\,kg\,ha^{-1}$, respectively. In contrast, no fish were stocked in Lake Vedia 2. Following fish removal, large *Daphnia* appeared in these lakes and grazed intensively on the phytoplankton. In contrast, no *Daphnia* were found in the reference lake (Vedia 3). The stocking of *O. bonariensis* in lakes Capurro, Longinotti and Vedia 1 led to a decrease in the percentage of large cladocerans and a rise in the phytoplankton biomass:TP ratio. Moreover, the lakes mentioned were stocked with different quantities of silversides over different periods of time. These differences were reflected temporarily in the plankton dynamics, affecting mainly larger sized zooplankton. Nevertheless, the presence of *Daphnia* was short lived in the lake where fish had been removed and no *O. bonariensis* were stocked. Competition for resources and recruitment of remaining fish probably caused a collapse in the zooplankton biomass. Our results support the idea that fish predation on zooplankton and its effect on phytoplankton is very intense in small pampean lakes. Fish removal was short lived, however. This could be because in small pampean lakes fish recolonization is favored, and minnows are highly prolific. Moreover, if manipulation of the trophic structure of lakes is undertaken in the pampean region, high nutrient loading from the watershed, climate and hydrology should also be taken into account.
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Introduction

During the last 40 years, organization of the food-web structure and dynamics in the pelagic zone of lakes has been subject to intense debate (Jeppesen et al. 2000). The classic limnological approach to lake ecosystem structure was focused on the food chain, encompassing nutrients, phytoplankton, zooplankton and fish ("bottom-up" control; Dillon and Rigler 1974; McQueen et al. 1986). The pioneering work of Hrbácek et al. (1961) and Brooks and Dodson (1965) indicated that fish could be important driving components of the food web, regulating plankton community structure. Two decades ago, investigations showed that food webs may rather be regulated by fish ("top-down" control; Shapiro 1980; Carpenter et al. 1985; Gulati et al. 1990).

The importance of top-down control may vary with lake trophic state. Many authors believe that the regulatory role of fish is more pronounced in nutrient-rich lakes, so that freedom from fish predation (e.g. by fish removal) will lead to higher zooplankton grazing of algae, and clear water (Jeppesen et al. 1997a; Quirós 1998). However, McQueen et al. (1989) and Elser and Goldman (1991) suggested that, instead, "top-down" control is low in these lakes, because the phytoplankton is dominated by grazing-resistant species, such as cyanobacteria. Therefore, trophic cascades are expected to be decoupled at the zooplankton–phytoplankton linkage (McQueen and Post 1988; DeMelo et al. 1992).

In hypertrophic shallow lakes, the fish biomass is typically very high. Moreover, planktivorous fish are highly successful in such lakes, and their impact on the plankton community may be important (Persson et al. 1988; Jeppesen et al. 2000). The pampean lakes of Argentina are very shallow; geologically they have very high nutrient levels, ranging from eutrophic to highly hypertrophic (Quirós and Drago 1999). Both the phytoplankton biomass (Quirós et al. 2002b) and the proportion of cyanobacteria are high (Izaguirre and Vinocur 1994; Gabellone et al. 2001). The most abundant fish in large pampean lakes, the pampean silverside (*Odontesthes bonariensis*, Atherinidae; Quirós et al. 2002b), is a visually guided planktivorous (Boveri and Quirós 2002) and benthivorous fish. Its total length at first maturity is 20 cm on an average. However, the relative abundance of *O. bonariensis* is greatly decreased in highly hypertrophic and small lakes situated in agricultural landscapes (Quirós et al. 2002b). *Cnesterodon decemmaculatus*, *Jenynsia multidentata*, *Cheirodon interruptus* and *Astyanax* spp. are present in large numbers in these ecosystems. These fish are small, omnivorous and prolific (Rosso 2006). The cascading effect of the pampean silverside has been studied in pampean lakes (Quirós 1995; Rennella and Quirós 2002) and in mesocosm experiments (Boveri and Quirós 2002). However, no whole-lake food web manipulation has been carried out in the pampean lakes.

The main objective of our study was to elucidate the effects of fish on plankton structure and dynamics in the highly variable pampean region. To this end, fish manipulation was carried out in small lakes.

Study site

This study was carried out in five small turbid lakes, Vedia 1 (V1), Vedia 2 (V2), Vedia 3 (V3), Capurro and Longinotti, located in the Pampa Plain (33–39°S, 57–64°W; Table 1). This region is sprinkled with several thousand lakes of varying size which function as a large wetland (Quirós et al. 2006). The climate of this region is temperate warm (Köppen 1931), with a mean annual temperature of 17 °C. Seasonal differences in nutrient concentration and algal biomass are observed as in other temperate regions (Sommer et al. 1986). Mean annual precipitation is 900–1000 mm, with marked interannual variability (Sierra et al. 1994). The main climatic characteristic of the Pampa Plain is the alternation between periods of drought and flood (Vervoorst 1967), which is reflected in the water depth and conductivity (Fig. 1) as well as in the operation of the freshwater ecosystems (Quirós et al. 2002a). The Pampa Plain is the most highly developed agricultural region in Argentina, and this contributes even more to the eutrophication process of its water bodies. Intensive row-crop agriculture is practiced in the watersheds of the study lakes, mainly in V1, V2 and V3, where nitrogen fertilization reaches $110 \, \text{kg} \, \text{ha}^{-1} \, \text{year}^{-1}$ (Sosnovsky and Quirós 2005). Maximum depth is similar for lakes V1, V2, Capurro and Longinotti, while Lake V3 is the largest and the deepest (Table 1). Input and output seasonal streams are present in all the lakes.

Materials and methods

A whole-lake study was carried out from April to December 2000. Four lakes (V1, V2, Capurro and Longinotti) were fish-manipulated, while the fifth (V3) was left undisturbed as a reference system. Fish were removed from lakes V1, V2, Capurro and Longinotti in May using the organochlorine Endosulfan at a dosage of $10–20 \, \text{mL}/1000 \, \text{m}^3$. Endosulfan at this concentration is tolerable to crustacean organisms but not to fish. Dead fish were removed with beach seine nets. Before stocking with juvenile silversides, water chemistry harmlessness was tested by leaving fish alive in cages in the pelagic zone of two of the lakes. Once the effect of Endosulfan had passed, fish were stocked in Lake V1, Lake Capurro and Lake Longinotti. Table 2 shows the

Table 1. Location and limnological characteristics of the study lakes for the period April–December 2000

Lake	Location		A (ha)	Z_{max} (m)	K_{25} (mS cm^{-1})	SD (cm)	TP (mg m^{-3})	TN (mg m^{-3})
	Latitude	Longitude						
Vedia 3	34°20′38″S	61°37′57″W	46.6	1.8 (1.3–2.0)	2.33 (1.85–3.22)	15 (10–17)	2702 (1313–5169)	14767 (8355–32543)
Vedia 2	34°24′41″S	61°33′51″W	20.6	0.8 (0.5–1.0)	1.38 (0.93–2.64)	20 (4–40)	2314 (968–5321)	12026 (2959–53176)
Capurro	34°54′53″S	60°51′16″W	7.6	0,8 (0.3–1.0)	0.93 (0.57–1.53)	45 (10–77)	2196 (1476–4909)	5500 (1822–21026)
Vedia 1	34°23′12″S	61°33′19″W	23.9	1.2 (1.2–1.4)	1.46 (1.18–2.30)	26 (10–45)	1609 (688–4755)	5479 (2368–18718)
Longinotti	34°40′21″S	60°56′38″W	14.0	0.9 (0.4–1.1)	0.89 (0.55–1.15)	31 (4–46)	2190 (1439–4528)	3556 (1224–14187)

A, surface area; Z_{max}, maximum depth; K_{25}, electrical conductivity at 25 °C; SD, Secchi disk depth; TP, total phosphorous concentration; TN, total nitrogen concentration.
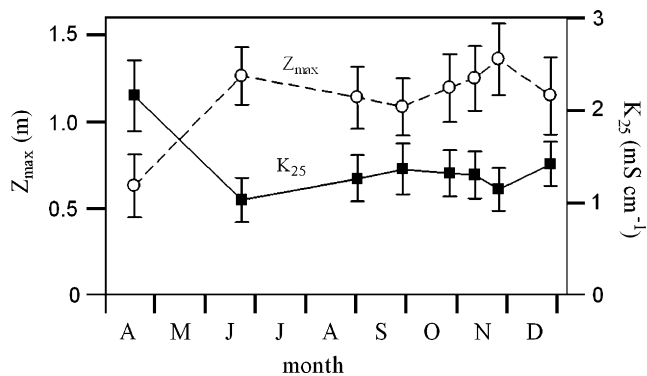

Fig. 1. Maximum depth, Z_{max}, and electrical conductivity at 25 °C, K_{25}, variations. Mean and standard deviation values are shown for all the studied lakes (modified from Sosnovsky and Quirós 2006).

stocking periods in each lake, the time needed for the three lakes being 60 days. Longinotti was the first and most intensively stocked lake, while *O. bonariensis* stocking started latest in Lake Capurro.

Fish were sampled with gill nets. Experimental gill nets composed of a 100 m length panel ranging from 30 to 180 mm stretched mesh size were set at night, both before (May) and after (December) *O. bonariensis* stocking. Catch per unit effort (CPUE, number of fish h^{-1} gill net^{-1}) was used to estimate fish abundance. However, as fish data from 2000 are scarce, the zooplankton:phytoplankton biomass (Zoo:Phyto) ratio was used as an indicator of predation pressure on zooplankton (Jeppesen et al. 1997a).

Zooplankton, phytoplankton and nutrients were sampled at the center of each lake. Water transparency as Secchi disc depth (SD) and water conductivity, corrected by temperature (K_{25}), were measured "*in situ*". Zooplankton was sampled with vertical tows of 69 μm conical plankton net without a flowmeter. We assumed 100% net efficiency. All samples were preserved in 4% sucrose–formalin and counted under a dissecting microscope in a Bogorov chamber. Cladocerans and copepods were grouped as mesozooplankton because of their size, which ranges from 0.2 to 2.0 mm. Zooplankton biomass was calculated as dry weight

using length–weight regressions (Bottrell et al. 1976). To evaluate phytoplankton biomass and nutrient concentrations, water samples were collected from 0.4 m beneath the surface. To estimate phytoplankton biomass as chlorophyll *a* concentration (Chl *a*), samples were filtered onto GF/F filters, extracted with a chloroform–methanol solution during 48 h and Chl *a* absorbance was measured at 665 nm using a spectrophotometer with 10-cm path width (APHA 1995). Phytoplankton biomass (dry weight, DW) was estimated using a Chl *a*:C ratio of 30 and a DW:C ratio of 2.2 (Jeppesen et al. 1994). Total phosphorus (TP) was analyzed using persulfate digestion and the ascorbic acid method (APHA 1995). Total nitrogen (TN) was estimated as the sum of organic nitrogen and nitrate nitrogen (NO_3^--N). Total organic nitrogen was estimated by the Kjeldahl method, and ammonia in the digested samples was determined using an ORION specific electrode (APHA 1995). The concentration of NO_3^--N was read with an ORION specific electrode following standard procedures (APHA 1995).

Results

Both fish abundance and community structure varied greatly in the lakes. Throughout the year, planktivorous minnows (*J. multidentata* and *C. interruptus*) dominated the fish community in Lake V3; however, they could generally not be caught with the gill nets because of their small size. In May, after fish removal, no fish were captured with gill nets from the pelagic zone of Lakes V1, V2, Longinotti and Capurro. In December, gill net sampling indicated that fish were present in the pelagic zone of these lakes. The planktivorous pampean silverside was, as expected, the dominant fish species in Lake V1 (CPUE = 15 fish h^{-1} gill net^{-1}). Nonetheless, a recolonization of fish from adjacent waters was observed in the other lakes. While *Hoplias malabaricus* (CPUE = 1 fish h^{-1} gill net^{-1}) dominated the fish community in Lake Capurro, *Cyphocharax voga* (CPUE = 1 fish h^{-1} gill net^{-1}) dominated in Lake

Table 2. Fish removal and *O. bonariensis* stocking in the study lakes

| Lake | Fish removal | Total *O. bonariensis* stocking (kg) | Biomass (kg ha^{-1}) (and abundance, ind ha^{-1}) of fish stocked | | | | | |
| | | | July | | August | | September | Total |
			1st fortnightly	2nd fortnightly	1st fortnightly	2nd fortnightly	1st fortnightly	
Vedia 3	No	0	–	–	–	–	–	–
Vedia 2	Yes	0	–	–	–	–	–	–
Capurro	Yes	182	0 (0)	0 (0)	14 (379)	6 (159)	4 (105)	24 (643)
Vedia 1	Yes	454	1 (42)	9 (252)	0 (0)	6 (154)	3 (100)	19 (547)
Longinotti	Yes	462	11 (327)	14 (398)	6 (159)	2 (71)	0 (0)	33 (956)

Longinotti. Likewise, small carnivores (*Oligosarcus jenynsi*) and small omnivores (*C. interreuptus*) were present in Lake V2 (CPUE = 12 and 3 fish h^{-1} gill net^{-1}, respectively). During the summer of 2001, adult silversides practically disappeared from the pelagic waters of all the study lakes, and their fish community was similar to the one we had found before the manipulation period.

During the study period, all the lakes showed hypertrophic characteristics (Table 1). Water temperature was on an average 17.3 °C for all study lakes. Minimum values were recorded in June (9.2 °C) and maximum values were recorded in November (22.8 °C). Lakes Capurro and Longinotti gave similar SD and K_{25} readings. Lakes Vedia 1, Vedia 2 and Vedia 3 showed similar values for these characteristics and were, on an average, the most turbid. At the beginning of this study, the pampean region was going through a period of drought. In consequence, low water depth and high water conductivity characterized the study lakes. Similarly, in April, the highest values for nutrient concentration and Chl *a* for the year 2000 were recorded (Table 1). The following period was very rainy and total precipitation reached the value of 400 mm during the next 30 days. As a result, water depth increased and water conductivity decreased (Fig. 1).

In the non-manipulated lake V3, zooplankton biomass was dominated exclusively by copepods during the entire study period (Fig. 2a). Cyclopoid copepods dominated during April and December, while calanoid copepods dominated from August until November, and during this period, the mesozooplankton size increased (Fig. 2b). Cladocerans were rarely present and when present were small-sized species (Fig. 2c). Whereas the Zoo:Phyto ratio of lake V3 was on an average the lowest of all the study lakes, the Chl *a*:TP ratio was the highest. However, the correlation between these two ratios was not significant.

As in Lake Vedia 3, the zooplankton was mainly composed of cyclopoid copepods during the month of April in Lake Vedia 2 (Fig. 3a). The zooplankton

structure changed dramatically after fish removal, however. The proportion of cladocerans within the plankton increased (Fig. 3a), with *Daphnia* as the dominant species (Fig. 3c). While *Daphnia* was present, the proportion of large cladocerans increased steadily (Fig. 3d). A sudden decrease of 14-fold in the zooplankton biomass between October and November was observed. In coincidence, a depletion of *Daphnia* occurred and cyclopoid copepods (Fig. 3a) and small-sized cladocerans (Fig. 3c) became the only species present. This was reflected in a decrease in the grazing pressure of zooplankton on phytoplankton (Fig. 3e), resulting in an increase in the Chl:TP ratio (Fig. 3f). Unlike the observations in Lake Vedia 3, the correlation between Chl *a*:TP and Zoo:Phyto was significant ($r = -0.90$, $P = 0.002$).

As in lakes V3 and V2, in Capurro, V1 and Longinotti, copepods formed the main plankton component in the month of April (Fig. 4a). Likewise, the Chl *a* concentration per unit TP was relatively high (Fig. 4f). As in Lake V2, fish removal resulted in an increase in the proportion of cladocerans in the zooplankton community (Fig. 4a) and *Daphnia* appeared. Fish stocking started last in Capurro (Table 2). Correspondingly, in this lake, both the main development of *Daphnia* (Fig. 4c and d) and a decrease in the Chl *a*:TP ratio (Fig. 4f) were observed during a longer period of time. Following the *O. bonariensis* stocking, changes appeared in the zooplankton community, these being more evident in Lake Longinotti, where stocking was more intense and conducted earlier in the season. The proportion of *Daphnia* began to decrease (Fig. 4c), as did the body size of the mesozooplankton (Fig. 4b). In the three lakes where silverside stocking was carried out, as well as in Vedia 2, the ratios Zoo:Phyto and Chl:TP showed negative correlations (Capurro: $r = -0.93$, $P = 0.0009$; Vedia 1: $r = -0.79$, $P = 0.02$; Longinotti: $r = -0.93$, $P = 0.0009$). Nevertheless, differences in plankton dynamics and structure were detected between these three lakes and Lake V2, from where fish were only removed. The largest sized mesozooplankton were
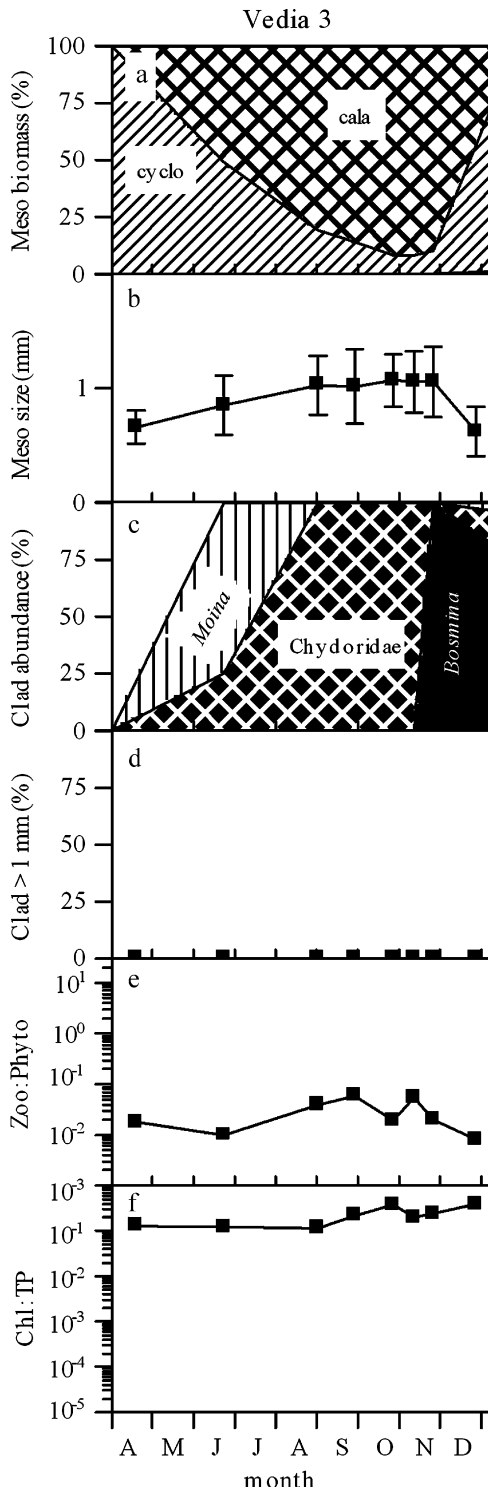
Fig. 2. Plankton dynamics in the reference lake. Meso, mesozooplankton; cala, calanoid copepods; cyclo, cyclopoid copepods; clad, cladocerans; Zoo:Phyto, zooplankton–phytoplankton biomass ratio; Chl:TP, Chl *a* per unit of TP.
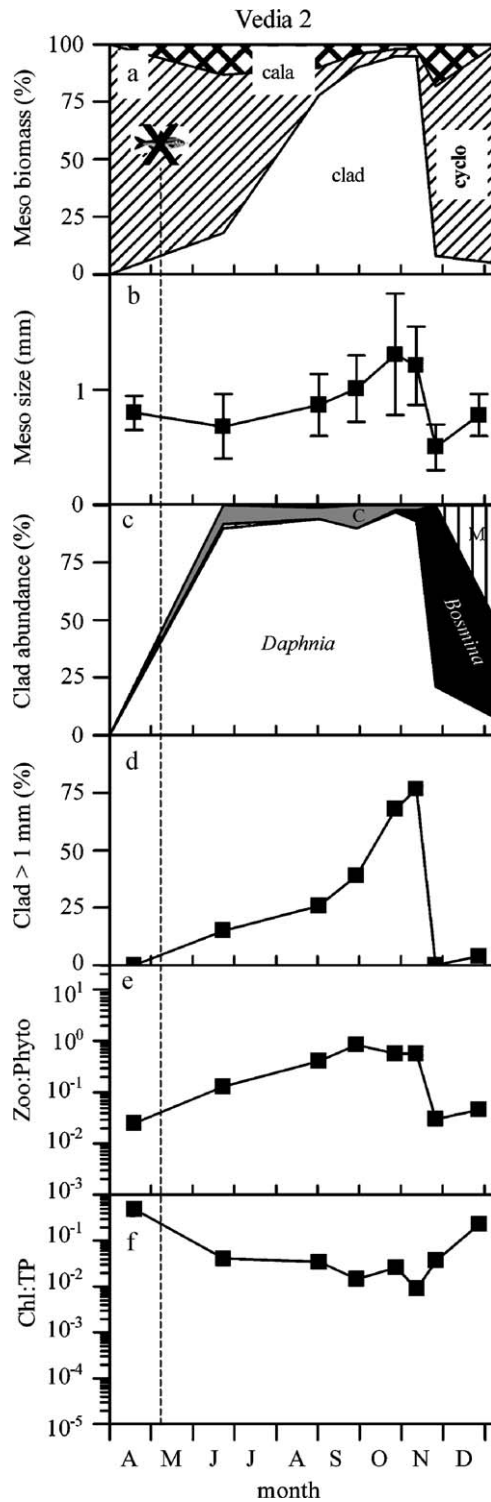
Fig. 3. Plankton dynamics in the lake where fish were removed (✳). Meso, mesozooplankton; cala, calanoid copepods; cyclo, cyclopoid copepods; clad, cladocerans; C, *Ceriodaphnia*; M, *Moina*; Zoo:Phyto, zooplankton–phytoplankton biomass ratio; Chl:TP, Chl *a* per unit of TP.

registered in Lake V2 where zooplankton was mainly composed of *Daphnia* cf. *obtusa* and *Daphnia spinulata*. Moreover, *Daphnia* abundance was highest in LakeV2

(data not shown). Above all, the biggest difference occurred in the dynamics of cladoceran size. While in the silverside stocked lakes, the first organisms to
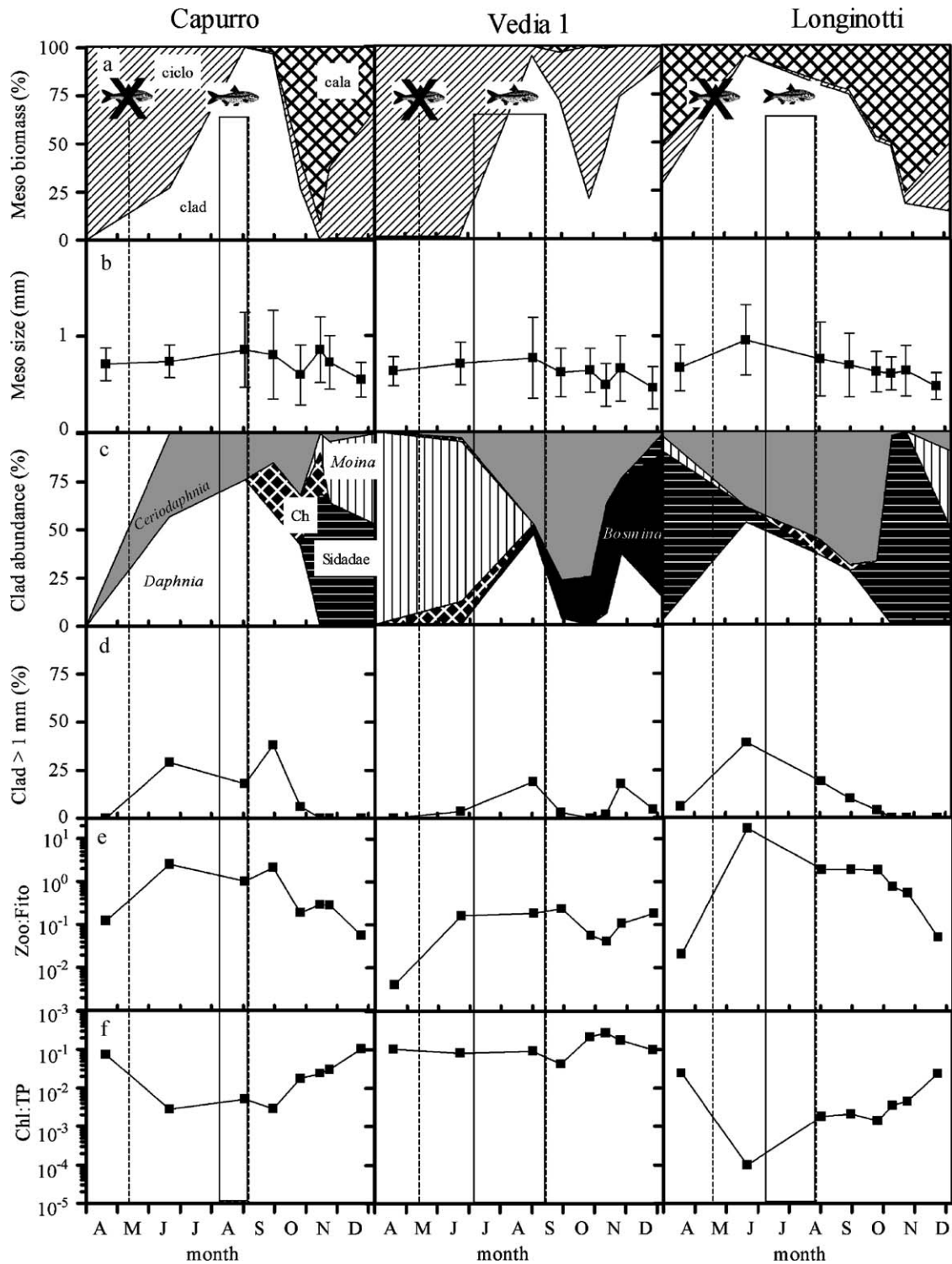
Fig. 4. Plankton dynamics in the lakes where fish had been removed (✖) and *O. bonariensis* was stocked (🐟). Meso, mesozooplankton; cala, calanoid copepods; cyclo, cyclopoid copepods; clad, cladocerans; Ch, Chydoridae; Zoo:Phyto, zooplankton–phytoplankton biomass ratio; Chl:TP, Chl *a* per unit of TP.

disappear were those measuring more than 1 mm (Fig. 4d; mainly in Longinotti), in Lake Vedia 2, the percentage of large cladocerans increased steadily until November (Fig. 3d).

Independent of fish manipulation, changes in predation pressure were reflected in zooplankton structure and phytoplankton biomass in all the study lakes. High Zoo:Phyto ratio (as a proxy for low fish predation)

coincided with both an increase in *Daphnia* biomass (Zoo:Phyto vs. *Daphnia* biomass: $r = 0.62$, $P = 0.007$) and a decrease in the Chl *a* concentration per unit of phosphorus (Zoo:Phyto vs. Chl:TP: $r = -0.84$, $P < 0.0001$).

Discussion

All study lakes showed hypertrophic characteristics. These lakes are amongst the most hypertrophic shallow lakes in the world (Kalff 2002), although similar values of nutrients are often found in shallow lakes located in agricultural areas (Jeppesen et al. 1999). In addition to the effects of agriculture, the climatic characteristics of the pampean region contribute even more to the eutrophication of the water bodies (Quirós et al. 2002a). Drastic changes are observed in the dynamics and structure of aquatic ecosystems during the drought and flood periods of the Pampas (Quirós et al. 2002a). During the periods of drought, pampean lakes concentrate both nutrients (Quirós et al. 2002a) and algal biomass (Izaguirre and Vinocur 1994), thus increasing water turbidity in these ecosystems. Moreover, the drought effects are much more pronounced in small-surface water bodies (Sosnovsky and Quirós 2006), which could dry up completely. At the beginning of year 2000, the pampa region was going through an extremely dry period. This explains the extreme values for limnological variables found in the study lakes. At the end of April and beginning of May, autumn precipitation diluted the salinity, nutrients and algal biomass of the study lakes (Sosnovsky and Quirós 2006). An inverse relationship between water depth and water conductivity is often found in the water bodies of the Pampa Plain (Gabellone et al. 2001; Quirós et al. 2002a; Mugni et al. 2005). Within this complex temporary dynamics, whole-lake studies were carried out. However, all experimental lakes were exposed to the same environmental dynamics.

Jeppesen (1998) hypothesized that predation pressure is high in hypertrophic lakes where the fish community is completely dominated by highly abundant planktivorous fish. Data from years 2001 and 2002 showed that *J. multidentata* and *C. interruptus* abundance was 9 individuals m^{-2} in our nonmanipulated Lake Vedia 3, which was on an average one order of magnitude higher than in the other lakes. Such a difference could be explained by the high nutrient levels and the characteristic absence of piscivorous fish in this lake (Sosnovsky 2007). As in the following years, Lake Vedia 3 was dominated by *J. multidentata* and *C. interruptus* during the study period. Because they are omnivorous fish (Ringuelet 1975), it would be expected that fish predation on zooplankton would be particularly high

in this lake, as the fish can be facilitated by food items other than zooplankton and therefore maintain a high abundance even when zooplankton are scarce (Jeppesen et al. 1997a).

A clear pattern in the zooplankton structure of this lake emerged during the year 2000. The zooplankton composition was dominated by calanoid copepods from August to November. In contrast, during April and December, cyclopoids were dominant in numbers. This alternation between copepods was observed again in the year 2001 (Sosnovsky 2007).

The calanoid:cyclopoid ratio is typically low at high predation pressure by fish (Jeppesen et al. 1997b). Moreover, there is evidence of higher predation pressure on zooplankton following fish spawning (Mehner 2000). Therefore, the variation in the calanoid:cyclopoid ratio in Vedia 3 could be explained by way of differences in predation intensity during the year. The level of predation would be higher from the end of spring and during the summer due to the presence of age-0 fish and a higher metabolic rate of the fish, respectively. In contrast, during the colder seasons, the lower level of predation would allow the development of large copepods.

Higher copepod than cladoceran biomass within the plankton community has been observed in other water bodies in the pampean region (Claps et al. 2004). Before fish removal, copepods formed the main component of the plankton in the study lakes. From May, the absence of fish allowed groups with a short life cycle to colonize the lakes. Examples of this are rotifers and cladocerans: the superior filtration rate of the latter would favor their dominance over the former.

Daphnia is a successful competitor in the plankton community. This explains its increase following the removal of fish from the ecosystem in the study lakes. Such an increase has been observed frequently in the past, for example, during massive fish mortality due to seasonal anoxia during winter months (Schindler and Comita 1972; Sarnelle 1993) or due to intentional fish removal (Hansson et al. 1998). Furthermore, the presence of *Daphnia* coincided with an increase in the Zoo:Phyto ratio. If we compare this ratio for the month previous to fish removal with the month following removal, there was a considerable increase in Lakes Capurro, Vedia 2 and Longinotti. The increase ranged from at least 20 times for Lake Capurro up to 800 times for Lake Longinotti. In contrast, during the same period, this ratio decreased by half in Lake Vedia 3, from which fish had not been removed.

There is probably a causal relationship between fish removal, the subsequent increase in mesozooplankton size and the increase in the Zoo:Phyto ratio, since this has been observed following zooplanktivorous fish removal in 17 whole-lake studies carried out in Denmark (Jeppesen et al. 1990; Søndergaard et al. 1997).

However, the Danish values found for Zoo:Phyto ratios following fish removal were much lower than those found in the present study. It is likely that the difference we found in the Zoo:Phyto ratios measured 1 month before and 1 month after fish removal also reflects the strong dilution effect on phytoplankton biomass caused by regional hydrology (Sosnovsky and Quirós 2006).

Total removal of planktivorous fish could leave the planktivore niche unoccupied, allowing other groups that prey on daphnids, such as invertebrate predators (Wissel et al. 2000) to invade and fill the gap. *Mesostoma* spp. (Rhabdocoela), *Buenoa* spp. (Hemiptera) and Odonata larvae were found in two pampean lakes dominated by macrophytes after fish had been removed (unpublished results). Nevertheless, such invertebrate predators were not found after fish removal in our turbid lakes. Thus, invertebrate predation pressure on zooplankton would be different between these two highly contrasting ecosystems. More research on the role of macrophytes is needed in pampean lakes, however.

In Lake Vedia 2, a lower predation pressure on the zooplankton was observed for the longest period of time. From June to October, both the size of mesozooplankton and the percentage of large *Daphnia* increased steadily as did zooplankton biomass. Average size was over 1.35 mm, and the *Daphnia* percentage among the cladocerans was over 90%. However, in Lake Vedia 2, this dominance of large cladocerans did not last in time. The increased level of zooplankton biomass fell abruptly due to the disappearance of *Daphnia* in the month of November. It is important to mention that the *Daphnia* disappeared sequentially, i.e., the smallest first followed by the largest. Recent results show that the depression of the *Daphnia* population in early summer is caused by a complex combination of top-down and bottom-up forces (Gliwicz 2002; Wagner et al. 2004). Thus, a combination of two processes could have occurred in Lake V2. The first is related to the predation of age-0 fish during spring and summer, as observed by Schael et al. (1991). Fish are gape-limited predators (Zaret 1980), thus the smaller daphnids could have been eaten by 0+ fish earlier than the larger ones. However, strong demographic effects in *Daphnia* population would only occur when fish feed preferentially on mature, egg-bearing daphnids (Mehner 2000). The second process is related to competition for resources (Meijer et al. 1994). *D.* cf. *obtusa* and *D. spinulata* were both present in Vedia 2. *D.* cf. *obtusa* has a smaller body size than *D. spinulata*. During the seasonal analyses of the zooplankton dynamics, both species were registered under the genus *Daphnia*, with the result that the seasonal dynamics of each species is not known. Since competition for resources favors larger individuals because of their greater filtration efficiency and lower metabolic rate (Brooks and Dodson 1965), it is likely that before the

dramatic fall in *Daphnia* abundance, there had been competition favoring *D. spinulta* over *D.* cf. *obtusa*. The latter could be excluded completely if competition lasted long enough.

Supposedly, therefore, starvation was an important reason for the collapse of the *Daphnia* population in late November. The abundance of *Daphnia* fluctuated between 67 and 159 individuals L^{-1} between August and November. Calculating the *Daphnia* filtration rate in relation to its size alone (filtration rate- $0.54 \times$ length$^{1.55}$; Porter et al. 1983) and multiplying by their abundance, we can obtain the volume of water filtered daily by *Daphnia* present in 1 L. Minimum and maximum values for V2 were 1196 and 2278 mL, respectively. During this period, therefore, *Daphnia* could have filtered the entire volume of the lake more than once per day, and up to more than twice in the same day, which is a strong indicator of starvation.

A number of characteristic features indicated a marked top-down control in Lakes Capurro, Vedia 1 and Longinotti after silverside stocking. Stocking of pampean silverside led to depletion of large cladocerans and an increase in the abundance of *Bosmina* spp. and *Ceriodaphnia* spp. and copepods. High abundance of *Bosmina* is typically observed in lakes with a relatively high abundance of zooplanktivorous fish (Stenson et al. 1978; Benndorf et al. 1988) and is considered to be a consequence of improved growth conditions for *Bosmina* at low *Daphnia* densities. The lakes mentioned were stocked with different quantities of pampean silverside over different periods of time. These differences were reflected in the seasonal zooplankton dynamics, mainly the large cladocerans. Lake Longinotti was the first and the most intensively stocked. Signs of predation on zooplankton were detected earlier and with more intensity in this lake than in the others. In contrast, in Capurro, the lesser quantities and late stocking allowed greater development of the large cladocerans in time. In Lake Vedia 1, the relationship between the level of stocking and its timing with its effect on the zooplankton was not as clearly marked as with the two previously mentioned lakes.

Nutrient availability, particularly of phosphorus (Schindler 1977), determines the potential phytoplankton biomass, whereas grazing by zooplankton determines the current strength of this potential (Carpenter et al. 1985). Zooplankton grazing is, in turn, influenced by the abundance of zooplanktivorous fish (Hrbácek et al. 1961; Brooks and Dodson 1965). Therefore, lakes with planktivorous fish should have more Chl *a* per unit of total phosphorus than lakes where planktivorous fish are absent from the system (Quirós 1995, 1998; Jackson et al. 2007). Our results support this idea. On one hand, fish removal allowed zooplankton to exert increased pressure on phytoplankton, mainly through *Daphnia*. On the other hand, subsequent stocking of planktivorous fish which preyed on *Daphnia* led to an increase in algal

biomass per unit of TP. In addition, the high abundance of minnows in Lake Vedia 3 and the lack of top predators partly explain the absence of *Daphnia* and therefore the high Chl *a*:TP ratio in this lake.

Fish manipulation and in consequence its effects were short-lived. Eight months after fish had been removed, fish structure was similar to the original one. A simple reason could explain this fact: the recruitment of those remaining will probably be very successful in the next breeding season. Besides, shallow lakes are the main component of the pampean wetland (Quirós et al. 2006), and they are connected by a network of streams, rivers and channels, which could allow fish movement between them. The small size of the omnivorous fish would make it difficult to control these movements with simple management measures (e.g. the implementation of gates). In addition, fish recolonization has already been observed in other whole-lake studies (Mehner et al. 2002). Moreover, the goal of totally removing planktivorous fish from a lake may be undesirable and will not cause lasting effects (Wissel et al. 2000).

Within trophic interactions, our study gives additional support to the view that changes in fish assemblage composition and fish stock abundance may influence both the structure and size of zooplankton in small hypertrophic pampean lakes. Moreover, these effects may cascade down the food web to phytoplankton in these ecosystems. Fish removal may be short-lived, however, because the fish community returns quickly to its initial state (see also Jeppesen et al. 2007). Therefore, repeated planktivorous fish removal is recommended.

In addition, agricultural activity, climate and hydrology should be taken into account if manipulation measures are implemented in pampean lakes. Reducing nutrient loading below a critical threshold for successful biomanipulation measures (Benndorf et al. 2002) would be difficult to achieve in many lakes because of heavy fertilization. Moreover, relatively high concentrations of nutrients and algal biomass will naturally occur in turbid lakes during the summer season, which makes the establishment of a macrophyte dominated state difficult, because of both low light availability and anoxic sediments. Finally, the alternation of periods of flood and drought causes enormous variability in the biotic and abiotic parameters of the water bodies. Because of the sum of all these characteristics, pampean lakes are suitable systems for the evaluation of the strength of trophic interactions in an ecosystem. Therefore, additional whole-lake studies should be undertaken in these ecosystems.

Acknowledgments

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