SHALLOW LAKES

Cascading trophic effects in pampean shallow lakes: results of a mesocosm experiment using two coexisting fish species with different feeding strategies

María B. Boveri · Rolando Quirós

Abstract Planktivorous fish, both visual predators and filter feeders, enhance eutrophication processes in lakes. In pampean shallow lakes several planktivorous species may coexist but often two species dominate: silverside (*Odontesthes bonariensis*), a visual planktivorous fish when young adult, and sabalito (*Cyphocharax voga*), an omnivorous filter feeder. To assess the relative strength of the cascading trophic effects of the two species, a mesocosm experiment was conducted using different proportions of both species as treatments. Differences were found in water transparency, phytoplankton biomass, crustacean abundance, individual size and biomass. Our results suggest that visual predators intensify eutrophication effects more strongly than filter feeders do.

Keywords Planktivorous fish · Trophic interactions · Pampean shallow lakes · Mesocosm experiments

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Introduction

Planktivorous fish enhance eutrophication processes in lakes. Feeding by visual predators or filter feeders usually cascades through zooplankton to the base of the food web and thus promote algal growth via suppression of large herbivorous zooplankters (Hurlbert et al., 1972; Carpenter et al., 1985), though the strength of the cascade may depend on various lake ecosystem characteristics (Jeppesen et al., 2003; Borer et al., 2005).

The Pampa plain in South America covers approximately 500,000 km^2 and is sprinkled with several thousand shallow lakes whose state range from eutrophic to highly hypertrophic (Quirós & Drago, 1999). Phytoplankton biomass is usually high, with chlorophyll levels often exceeding 50 mg m^{-3} during summer (Quirós et al., 1988). Because of their shallowness, the lakes are strongly influenced by wind and therefore polymictic (Rennella & Quirós, 2002). Several planktivorous fish species may coexist, though in different proportions depending on the condition of the aquatic environment. However, two species tend to dominate: silverside (*Odontesthes bonariensis*, Valenciennes 1835, Atherinidae) and "sabalito" (*Cyphocharax voga*, Hensel 1870, Curimatidae). As young adult silverside is a visual planktivore (Boveri & Quirós, 2002). Sabalito is described as a planktivore, feeding on benthos by Destefanis & Freyre (1972), as a

planktivore and periphyton sucker by Grosman et al. (1996), and as a detritivore by Brassesco et al. (2004). Sabalito dominance in shallow lakes occurs most frequently in eutrophicated lakes and lakes impacted by siltation (Rosso, personal communication). As silverside is an important angling fish, there is some concern to understand which factors may affect the development of its populations, particularly if other fish species outcompete silverside populations.

To obtain more insight into the trophic relationships between silverside and sabalito, and the relative strength of their cascading trophic effects, a mesocosm experiment was conducted using different combinations of the two species as treatments. Previous studies suggest that the two planktivores have different trophic cascade pathways (Drenner et al., 1986), but comparisons between the strength of this effects are only few (Lazzaro et al., 1992; Williams & Moss, 2003). Although mesocosm experiments with visually and filter-feeding planktivorous fish are not new (Drenner et al., 1990), our experimental design using similar abundances but different species proportions is unique.

Materials and methods

The experiment was run for a 5-week period in late summer—early fall 2000 (March 15th–April 17th) in ten outdoor mesocosms located at the Agronomy Faculty of Buenos Aires University. All ten tanks hosted 16 young individuals of pampean silverside and sabalito in five different densities of each species.

The mesocosms consisted of large white fibreglass tanks, 2 m in diameter and 2 m high, holding approximately 5500 l. To prevent stratification and simulate the wind-induced mixing of shallow lake systems, each mesocosm was continually mixed with air that was softly pumped into the tank near the bottom.

In a 70 m^3 reservoir we prepared the experimental medium with groundwater enriched with 4750 g NH_4Cl and 230.5 g KH_2PO_4 and salt (120 kg NaCl) which dissolution were stimulated by a vigorous bubbling of air from eight 1/2″ hoses distributed near the reservoir bottom. Thus, the

following average concentrations in the tanks on the first sampling day were achieved: 17.83 mg TN l^{-1}, 1.21 mg TP l^{-1}, achieving a N:P ratio of 31.75 on molar base, and a salinity of 0.28%. The experimental medium mimicked the average conditions of salinity, nutrient contents and ratios of a typical pampean shallow lake and was inoculated with natural phytoplankton and zooplankton imported from de Gomez shallow lake, a typical pampean hypertrophic shallow lake (Quirós et al., 2002). All tanks were filled by pumping at the same time during a 48-h period prior to the onset of the experiment.

Fish were caught by seining in Lake de Gomez. On average, stocked silversides (sil) weighed 3.5 ± 0.8 g (mean weight ± SD) and were 86 ± 7 mm long (mean total length ± SD), while the sabalitos (sab) weighed 6.5 ± 2.1 g and were 73 ± 0.8 mm long.

Silversides and sabalitos differed in individual body weight, and the resulting overall fish biomass was distinct between fish treatment combinations. However, we found that, in our study, fish number was more critical than fish biomass, because we focused at differences between the impacts of two species differing in foraging modes and activity levels. Indeed, silverside is an active open water swimmer, while sabalito is less mobile, and it is well-known that fish with different activity levels have different food demands (Margalef, 1983).

The experimental design comprised five treatment combinations with duplicate replication. Each tank received 16 young individual fishes. The five treatments consisted of five different proportions of Pampean silversides and sabalitos: 0 sil + 16 sab, 4 sil + 12 sab, 8 sil + 8 sab, 12 sil + 4 sab, and 16 sil + 0 sab. Treatments were randomly assigned to tanks, by stocking fish on 15 March (day 1).

Because fish mortality may potentially result in release of nutrients, potentially affecting the outcome of tank mesocosm experiments (Threlkeld, 1988), sick and dead fish detected at the surface or at the bottom were removed during daily inspections of the tanks and replaced by healthy specimens. Due to high undetected mortality rates common of experiments involving silversides (Boveri & Quirós, 2002), we assumed a weekly

undetected mortality rate for silverside of 10%. Then, 8 and 24 days after the onset of the experiment we added 0/1/2/3/4 silversides to the tanks with 0 sil + 16 sab, 4 sil + 12 sab, 8 sil + 8 sab, 12 sil + 4 sab, and 16 sil + 0 sab, respectively.

Tanks were monitored daily at noon for pH, electrical conductivity (mS cm^{-1}), turbidity (NTU), dissolved oxygen content (mg l^{-1}), and water temperature (°C) with a HORIBA-U10 limnological probe, and for Secchi disk depth. Water and plankton samples were taken on five dates (days 1, 6, 17, 27, and 34). The first sampling was done prior to fish release on day 1.

Zooplankton was sampled with four vertical tows using a plankton net (mesh size: 69 μm, diameter: 14 cm), pooled, and preserved in 5% sucrose—formalin. The zooplankton was then counted and measured under a dissecting microscope in a Bogorov chamber. Zooplankton biomass was calculated using length-weight regressions (Bottrell et al., 1976).

Integrated water-column samples were taken for analyses of chlorophyll-a (Chl), total phosphorus (TP) and total nitrogen (TN). Samples were collected with a 1.5 cm diameter PVC hose which was lowered to 10 cm above the tank bottom and then slowly moved upwards while water was siphoned into the can. To determine Chl, water was filtered through Whatman GF/F filters, which were subsequently wrapped in aluminium foil and cooled. Chl was extracted in chloroform—methanol in the dark at 4°C for 48 h and absorbance was then read at 665 nm (Wood, 1985).

TP was analysed by the ascorbic acid method corrected for turbidity following current APHA procedures (American Public Health Association, 1995). With a sub-sample of collected water, particles were retained on a Whatman GF/C filter to allow distinction between the soluble and particulate fraction.

Total organic nitrogen was determined by the Kjeldahl method and ammonia in the digested samples was determined using an ORION specific electrode (American Public Health Association, 1995). The concentration of NO$_3^-$ was read with an ORION specific electrode following standard procedures (American Public Health Association, 1995). TN is considered as the sum of both fractions of nitrogen.

At the end of the experiment the water of the tanks was carefully drained through a small mesh seine and all remaining live fish were recovered, weighed and measured. Fish unaccounted for at the time of the tank emptying were assumed dead and decomposed in the tanks during the experiment (on average: 45% and 60%, respectively, of the silversides and sabalitos introduced). Both detected and undetected mortality turned out to be relatively high in our experiment. Thus, the number of live silversides recovered by the end of the experiment was 13 and 11 in the 16 sil tanks, 12 and 8 in the 12 sil tanks, 7 and 5 in the 8 sil tanks, and 4 and 4 in the 4 sil tanks, allowing us to interpret the treatments as they were planned.

Data were analysed by one-way ANOVA with NCSS 2000 (Hintze, 1998). Because of low replication and statistical power, we chose a probability level of $\alpha < 0.10$ to reduce the risk of making the type II error of failing to reject a false null hypothesis. We present here the probability values for the comparison between the 0 sil + 16 sab and the 16 sil + 0 sab treatments.

ANOVA of response variables did not reveal any effects due to tank location or pre-treatment variation, except for a few zooplankton variables. Thus, cladoceran abundance ($P = 0.02$), cladoceran biomass ($P = 0.02$), macrozooplankton abundance ($P = 0.02$), macrozooplankton biomass ($P = 0.02$), and *Daphnia* biomass ($P = 0.02$), were significantly different between the tanks before the start of the experiment. However, this may be ignored because the association between these differences and the treatments applied did not coincide with the differences expected to occur as a result of treatments. On the other hand, the differences disappeared within the first 5 days of the experiment ($P = 0.32$, 0.56, 0.42, 0.57, and 0.57 on the second sampling date, respectively).

Results

Growth of each fish species was inversely proportional to its density in tanks (Fig. 1). At the end of the experiment, silversides had grew by $150 \pm 48\%$ above their initial weight in the 4 sil
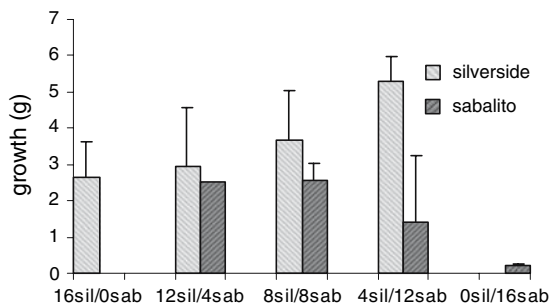
Fig. 1 Average fish growth of silverside and sabalito (final weight – initial weight) recorded at the end of the experiment in each treatment. Vertical lines represent 1 SD

tanks, while sabalitos had enhanced their weight by approx. $38 \pm 14\%$ in the 4 sab tanks.

There were no significant differences in macrozooplankton biomass between the treatments ($P = 0.46$, Fig. 2). However, the effects of filter feeding and visual planktivorous fish on the zooplankton community differed.

In the tanks where visual planktivores were most abundant, cladoceran abundance was continuously low and by the end of the experiment they had completely disappeared. In contrast, cyclopoid abundance increased during the first week of the experiment after which it declined (Fig. 3a). In the tanks containing only filter feeders, cladocerans and cyclopoids seemed to be equally controlled by fish (Fig. 3e). Tanks with both visual planktivores and filter feeders exhibited intermediate levels (Fig. 3b–d).

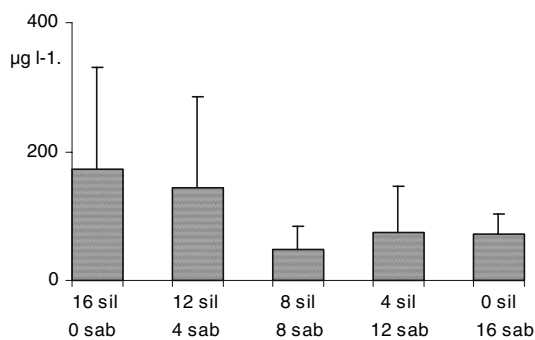During the experiment, cladoceran size decreased markedly ($P = 0.01$ in comparison

Fig. 2 Effect of the different proportions of visually and filter-feeding planktivores on macrozooplankton biomass (μg DW l^{-1}). Vertical lines represent 1 SD
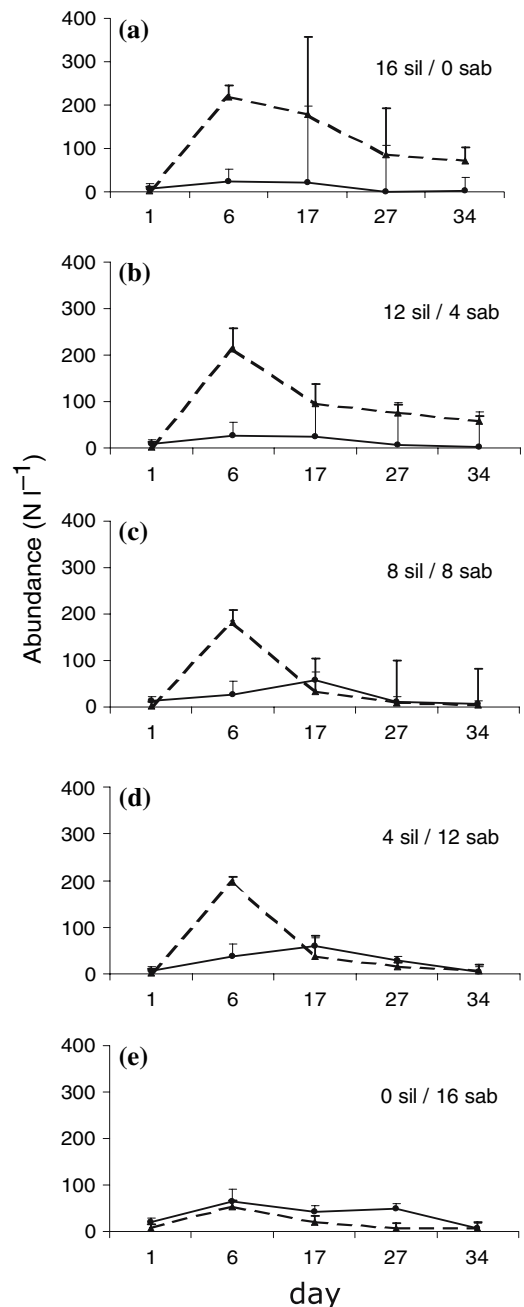

Fig. 3 Average cladoceran (full line) and cyclopoid (broken line) abundance (number of individuals l^{-1}) at all sampling dates for the five treatments. Vertical lines represent ± 1SD

between the last and the first day of the experiment), and so, though less pronouncedly, did that of cyclopoids ($P = 0.20$) in the silverside-only tanks (Fig. 4a). However, neither cladoceran
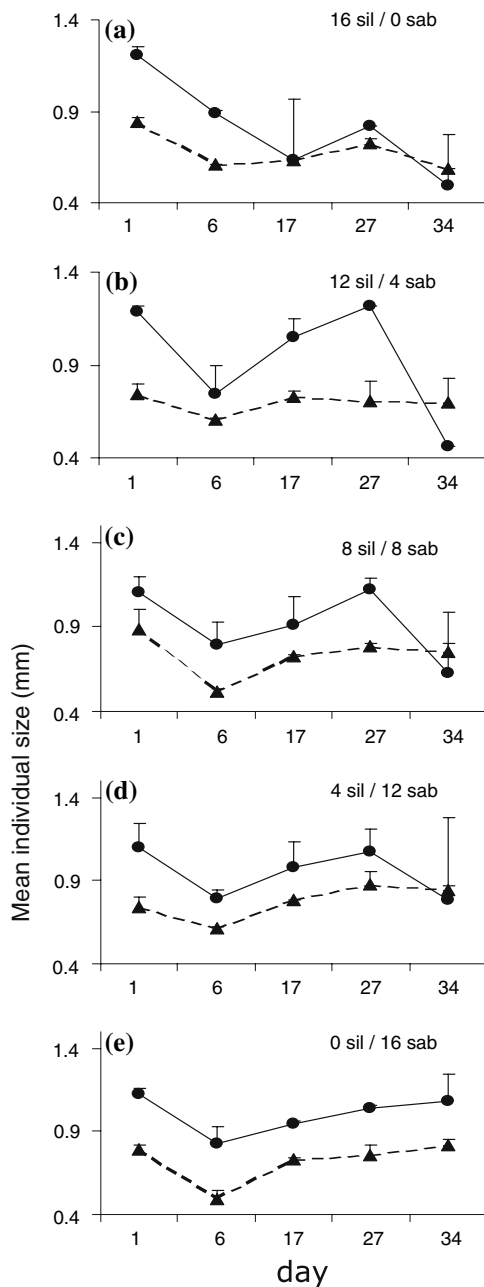
Fig. 4 Average cladoceran (full line) and cyclopoid (broken line) size (mm) at all sampling dates for the five treatments. Vertical lines represent ±1 SD

($P = 0.77$) nor cyclopoid size ($P = 0.42$) decreased in the tanks containing only sabalitos (Fig. 4e).

At the end of the experiment, the sabalito-dominated mesocosms exhibited larger cladocerans ($P = 0.05$), insignificant differences in cladoceran abundance ($P = 0.49$), and an enhanced, though not

significantly so, cladoceran biomass ($P = 0.13$) compared to the silverside-mesocosms (Table 1). Despite limited abundance, the cladoceran community was dominated by *Daphnia* in the sabalito tanks, *Daphnia* constituting <20% in the silverside-tanks ($P = 0.04$, Table 1). Moreover, cladocerans larger than 1 mm were present only in the tanks with few or no silversides ($P = 0.02$, Table 1).

The fish effects on cyclopoids differed from those on cladocerans. At the end of the experiment, cyclopoids were more abundant in tanks dominated by silversides ($P = 0.06$, Table 2). In tanks with only filter feeders, cyclopoids were controlled in the same manner as the cladocerans. Silverside prompted only a small reduction of cyclopoid size ($P = 0.25$, Table 2), especially when compared with the large reduction observed in cladoceran size. Cyclopoid biomass was not affected particularly by silverside density ($P = 0.33$, Table 2. However, cyclopoids dominated the macrozooplankton community in the silverside-dominated tanks ($P = 0.08$, Table 2).

During the first week of the experiment, water turbidity increased in all the tanks, after which it declined steadily. In tanks with only visual planktivores (16 sil/0 sab), turbidity increased consistently from the 12th day until the end of the experiment (excepting the effect of a clearwater state due to 100 mm precipitation on the 24th day after the onset of the experiment). For intermediate treatments, turbidity increased as from the 18th day (12 sil/4 sab), 23th day (8 sil/8 sab), and 30th day (4 sil/16 sab). In tanks with only filter feeders (0 sil/16 sab), water turbidity remained low from the third day until the end of the experiment.

At the end of the experiment, tanks with visual planktivores had more turbid water ($P = 0.09$, Fig. 5a). Moreover, tanks holding only silversides had more than 200 times the chlorophyll concentration than tanks with only filter feeders ($P = 0.0008$, Fig. 5b). The more visual planktivores, the more turbid the water and the more abundant the phytoplankton, compared with tanks dominated by filter feeders.

During the experiment, nutrient concentrations tended to decrease ($P = 0.0001$ for TN; $P = 0.0001$ for TP in a comparison between the last and the first day for all the tanks). The fish stock composition did not affect nitrogen or phosphorus concentrations.

Table 1 Effect of the different proportions of visual predators and filter-feeding planktivores on cladoceran variables at the end of the experiment: abundance (number $l^{-1}$); mean individual size (mm); biomass ($\mu g\ l^{-1}$); proportion of Daphnia of total cladoceran number (%); and proportion of cladocerans larger than 1 mm (%). In brackets: 1 SD

Cladoceran	16 sil 0 sab	12 sil 4 sab	8 sil 8 sab	4 sil 12 sab	0 sil 16 sab
Abundance (number l^{-1})	2.1 (1.1)	1.1 (1.6)	6.0 (7.1)	5.5 (6.4)	6.6 (6.2)
Mean individual size (mm)	0.5 (0.1)	0.5 (–)	0.6 (0.4)	0.8 (0.5)	1.1 (0.2)
Biomass ($\mu g\ l^{-1}$)	2.2 (0.8)	0.8 (1.2)	27.6 (38.5)	45.8 (63.9)	43.9 (24.0)
% of Daphnia of total clad.	17 (23)	0 (–)	45 (64)	78 (67)	100 (0)
% of clad. larger than 1 mm	0 (0)	0 (–)	27 (37)	35 (49)	36 (8)

Table 2 Effect of the different proportions of visual predators and filter-feeding planktivores on cyclopoid variables at the end of the experiment: abundance (number l^{-1}); mean individual size (mm); biomass ($\mu g\ l^{-1}$); and proportion of cyclopoids of total macrozooplankton number (%). In brackets: 1 SD

Cyclopoids	16 sil 0 sab	12 sil 4 sab	8 sil 8 sab	4 sil 12 sab	0 sil 16 sab
Abundance (number l^{-1})	70.4 (23.9)	58.7 (69.1)	5.2 (0.3)	5.9 (2.2)	6.0 (2.3)
Mean individual size (mm)	0.6 (0.2)	0.7 (0.1)	0.8 (0.1)	0.8 (0.0)	0.8 (0.0)
Biomass ($\mu g\ l^{-1}$)	170 (158)	143 (141)	20.5 (3.4)	28.4 (8.8)	27.2 (7.8)
% of cyc. of macrozooplank.	97 (0)	91 (13)	58 (39)	62 (28)	54 (18)

Fig. 5 Effect of the different proportions of visually and filter-feeding planktivores on (**a**) water transparency (SDL, cm); (**b**) phytoplankton biomass (chlorophyll concentration, $\mu g\ l^{-1}$); and (**c**) proportion of particulate phosphorus of total phosphorus (%). Vertical lines represent ±1 SD
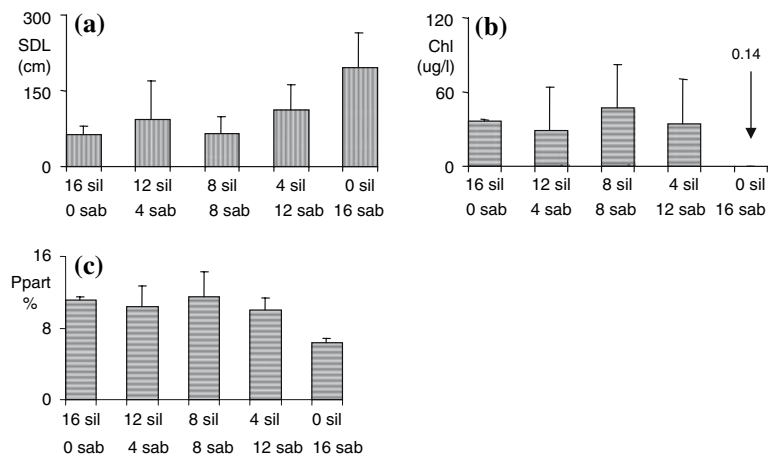
However, there were significant differences for phosphorus fractions between treatments. Tanks with more visual planktivores had a higher proportion of particulate phosphorus than tanks dominated by filter feeders ($P = 0.09$, Fig. 5c).

Discussion

Our results show that the feeding strategy of planktivorous fish is an important factor for the outcome of cascading trophic effects.

While filter feeders controlled both cladoceran and copepod size and abundance, visual planktivores selected strongly for cladocerans, cyclopoid abundance thus remaining high. These results agree with those of Janssen (1976) who experimentally showed that a suction feeding device is less effective at catching calanoid copepods than a filtering device. We found that this was true for cyclopoids as well. Moreover, our observations on the behaviour of visual planktivores in the mesocosms also agree with those of Hairston et al.

(1982) concerning the attack of visual planktivores upon their selected prey items.

Our results show that visual planktivores strongly suppressed the largest prey items, the opposite being true for the filter feeders. In consequence, even though the final communities of the silverside- and sabalito-dominated mesocosms had the same total crustacean biomass, the types of macrozooplankton communities differed widely. Thus, the macrozooplankton in the silverside tanks was dominated by cyclopoids and a few small cladocerans, while that of the sabalito tanks was composed of equal proportions of cyclopoids and cladocerans.

The silverside mesocosms were turbid due to a higher phytoplankton biomass, while the sabalito tanks were clearer. This was to be expected from the different composition of the grazer communities (Brooks & Dodson, 1965; Carpenter et al., 1985; Bergquist et al., 1985; Declerck et al., 1997). The grazer community dominated by cyclopoids and small cladocerans should be, and was, less efficient at removing algae than the other dominated by large-sized cladocerans. However, the observed effect of zooplankton on phytoplankton may be the consequence not only of grazing, but the result of direct as well as indirect impacts, such as the recycling of nutrients or removal of competitors (Sommer et al., 2001).

We conclude that through both processes—the preference of visual planktivores for large-sized cladocerans, and the filter feeders' reliance on both cladocerans and cyclopoids as prey items—visual predators enhance eutrophication effects more than filter feeders. Visual planktivorous fish have stronger cascading effects on phytoplankton biomass. Fish directly act on the herbivorous zooplankton via predation, with indirect effects on the phytoplankton. The effects of the visual planktivores on the most efficient herbivores, large-sized cladocerans, cascade strongly down the food web and lead to a marked deterioration of water transparency via the growth of the algal standing crop.

Our results are not in agreement with those of Lazzaro et al. (1992), who found that cyclopoid density was higher in tanks with the filter feeder gizzard shad (*Dorosoma cepedianum*) than with the visual feeder bluegill (*Lepomis macrochirus*), and our results on phytoplankton growth are also the opposites.

The results obtained allow us to elucidate some of the trophic relations occurring in the complex pelagic system of pampean shallow lakes of relevance for managers.

Our results do not support the hypothesis proposing that the replacement of visual planktivores by filter feeders in hypertrophic shallow lakes is a result of exploitative competition. There are important differences in many characteristics of the zooplankton community resulting from the feeding behaviour of both fish species. In fact, where filter feeders and visual planktivores coexist, the size reduction of cladocerans is similar to that observed in tanks inhabited only by visual planktivores. This important effect on the largest cladocerans is hardly attributable to a cladoceran enlargement in the filter feeder tanks but rather to the feeding activities of the visual predators, as concluded also in previous studies (Boveri & Quirós, 2002). We therefore hypothesize that the two species only have a few prey items in common, which contradicts the argument of competitive displacement of visual planktivores by filter feeders.

We suspect that changes in the environment of pampean shallow lakes induced by human activities may affect the survival of silverside. The current intensification of agriculture, stockbreeding activities and urbanization have triggered intense eutrophication processes (Quirós et al., 2002) that may potentially lead to dominance by other fish species than those dominant today. Filter feeders, detritivores, and omnivores often substitute visual predators at increasing eutrophication (Horne & Goldman, 1994). Because silverside and sabalito often dominate the fish communities in pampean shallow lakes, the ecological relationships among fish species, plankton communities and water quality may have important implications for lake management, and the intensified land use in the lake catchments calls for the implementation of new management measures in our shallow lakes.

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