



Fish as links between pelagic and littoral zones: feeding strategy of "Sabalito" (*Cyphocharax voga*) in a mesocosm experiment

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Abstract. In shallow lakes, energy and matter transfers often occur mediated by currents, diffusive processes and organisms, particularly fish. In Pampean shallow lakes, "Sabalito" (*Cyphocharax voga*), an omnivorous feeder, is a common species in the open water and near the shoreline. There is increasing evidence that, when available, periphyton is an important source of carbon for secondary production in the pelagic thus, insights on factors affecting periphyton production are extremely important for evaluating possible limitations within fish yield. To clarify the interactions between littoral and pelagic food webs in shallow lakes, mediated by the presence of *C. voga*, a 32 day mesocosm experiment was conducted examining the response of the pelagic and periphytical sub-systems to different densities of *C. voga*. *Cyphocharax voga* did not affect the macrozooplankton community neither on its biomass as a bulk nor by promoting inner changes in the relative proportion of cladocerans and cyclopooids or in its average individual size. Within the fish densities evaluated, no cascading "top-down" effects were observed. Nevertheless, *C. voga* pressure affected the peripheric community: on one side, treatments with higher number of individuals exhibited lower periphytic algae biomass; on the other, a positive and a negative effect on attached chironomid larvae occurred. *Cyphocharax voga* feeding strategy might include periphytical elements as an important source of food. Thus, moving in and out open water and shoreline, it can promote energy and matter transfers between littoral and pelagic zones in Pampean shallow lakes.

Key words: littoral-pelagic transfers – trophic interactions – Pampean shallow lakes

Resumen: Peces como enlaces entre las zonas pelágica y litoral: la estrategia de alimentación del "Sabalito" (*Cyphocharax voga*) en un experimento en mesocosmos. En los lagos poco profundos, la transferencia de materia y energía ocurre mediada por corrientes, procesos de difusión y por organismos del sistema, particularmente los peces. En los lagos someros de la región Pampeana, el "Sabalito" (*Cyphocharax voga*) es una especie omnívora muy común que habita tanto la zona de aguas abiertas (pelágica) como la zona litoral. Existe evidencia de que, cuando está disponible, el perifiton puede ser una importante fuente de carbono que sostiene la producción secundaria de la zona pelágica; de manera que el conocimiento de los factores que afectan a la producción de perifiton es extremadamente importante para la evaluación de las posibles limitaciones en el rendimiento pesquero de estos cuerpos de agua. Para esclarecer las interacciones entre las redes tróficas litoral y pelágica en lagos poco profundos y estimar su influencia sobre los diferentes subsistemas, se llevó a cabo un experimento en mesocosmos de 32 días de duración en el cual se midió la respuesta de los subsistemas pelágico y perifítico ante tratamientos que involucran distintas densidades de *C. voga*. *Cyphocharax voga* no afectó a la comunidad del macrozooplancton en su biomasa general, no provocó cambios internos en la proporción relativa de cladóceros y ciclopoideos, ni

en el tamaño promedio de los individuos. Dentro de las densidades de peces evaluadas, no se observaron efectos “top-down” en cascada. Sin embargo, la presencia en diferentes densidades de *C. voga* afectó a la comunidad perifítica resultando en: por un lado, los tratamientos con mayor número de individuos exhibieron menor biomasa de algas del perifiton y por el otro, se evidenció un efecto simultáneo de promoción y de predación sobre las larvas de quironómidos presentes en un soporte sólido dentro de cada unidad experimental. La estrategia de alimentación de *C. voga* podría incluir elementos de la comunidad perifítica como una importante fuente de alimento. Por lo tanto, el desplazamiento de *C. voga* entre la zona pelágica y la zona litoral puede significar una transferencia de materia y energía desde una zona a la otra en sistemas someros de la región Pampeana.

Palabras Clave: Transferencias litoral-pelágicas - Interacciones tróficas - Lagos poco profundos pampeanos

Introduction

Littoral and pelagic food webs have commonly been regarded as relatively separate systems (Vadeboncoeur *et al.* 2002). However, interactions between littoral and pelagic energy-flow pathways have recently received more attention, because coupling between these habitats can have important consequences over ecosystem structure and function (Polis & Strong 1996, Polis *et al.* 1997, Schindler & Scheuerell 2002).

The energy flow through the system from the base of the food web to top consumers is of fundamental importance for the function of lake ecosystems. Energy transfer within the food web sets the limit for production at higher trophic levels, and the presence of several diverse energy-flow pathways may affect ecosystem properties such as nutrient cycling, among others (Polis *et al.* 1997). This energy limit is set because only 5–15 % of the energy produced in one trophic level transfers to the next (Wetzel 2001). Consequently, in a particular lake ecosystem, the energy source basis of top consumers typically reflects the dominant primary production pathway and the associated food web (McCann *et al.* 2005, Schindler & Scheuerell 2002).

In shallow lakes, littoral – pelagic limits can be easily surpassed by physical, chemical and biological processes that minimize rigid zonation. Energy and matter transfers often occur mediated by currents (Marti & Imberger 2008), diffusive processes (James & Barko 1991) and organisms (Bouchard & Bjorndal 2000), particularly fish (Karlsson & Byström 2005, Reissig *et al.* 2003). Because of their high mobility and flexible feeding, on both littoral and pelagic resources, fishes play a particularly important role as integrators of littoral and pelagic food webs linking these two ecological systems through inter-habitat omnivory (Schindler & Scheuerell 2002, Vander Zanden & Vadeboncoeur

2002) and also as top-down controllers of organisms at lower trophic levels (McCann *et al.* 2005, Schindler & Scheuerell 2002). Nevertheless, fish effects on ecosystem functioning are not only related to prey consumption. Fish can forage in one habitat and excrete in another, thus translocating nutrients and affecting the phytoplankton community structure by altering the supply rates and ratios of limiting nutrients (Attayde & Hansson 2001, Sereda *et al.* 2008). Consequently, this behavior can have a strong influence on the structure and dynamics of the pelagic pathway by providing energy that sustains higher densities of consumers than would otherwise be maintained if these consumers feed exclusively on energy derived from the pelagic pathway (Havens *et al.* 1996, Polis *et al.* 1997). Understanding sources of food responsible for sustaining consumers is critical in providing effective management (Bunn *et al.* 2006). Consumers can affect resources through different mechanisms both, positively (i.e., nutrient regeneration, physical stimulation) and negatively (i.e., consumption); the net impact of consumers on primary producers will depend on the relative magnitudes of deleterious and stimulatory effects (Geddes & Trexler 2003). McCann *et al.* (2005) suggested that fishes not only link food webs in space but can also strongly affect their dynamics and stability with their rapid behavioural responses. All these processes were called “ecological habitat coupling” by Schindler & Scheuerell (2002) and are critical for the whole lake ecosystem function understanding.

The Pampa plain in South America covers approximately 500.000 km² 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 are, therefore, polymictic (Rennella & Quirós 2002). Several planktivorous fish species may coexist, though in different proportions depending on the condition of the aquatic environment. In Pampean shallow lakes, "Sabalito" (*Cyphocharax voga*, Hensel 1870, Curimatidae), is a common species in the fish communities (Rosso 2006). *Cyphocharax voga* 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). *Cyphocharax voga* dominance in shallow lakes occurs most frequently in eutrophicated lakes and on aquatic systems impacted by siltation (Rosso, personal communication¹) in agreement with the idea that in eutrophic and hypereutrophic lakes, visual detection of prey by specialist fish predators (piscivores) can be limited while filter feeders and suckers are favoured. In particular, the contrast degradation theory predicts that an organism that feeds on large prey (such as piscivores) would be more affected by the increment of turbidity than an organism that feeds on small prey (such as planktivores, benthic feeders) (Utne-Palm 2002). *Cyphocharax voga* is habitually found in the open water and also near the submerged macrophyte beds at the shoreline. When analyzing stomach content of *C. voga*, Grosman & Sanzano (2003) found a diverse number of preys including: periphyton, phytoplankton, zooplankton, and sedimentary organic matter. More recently, Sagrario & Ferrero (2013), analyzing digestive tracts of *C. voga*, found sediment, diatoms, plant debris (decaying when eaten), chydorids, ostracods and chironomids in different proportions, revealing that *C. voga* forages in different lake areas, but mainly supports its maintenance on benthic resources. Omnivores represent an interesting case in this framework, because they can: (1) decrease herbivorous grazers and thus increase algal biomass via trophic cascades, and (2) mobilize nutrients from ingested herbivores, providing a nutrient subsidy to primary producers that can even overcompensate for their herbivory (de Mazancourt *et al.* 1998).

Despite the significance of the feeding strategy regarding the function of lake ecosystems, there exist very few estimates of the relative

importance of littoral versus pelagic energy sources for ecosystem energy flow in lakes. Thus, to clarify the interactions between littoral and pelagic food webs in shallow lakes, mediated by the presence of *C. voga*, and to estimate its influence over different sub-systems, we conducted a mesocosm experiment evaluating a range of fish densities as treatments.

The aim of this study is to contribute in the understanding of the role of fish in shallow lake ecosystems. Assessing the influence of *C. voga* over the peripheric sub-system, particularly over periphyton growth and chironomid larvae abundance, we could hypothesize that, feeding on border waters, *C. voga* can act as a carrier of energy and matter between littoral and pelagic zones in Pampean shallow lakes.

Materials and Methods

The experiment took place in summer and lasted 4 weeks and a half (February 1st to March 3rd). It was run in a ten outdoor mesocosm facility located at the Facultad de Agronomía, Universidad de Buenos Aires. All ten tanks simulated some principal characteristics of Pampean shallow lake's environment such as elevated trophic state, showing high phytoplankton biomass and nutrient concentrations.

The mesocosms consisted of large white fibre-glass tanks, 2 m in diameter and 2 m high, holding approximately 5,500 l of water. To prevent stratification and reproduce 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. The experimental units hosted five different densities of fish.

In a 70 m³ reservoir the experimental medium was prepared with groundwater enriched with 4750 g NH₄Cl and 230.5 g KH₂PO₄ and salt (120 kg NaCl); all dissolutions 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 representative Pampean shallow lake. The experimental medium was inoculated with natural phytoplankton and zooplankton imported from de Gomez shallow lake, a typical Pampean hypereutrophic shallow lake (Quirós *et al.* 2002); plankton was collected and held in a large container.

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It was then mixed and distributed in several aliquots to stock the whole tank volume aleatoriously. 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 Gomez on January 31st. On average, stocked *C. voga* weighed 6.2 ± 0.9 g (mean weight \pm SD) and were 71 ± 6 mm long (mean total length \pm SD).

The experimental design comprised five treatments with two replicates for each of them. The five treatments consisted of five different fish densities: 0, 5, 10, 15 and 20 young individuals of *C. voga*. Treatments were randomly assigned to tanks, by stocking fish on February 1st (sampling date: Initial). As the water was very clear in the first week of the experiment, it was possible to see *C. voga* schooling in all tanks. It was also likely to see the feeding behaviour of fish, catching zooplankton in the water column and chironomid larvae on wall's tanks surface. This natural resembling behaviour allows us to state that fish might have not suffered any stress inside the mesocosms. Moreover, the survival of the individuals was complete; all fish were caught alive at the end of the experiment. This experimental design prioritized the generation of a predation pressure gradient (0, 5, 10, 15 and 20 Fish), so as to avoid a scheme that only addressed the effect of the presence or absence of sabalito. Furthermore, we sought a design that could explore and find a threshold of sabalito individuals that could trigger cascading trophic effects over lower trophic levels. Unfortunately, the experimental system available ($n = 10$) limited the possibility of implementing designs that could address a larger number of replicates preserving the objective of exploring different densities of predators.

Tanks were monitored daily at noon for pH, electrical conductivity ($\text{mS}\cdot\text{cm}^{-1}$), turbidity (NTU), dissolved oxygen content ($\text{mg}\cdot\text{l}^{-1}$), and water temperature ($^{\circ}\text{C}$) with a HORIBA-U10 limnological probe, and for Secchi disk depth. Water and plankton samples were taken on five dates (day 1: "Initial", day 7 "t1", day 17 "t2", day 24 "t3", and day 32 "Final"). In sampling the mesocosmos, we focused on the responses of the zooplankton and periphytic community on a weekly time scale. This frequency is adequate according to the average zooplankton doubling time, thus, providing us with sufficient information to reach our goal of understanding the effects of sabalito over the system. 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) filtering 30.78 l each time, pooled, and preserved in 5% sucrose-formalin. The zooplankton was then counted following the method outlined by Bottrell *et al.* (1976), and measured under a dissecting microscope in a Bogorov chamber. Identification level reached was "Order", discriminating between cladocerans and copepods. Zooplankton biomass was calculated using length-weight regressions (Bottrell *et al.* 1976).

Integrated water-column samples were taken for analyses of chlorophyll-a (Chl a), total phosphorus (TP) ammonia, NO_3^- Kjeldahl nitrogen (Nk) and total nitrogen (TN). Five litre 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 Chlorophyll, water was filtered through Whatman GF/F glass fibre filters, which were subsequently wrapped in aluminium foil and cooled. Chlorophyll 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.

Periphyton and their hosts communities were evaluated in glass surfaces "plates" disposed in mesocosm walls. The plates were 6 cm width by 10 cm high and hooked from the border into the water by a wire and a rope at 10 cm depth in the east side of each tank.

Four glass surfaces in each tank were bare, exposed to direct fish action, but one glass was protected from fish contact by a plastic net as a cage. The cage allows uncoupling positive and negative effects of fish on attached algae and its host invertebrate community. Bare plates were collected once in every sample date, and caged plate at the end

of the experiment. Periphyton dry weight was measured by grazing 50 cm² of glass surface, drying the flocks 24 h at 105°C in stove, and then weighting it in a precision scale (Kern 770 accuracy 0.1 mg).

Chironomid larvae were visually counted in the side facing the water on each plate before the grazing.

At the end of the experiment the water of the tanks was carefully drained through a small mesh seine and all fish were recovered live, then sacrificed, weighed and measured.

Data were analysed by ANOVA (One and Two Way) and followed by Tukey's test in order to identify differences between treatments and among sampling date. Shapiro-Wilks test was applied to check for normality. All the analyses were performed on Minitab® 16.2.3 Statistical Software. In all cases, differences were considered significant at an alpha level of 0.05.

Results

Initial Conditions: The composition of zooplankton assemblages resulted only in Cladocera (including *Daphnia* spp) and Cyclopoida. Initial macro zooplankton abundance (ind.l⁻¹) and composition did not significantly differ between treatments (One Way ANOVA $\alpha=0.05$; $p=0.559$).

Phytoplankton biomass and water transparency (Chlorophyll a and Secchi Disk Lecture SDL) was similar in all treatments (One Way ANOVA, Chl a: $p=0.728$; SDL: $p=0.737$). Analogous results were obtained for nutrient (NKjel and P) concentrations (One Way ANOVA, NKjel: $p=0.821$; TP: $p=0.454$).

Periphyton sampling plates were installed empty and clean on the initial date thus, there was neither periphyton nor chironomid larvae attached to them at this stage.

Zooplankton: Sabalito's density did not affect the macrozooplankton biomass as a bulk, but promoted, although not statistically significant ($p>0.05$), inner changes in relative proportion of cladocerans and cyclopoids. At the end of the experiment, cladocerans were absent in 10, 15, and 20 sabalitos treatments, while representing more than 75% of the macrozooplankton abundance in control tanks (Fig. 1). In these tanks (10, 15 and 20 Fish) the predating pressure was evident as from sampling date "t2" and cladoceran abundance did not recover ever since (Fig. 2). As for Copepods, their abundance reach zero only in one unit of the 20 Fish treatment and in one unit of the Control tanks, preventing us to draw

any conclusion on this aspect.

Regarding zooplankton biomass, Copepods average body size was not affected along the experiment by sabalitos, while cladocerans average body size exhibited slight changes between treatments (Fig. 3), although the very few individuals in 10, 15 and 20 samples (in many cases zero individuals) limit this asseveration, furthermore, temporal variation was considerable and there was no consistent pattern among treatments.

Annex I contains all the raw data.

Nutrient and chlorophyll evolution: During the experiment, the fish stock did not affect neither nitrogen nor phosphorus concentrations, in any of the measured fractions (i.e. kjeldahl nitrogen (shown here), total nitrogen nitrates (data not shown), total phosphorus (shown here), soluble reactive phosphorus, particulate phosphorus, % of particulate on total phosphorus (data not shown)) (Final date One Way ANOVA $\alpha=0.05$ Nkjel $p=0.986$; TP $p:0.885$) (Fig. 4), nor Chlorophyll a concentration (Final date One Way ANOVA $\alpha=0.05$ Chl a $p=0.620$) (Fig. 5).

Periphytic system: In the peripheric system, *C. voga* had a notorious influence. It is possible to see the difference among the low density treatments and the rest of the mesocosms regarding bare plates which, by the end of the experiment, had until three times the biomass than the one achieved in 15 and 20 *C. voga* tanks (ANOVA $\alpha=0.05$; $p=0.01$), moreover, during the experiment the effect of 15 and 20 fish treatment is observed (Two Way ANOVA $\alpha=0.05$ Date $p=0.000$; Treatment $p=0.003$; Interaction $p=0.112$) (Fig. 6) indicating that both, treatment and the elapsed time of the experiment affects periphyton abundance in bare glasses, particularly 15 and 20 fish treatments. As for the protected plates, differences between treatments were not statistically significant (ANOVA $\alpha=0.05$; $p>0.05$).

As for chironomid larvae density, initial conditions showed absence of larvae in every treatment. At the end of the experiment, only CONTROL treatment showed presence (10 ind.glass⁻¹ ± 2.828) of chironomid larvae in bare glasses. (One Way ANOVA $\alpha=0.05$; $p=0.002$). On plates protected from fish predation, at the end of the experiment lower values were found between CONTROL and 5 fish treatment when comparing them to 10, 15 and 20 fish treatment (One Way ANOVA $\alpha=0.05$; $p=0.005$). (Fig. 7).

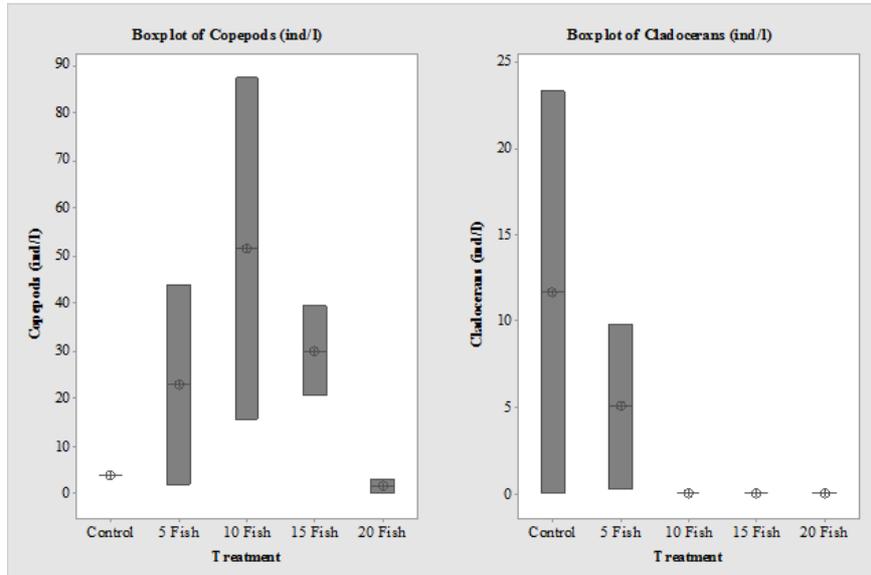


Figure 1. Zooplankton abundance (ind.l⁻¹). Copepod, left panel and Cladoceran, right panel for Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish for the final sampling date. Boxes represent the mean 95% confidence intervals. Note the differences on Y scales between panels.

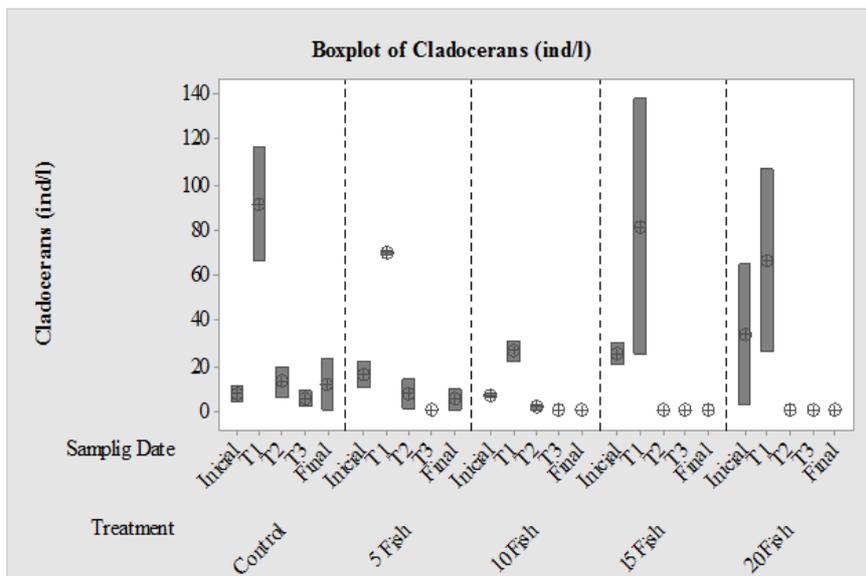


Figure 2. Cladoceran abundance (ind.l⁻¹) for every sampling date (one week spacing between sampling dates) and every treatment (Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish). Mean ± 95% confidence intervals. Note the evidence of predating pressure in 10, 15 and 20 Fish tanks as from sampling date “t2”

Finally, when analyzing the combined effect of fish density and the level of protection of the glass plate, data shows that the enhancement effect showed in Figure 5 is dependent of both variables (Two Way ANOVA (Treatment and Protection) $\alpha=0.05$ Protection $p=0.000$; Treatment $p=0.003$; Interaction $p=0.000$).

Discussion

Shallow lakes are complex systems where interactions among the pelagic, benthic and littoral

areas are strong. Recently it has been stated that predator foraging type has considerable effects on food webs and is a key factor controlling food web topology (Ings *et al.* 2009, Lazzaro *et al.* 2009, Sagrario & Ferrero 2013) and ecosystem functioning (Schmitz *et al.* 2004, Schmitz 2008), it has also been stated that the food strategy of planktivorous fish is a determining aspect towards the results of the transmission of trophic cascade effects (Threlkeld & Drenner 1987, Boveri 2009). Besides, daily movement by fish and zooplankton facilitates rapid

nutrient translocation across boundaries in freshwater (Kitchell *et al.* 1979, Vanni *et al.* 1980, Schindler *et al.* 1996). Such movement transports great quantities of matter rich in fertilizing nutrients within the water column (the "diel ladder"; Kitchell *et al.* 1979), between benthic and pelagic waters ("nutrient pump mechanism"; Vanni 1996), between onshore and offshore waters (Brabrand *et al.* 1990), and to refuge areas (Meyer *et al.* 1983, Ogden & Gladfelter 1983).

These spatial food web subsidies that move

across traditionally defined ecological or habitat boundaries, are energetically important in a wide range of ecosystems (Polis *et al.* 1997). The importance of cross-habitat linkages for trophic dynamics and stability is also supported by recent theoretical food web models (Huxel & McCann 1998, Post *et al.* 2000, Vadeboncoeur *et al.* 2005).

It has been stated that *C. voga* depends largely on benthic resources in turbid hypereutrophic shallow lakes (Sagrario & Ferrero 2013) behaving as a detritivorous fish species, while other studies have

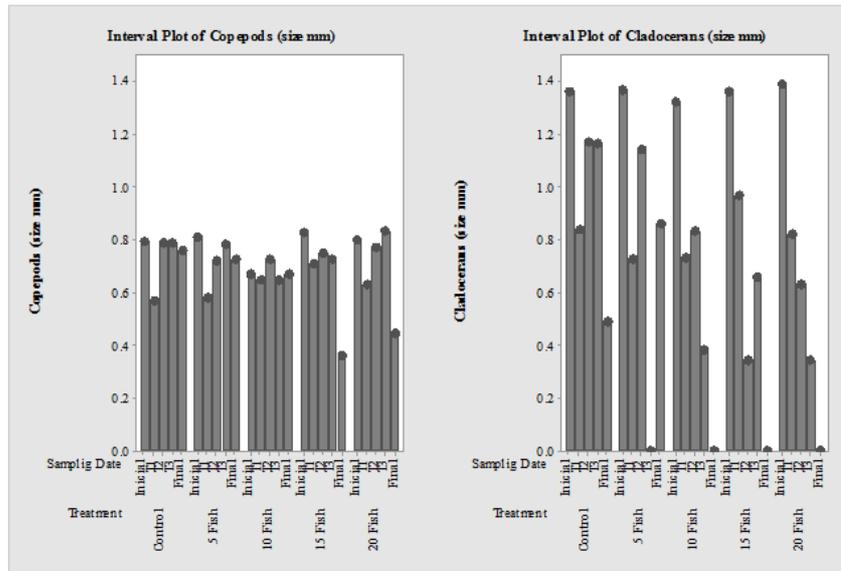


Figure 3. Interval plot for zooplankton mean body size (mm) copepods (left panel) and cladocerans (right panel) for every treatment (Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish) and every sampling date (one week spacing between sampling dates). p -value >0.05 for date, treatment and interaction effects. Note that zero values for cladocerans mean body size in 10, 15 and 20 fish treatments for final date correspond to zero individuals (0 ind.l⁻¹) (see Fig. 2).

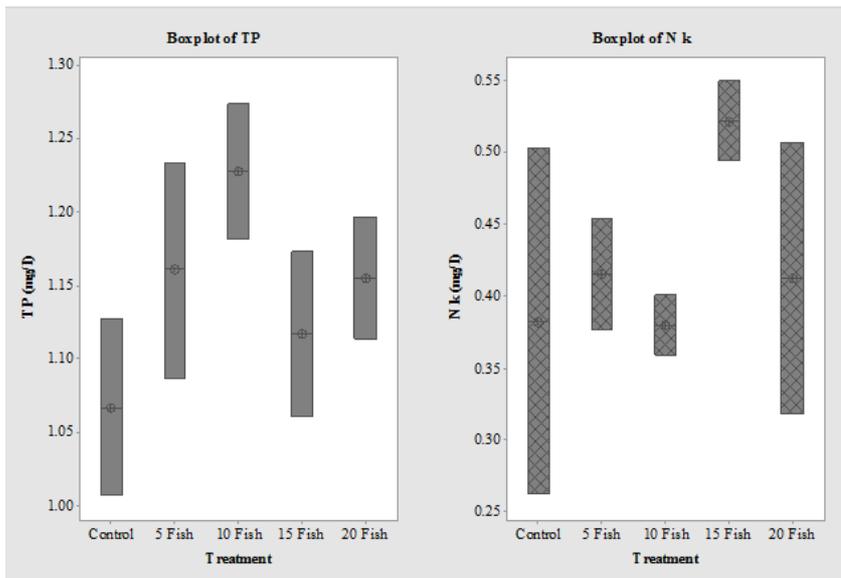


Figure 4. Total Phosphorous (TP) and Kjeldahl Nitrogen (N k) concentrations (mg.l⁻¹) for every treatment (Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish) for the final sampling date. Boxes represent the mean 95% confidence intervals. Note the differences on Y scales between panels.

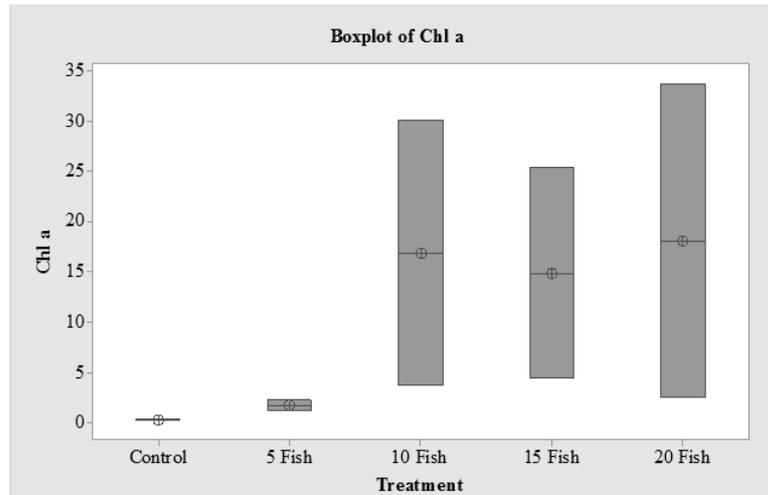


Figure 5. Chlorophyll a concentrations ($\text{mg}\cdot\text{l}^{-1}$) for every treatment (Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish) for the final sampling date. Boxes represent the mean 95% confidence intervals.

classified *C. voga* as a detritivorous-iliophagous fish associated with periphyton and phytoplankton consumption (Grossman *et al.* 1996, Corrêa & Noguez Piedras 2008).

Despite some studies have related *C. voga* diet with zooplankton consumption (Destefanis & Freyre 1972, Escalante 1984), in this study we had no impact on the zooplankton community, in accordance with Stein *et al.* 1995, who informed that *C. voga* can prey on different food items thus, not being limited by zooplankton presence. At the same time, when analysing the final date, similar zooplankton biomass and abundance were found despite of the fish density; these results are consistent with Horppila & Kairesalo 1990, 1992 who report no clear responses of fluctuations in cladoceran zooplankton for different levels of filter feeder fish predation.

Our results show the significative influence of *C. voga* in the periphyton community. With exposed and protected surfaces, this experiment was able to show positive and negative effects of fish at the same time: *C. voga* stimulates periphyton and chironimids development but also caused its disappearance by eating on it, this suggest that the littoral system might be a source of energy and matter transported to the pelagic zone by *C. voga*, but also that *C. voga* contributes with the littoral zone by bringing up some sort of inoculum or enhancement which results in the above mentioned periphytic development. In fact, while periphyton biomass achieved in protected plates was the result of stimulation effects, periphyton biomass achieved in exposed plates was a balance consequence among stimulation to grow and predation or perturbation by fish. The fact that

chironomid larvae were totally depleted when available, regardless fish density levels, suggests that they represent a valuable littoral food source for *C. voga* and provides food of high quality in terms of both protein and energy compared to primary food resources like detritus, macrophytes or algae (Bowen *et al.* 1995).

In this study, *C. voga* did not have access to the benthic habitat because the experimental design did not recreate this zone thus, forcing *C. voga* to depend only on pelagic and/or littoral components. In conclusion, we show that having only these two habitats accessible for foraging, *C. voga* prefers littoral resources rather than pelagic plankton components. This behaviour has its consequences over the structure and functioning of the whole system.

Cyphocharax voga can be found in the littoral and pelagic zones (Artioli *et al.* 2009) thus, it can move from open water to the littoral and back searching and consuming alternative preys (Sagrario & Ferrero 2013). Feeding on both, pelagic and border waters, *C. voga* may act as a carrier of energy and matter between littoral and pelagic zones in pampean shallow lakes thus, driving energy from the littoral food web to the pelagic food web. Related excretion effects may also be possible (see Vanni 1996), but this experiment didn't show any relationship among fish density and nutrients concentration; this can be explained because a) the high concentrations of nutrients present in the system did not limit the primary production during the length of the experiment, b) The experimental units enables a quick nutrient recycle resulting in no significant effects of fish density on this variable.

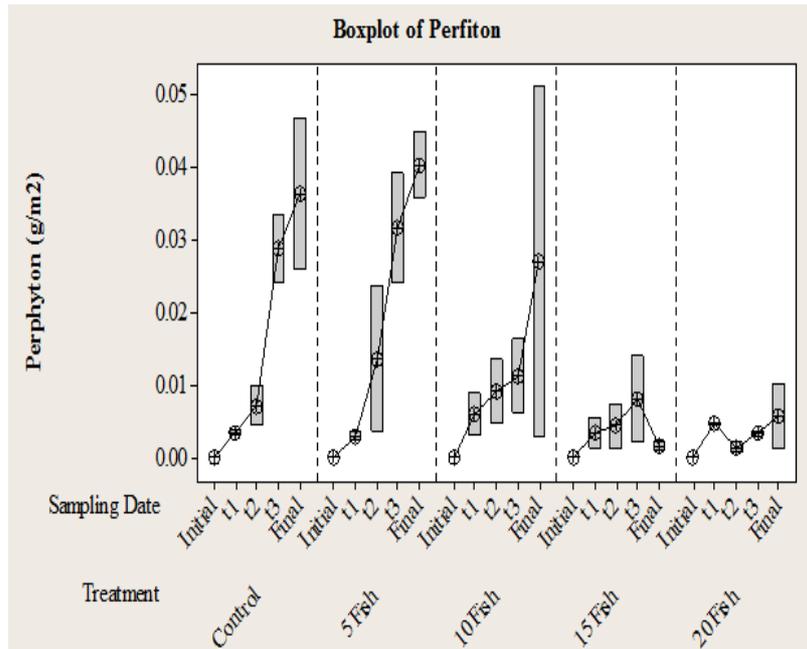


Figure 6. Temporal variation of periphyton abundance (g.m⁻²) for every treatment (Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish) and every sampling date (one week spacing between sampling dates). Mean ± 95% confidence intervals

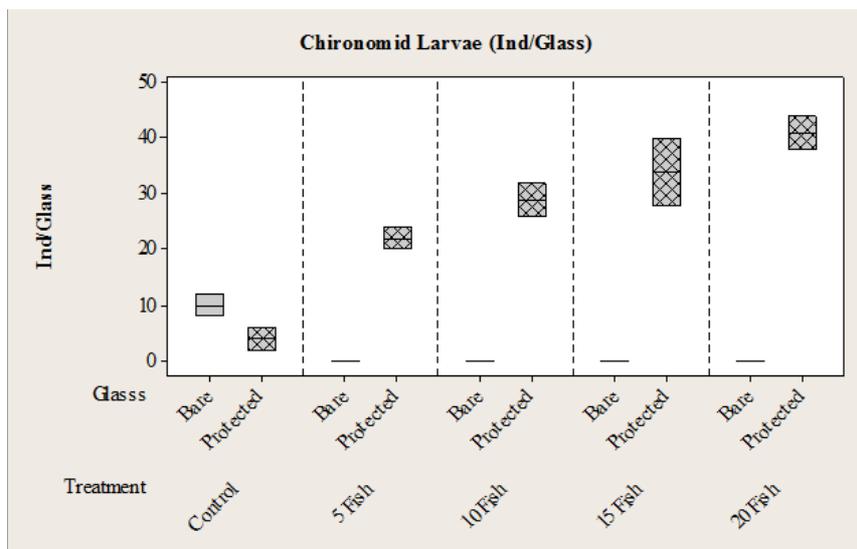


Figure 7. Chironomid larvae abundance (ind.glass⁻¹) for the final date in each of the treatments (Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish). Comparison between levels of protection (Bare=Unprotected; Protected=not exposed to fish predation showed as squared boxes).

In this way, it is possible to reinforce that littoral resources subsidize pelagic consumers and affect its trophic cascading effects (Schindler *et al.* 1996).

Increasing the number of links in the lake ecosystem, omnivorous fish brings stability to the components of the food web, allowing the uncoupling of those that enter at risk for depletion and enabling the incorporation of alternative resources.

Multi-channel omnivory, or allochthonous energy subsidies from adjacent ecosystems, can

facilitate or attenuate trophic cascades (Polis *et al.* 2000). Moreover, Bascompte *et al.* (2005) suggest that omnivory can reduce the probability of trophic cascades to occur, particularly it has been stated that predator exploitation of multiple resources within ecosystems profoundly affects the expression of top-down control (Schindler *et al.* 1996, Estes *et al.* 1998, Post *et al.* 2000, Ramcharan *et al.* 2001).

Because *C. voga* is an important species in fish community of pampean lakes, the ecological

relationships between these fishes, littoral, plankton communities, and water quality may have significant implications for managing Pampean very shallow lakes.

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Fish as links between pelagic and littoral zones: feeding strategy of "Sabalito" (*Cyphocharax voga*) in a mesocosm experiment

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ANNEX I

Table I: Raw data of zooplakton samples for every sampling date (one week spacing between sampling events) and for every treatment (Control (0 Fish), 5 Fish, 10 Fish, 15 Fish and 20 Fish). Variables included for cladocerans and copepods (in order): Abundance (ind.l⁻¹), Size (mm), Biomass (µg.l⁻¹).

SamplingDate	Treatment	Cladocerans (ind/l)	Copepods (ind/l)	Cladocerans (mm)	Copepods (mm)	Cladocerans (µg/l)	Copepods (µg/l)
Inicial	10Fish	5,550142103	1,490052781	1,388	0,83	87,73664637	6,964506699
Inicial	10Fish	7,074299635	1,179049989	1,259	0,509	96,17510353	1,998489647
Inicial	15Fish	29,67113276	8,594397077	1,378	0,837	471,2666017	41,63985384
Inicial	15Fish	20,00812018	10,9135201	1,337	0,819	296,9004953	49,60194884
Inicial	20Fish	2,377588307	2,773853025	1,421	0,831	41,56262119	12,82074868
Inicial	20Fish	64,55542022	9,744214373	1,356	0,768	1081,143727	36,99878197
Inicial	5 Fish	10,18595209	4,157531466	1,35	0,82	154,2051287	18,9666855
Inicial	5 Fish	21,82704019	2,545488023	1,378	0,796	356,6538368	10,75636541
Inicial	Control	3,771010962	2,933008526	1,265	0,775	53,24290378	11,22756664
Inicial	Control	10,69914738	2,773853025	1,451	0,808	198,0875128	12,06626066
T1	10Fish	30,82419813	20,69021518	0,762	0,594	117,5943159	50,85654892
T1	10Fish	21,45026391	63,52578157	0,708	0,708	57,16495381	224,3095347
T1	15Fish	24,73731222	3,092164028	0,909	0,891	134,3978173	17,29756557
T1	15Fish	138,0495381	67,74177882	1,021	0,53	1310,780317	115,0932814
T1	20Fish	26,06252538	144,0064961	0,853	0,675	145,5592042	451,7488784
T1	20Fish	106,772229	77,17417783	0,798	0,587	387,7967357	196,3311084
T1	5 Fish	69,18392205	25,82866423	0,729	0,57	209,3505481	55,50579943
T1	5 Fish	70,66504263	80,21437272	0,726	0,589	192,0675859	181,8458829
T1	Control	116,3264312	78,08526188	0,823	0,6	530,5648526	198,883162
T1	Control	65,98585059	37,74259034	0,853	0,53	368,2517255	80,4672026
T2	10Fish	2,572472594	11,14738124	0,925	0,716	13,12990012	36,75291596
T2	10Fish	0,237109216	8,654486399	0,737	0,735	0,898664637	30,75804466
T2	15Fish	0,461226147	1,844904588	0,684	0,788	0,970881089	8,26327649
T2	15Fish	0	37,09622412	0	0,713	0	120,7111133
T2	20Fish	0	37,47300041	0	0,791	0	159,0354137
T2	20Fish	0,441737718	15,01908242	1,268	0,744	4,730127487	54,92478441
T2	5 Fish	0,831505293	6,652050345	1,132	0,689	6,721065367	19,59028827
T2	5 Fish	13,64190012	7,795371488	1,15	0,752	130,3619976	28,14908648
T2	Control	19,63296793	24,25984572	1,108	0,758	195,0928023	91,38683881
T2	Control	6,119366626	3,569630532	1,224	0,816	68,63481608	16,0990337
T3	10Fish	0,148989088	33,40966301	0,763	0,496	0,419106163	57,3098173
T3	10Fish	0	8,550548112	0	0,799	0	37,21198538
T3	15Fish	0,389768575	26,11449452	1,316	0,659	4,651108404	73,14669915
T3	15Fish	0	19,50791717	0	0,796	0	85,01550305
T3	20Fish	0,107998376	7,127892814	0,684	0,847	0,227336581	35,25455786
T3	20Fish	0	12,42387383	0	0,816	0	56,08136419
T3	5 Fish	0	5,91317905	0	0,779	0	23,48714719
T3	5 Fish	0	4,894843687	0	0,782	0	19,70664068
T3	Control	9,062541616	10,9817296	1,116	0,799	121,6374336	47,99015834
T3	Control	1,611043443	3,624847747	1,211	0,778	22,37578238	14,43051888
Final	10Fish	0	15,38286642	0	0,665	0	45,94862201
Final	10Fish	0	87,12951685	0	0,667	0	600,9322777
Final	15Fish	0	20,46285018	0	0,724	0	68,59147381
Final	15Fish	0	39,31140885	0	0	0	0
Final	20Fish	0	2,728380024	0	0,886	0	14,39766139
Final	20Fish	0	0	0	0	0	0
Final	5 Fish	0,295964271	43,7320341	0,789	0,598	0,910682063	95,81688672
Final	5 Fish	9,789687373	1,779943159	0,925	0,851	0	8,844537556
Final	Control	23,23670321	3,798747462	0,977	0,885	194,9791766	20,20548888
Final	Control	0	3,559886317	0	0,632	0	9,960561916