



The trophic role of *Cyphocharax voga* (Hensel 1869) according to foraging area and diet analysis in turbid shallow lakes

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With 6 figures and 2 tables

Abstract: Detritivory is a widespread strategy that has been associated with shallow, warm and productive systems. Eutrophic and hypereutrophic lakes can be dominated by an assemblage of detritivorous fish species. The trophic role of the pelagic fish *Cyphocharax voga* in two temperate turbid shallow lakes was analyzed through the study of its diet and foraging area. The results showed that *C. voga* consumed detritus, zoobenthos and zooplankton (95.77%, 4.11% and 0.12% of total ash free dry mass ingested, respectively). Benthic invertebrates were the most abundant organisms ingested, representing 93% of the total biomass. In particular, *Leydigia louisii*, ostracods and harpacticoid copepods contributed most in abundance and biomass. Pelagic prey, represented mainly by *Bosmina (Neobosmina) huaronensis*, constituted 7% of the total biomass consumed by fish. Prey availability was determined in the open and littoral areas and in the lake bottom. *C. voga* showed a selectivity for crustaceans from the lake bottom. This evidence and the high consumption of detritus indicate that *C. voga* is exploiting the benthic food web. Thus, this fish can be considered a detritivorous species. This strategy seems suitable in turbid lakes (20–30 cm Secchi disc depth) where prey detection for visual predators is constrained. Moreover, as *C. voga* attains a high biomass in warm temperate eutrophic shallow lakes of South America, it might be contributing to the linkage of benthic and pelagic pathways, and detritus and benthic invertebrates may provide a subsidy for the pelagic food web.

Key words: *Cyphocharax voga*, detritivory, shallow turbid lakes.

Introduction

Detritivory can be considered a case of omnivory (the consumption of resources from more than one trophic level) when consumers feed on detritus (a low quality, but very abundant basal resource), and on intermediate consumers like invertebrates (a high quality, but less abundant food) (Polis et al. 1989, Diehl 2003). This strategy can stabilize food webs, enhancing its performance, and affecting the topology of food webs (e.g.

from chains to webs) (McCann & Hasting 1997, Krivan & Schmitz 2003, Lazzaro et al. 2009). Moreover, the foraging behaviour of the dominant top predator has an important impact on the number of links, the connectance and the configuration and composition of the food webs in an ecosystem (Lazzaro et al. 2009). Some evidence suggests that omnivorous or detritivorous fish can dampen trophic cascades, although this is not always the case (Thompson et al. 2012). For instance, the detritivorous tilapia (*Oreochromis niloti-*

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cus Linnaeus 1758) can generate a trophic cascade in tropical ecosystems (Okun et al. 2008).

It has been shown that there is an increasing trend in the relative and absolute richness of omnivorous and detritivorous fish species with decreasing latitude considering marine, estuarine and freshwater ecosystems of contrasting latitudes (González-Bergonzoni et al. 2012). Furthermore, the richness of omnivorous and detritivorous fish was higher in freshwater than in other aquatic ecosystems (González-Bergonzoni et al. 2012). For example, detritivorous fish, represented mostly by the families Prochilodontidae and Curimatidae, are highly important in tropical rivers of South America (Bowen 1983, Araujo-Lima et al. 1986, Fugi et al. 1996, Vaz et al. 1999). Omnivorous and detritivorous fish have also been related to warmer, productive and/or shallow lakes (Mehner et al. 2007, Vanni et al. 2006, González-Bergonzoni et al. 2012), and this evidence is in concordance with several models that predict an increase of these type of predators along a productivity gradient (Krivan & Schmitz 2003, Namba et al. 2008). For example, fish assemblages in lakes of Central Europe are dominated by percids and salmonids (piscivores) in deep “cold water” lakes and by cyprinids (bream and roach) in more shallow productive lakes. This fish replacement was explained by water temperature, lake depth and chlorophyll-*a* concentration (Mehner et al. 2007). Similarly, fish assemblages of shallow tropical and subtropical lakes in South America are composed of high densities of omnivorous and detritivorous small sized species and a low representation of facultative piscivores (Lazzaro et al. 2003, Jeppesen et al. 2005, Teixeira de Mello et al. 2009).

In eutrophic and hypereutrophic lakes, visual detection of prey by specialist fish predators (piscivores) can be severely limited. 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). Experiments have shown that increased turbidity had a negative effect on fish that feed visually (for example: Turesson & Brönmark 2007, Shoup & Wahl 2009). In a study of species composition relative to environmental gradients in some floodplain lakes of the Orinoco River in Venezuela, Rodríguez & Lewis (1997) found that fish with good sensory adaptation to low light (rod-cells dominant in retina) were dominant in turbid lakes, while visually oriented fish predominated in clear lakes (cone-cells dominant in retina). Therefore, turbid and productive

lakes are more likely to sustain a detritivore assemblage of consumers (Schaus et al. 2002, Vanni et al. 2006). Furthermore, as fish can function as a strong link between benthic and pelagic food webs (Vander Zanden & Vadeboncoeur 2002, Vadeboncoeur et al. 2002), the effect of a detritivore assemblage on lake processes and functioning should not be disregarded. Fish impact cannot only be addressed as consumptive effects. Nutrient release and bioturbation must be considered because it can facilitate the exchange of sediment-borne nutrients by perturbing the sediment and excreting nutrients derived from the benthos into the water column (Vanni et al. 2005). Consequently, detritivorous fish provide a substantial input to the pelagic nutrient cycle, stimulating phytoplankton development (Vanni et al. 2006, Torres & Vanni 2007). Accordingly, the Gizzard Shad, *Dorosoma cepedianum* (Lesueur 1818), sustains phytoplankton production through the recycling of detritus derived nutrients in warm eutrophic and hypereutrophic reservoirs of eastern North America (Vanni et al. 2005). Detritivores can dominate the fish assemblage in eutrophic lakes (e.g. Schaus et al. 2002, Lazzaro et al. 2003, Diovisalvi et al. 2010) and could have strong effects on the ecosystem, contributing to the resilience of the system and maintaining the lakes in a high productive state. For this reason, biomanipulation techniques must be focus on the removal of plankti-benthivorous and detritivorous fish (Drenner & Hambright 1999) to reduce fish-mediated nutrient cycling and sediment disturbance, favoring, as a consequence, a clear water state (Lazzaro & Starling 2005). As an illustration, the natural mortality event of the Nile Tilapia (*Tilapia nilotica*, Linnaeus 1758) in Paranoá reservoir (Brazil) induced an improvement in the water column conditions, reducing chlorophyll-*a* concentration (ca. 30 %) and total phosphorous (TP) concentration over a year, and, also, inducing the disappearance of bloom forming cyanobacteria (Starling et al. 2002). In this system, the fish removal resulted in a reduction of the internal recycling of phosphorous via excretion that was equivalent to a 12 % reduction of the external TP load (Starling et al. 2002).

This study clarifies the relevance of detritivory as a feeding strategy for the fish assemblage in turbid warm shallow lakes. *Cyphocharax voga* (Characiformes; Curimatidae) can attain a high biomass in warm temperate and subtropical shallow eutrophic lakes in Argentina and in the south of Brazil (Rosso 2006, Diovisalvi et al. 2010). Here we tested the hypothesis that *C. voga* forages in different lake areas and we predicted that it depends on more than one

food web. To confirm this assumption we investigated: (i) the trophic role of *C. voga* in warm temperate turbid lakes, by determining the contribution (abundance and biomass) of benthic, littoral and pelagic resources to the diet of adult individuals, (ii) the relevance in terms of abundance and biomass of the most important prey (iii) changes in the relative contribution of the different resources related to fish size, and finally, (iv) prey availability and selection in each lake zone (open water, littoral areas and lake bottom) with the purpose of determining the foraging area of *C. voga*.

Material and methods

C. voga distribution and characteristics

This fish is a fast growing species that reaches maturity during the first year and has several reproductive events during the spring and fall (Rosso 2006). *C. voga* is distributed from Brazil (Coastal rivers of Rio Grande do Sul and southern Santa Catarina), to Uruguay and Argentina (Uruguay, Paraná, Paraguay, de La Plata and south from the Salado river basins) (Liotta 2006). Related species such as *Cyphocharax nageli* (Steindachner 1881) and *C. modestus* (Fernández-Yépez 1948) have been identified as detritivorous-iliophagous in rivers and in a reservoir of Brazil (Vaz et al. 1999, Roquetti Velludo 2007, Lopes et al. 2009).

Study area

The existence of clear and turbid phases in shallow lakes of South America has been demonstrated (Kosten et al. 2012), and in particular, clear and turbid (organic and inorganic) lakes have been described in the Pampa plain (Quirós et al. 2002). Moreover, a high frequency of turbid lakes in this area has been reported and related to lake size: larger lakes tend to remain turbid (Kosten et al. 2012).

Lakes Hinojales (H) and Nahuel Rucá (NR) (H: 37° 24' S; 57° 24' W; NR: 37° 37' S; 57° 26' W; Buenos Aires Province, Argentina, South America) are warm temperate systems, and, in common with most of the lakes in the Pampa plain, are very shallow (mean depth: H: 0.9 m, NR: 1.1 m), and polymictic. These turbid lakes (Secchi disc depth ~20–30 cm) are hypereutrophic (total phosphorus NR: 380–500 µg L⁻¹), with alkaline waters (pH 8–9) and a total chlorophyll-*a* concentration ranging from 40 to 60 µg L⁻¹ (NR, no previous data available for Hinojales). The littoral zone of both lakes is dominated by *Schoenoplectus californicus* (Meyer) Steud. which forms an outer ring around the shore, while within or close to that ring, small free floating macrophytes, like *Lemna* sp., *Azolla filiculoides* Lam. and *Ricciocarpus natans* L., develop.

The pelagic fish assemblage in these lakes is composed of *C. voga* (curimatid), the inland silverside *Odontesthes bonariensis* (Cuvier & Valenciennes 1835) and *Oligosarcus jenynsii* (Günther 1864). In particular, *C. voga* comprises 30–80% of the biomass of the pelagic fish assemblage in these turbid systems (González Sagrario, unpublished data). The benthic fish assemblage is composed of *Rhamdia quelen* (Quoy & Gaimard 1824), *Pimelodella laticeps* (Eigenmann 1917) and *Corydoras paleatus* (Jenyns 1824) (González Sagrario, unpublished data).

Sampling and laboratory analyses

We estimated the total number of digestive tracts that should be analyzed ($n=45$) to detect rare prey species (McArdle 1990), using a probability of occurrence of rare prey in a single sample of $p=0.05$ and a confidence or probability to detect them of 0.9. However, the total number of digestive tracts analyzed ($n=55$) exceeded the number required (45), and, indeed, increased the confidence of detecting rare species to 0.94.

Cyphocharax voga was collected in lakes Hinojales and Nahuel Rucá, using a fish trap (Colautti 1998) during summer (January) and winter (July and August) of 2008. The fish trap was set in open waters in different sampling stations, remaining there 16–20 hours. Once caught, fish were euthanized in the field using a pointed knife. Fish were stored in a freezer until analysis. In the laboratory, total weight (g), total and standard length (TL, SL) (cm) were measured. The stomach and intestinal tract was preserved in 70% ethanol solution.

The contribution of sediment, detritus and invertebrates to the total mass ingested was estimated by a modification of the weight difference determination method (Bowen 1979, Ahlgren & Bowen 1992). This method was selected because silt, clay and amorphous detritus cannot be estimated by standard numerical or volumetric methodologies (Hyslop 1980). Gut content (stomach plus intestine) was examined under a stereoscopic microscope and the abundance of the organisms consumed was determined. When necessary, two subsamples were taken and all prey were counted in a fully replete digestive tract. The subsamples' volume was determined in each particular case and was chosen when at least 100 individuals of the most abundant prey were counted. Zooplankton and zoobenthos were identified to the lowest taxonomic unit. A subset of individuals (at least 30–50) of each taxon was measured (total length or head capsule width) under a microscope for estimation of the dry mass from their length according to published length-mass regressions (Dumont et al. 1975, Bottrell et al. 1976, Herman & Heip 1982, Benke et al. 1999). After that, gut samples ($n=43$) were rinsed into aluminum pans and oven-dried at 60 °C for 48 hours. Samples were weighed (to the nearest 0.0001g), ashed at 550 °C for 6 hours, and reweighed to determine total ash-free dry mass (AFDM). Estimates of zooplankton and zoobenthos biomass were divided by AFDM to determine the percent of AFDM that consisted of zooplankton and zoobenthos (Yako et al. 1996, Schaus et al. 2002). Detrital contribution to the diet was considered to be the remaining proportion of AFDM because phytoplankton was rarely observed in gut samples (Yako et al. 1996, Schaus et al. 2002).

To assess zooplankton, and benthic and littoral invertebrate availability in each lake area the following procedures were carried out. Six zooplankton samples were taken in open waters of each lake at noon using a van Dorn bottle, covering most of the water column obtaining a final volume of 1 L which was filtered through a sieve of 65 µm. Littoral invertebrates were collected inside *S. californicus* patches using a dip net that was pulled 15 times through the entire water column and the top of the sediment, covering a surface of 1 m² during 2 minutes ($n=6$). Benthic invertebrates were obtained with an Ekman birge ($n=3$) in the sediment of the open waters. Zooplankton, and benthic and littoral invertebrates were counted under a stereomicroscope and these samples were considered a reference of the potential prey assemblage in each lake zone.

Statistical analysis

Invertebrate habitat association was determined according to previous studies (Dumont et al. 1975, Thorp & Covich 1991, González Sagrario & Balseiro 2010). All comparisons were performed between benthic and pelagic prey as no invertebrate species associated with littoral plants or occurring in the water column of littoral areas were found in fish tracts.

Differences between total pelagic and benthic abundances and biomass of the organisms ingested within and between lakes were estimated performing a t-test (Gotelli & Ellison 2004). One-way analyses of variance (ANOVA) were carried

out to test for differences among mean abundance and mean biomass of each prey consumed and among the contribution of each food item to the total dry mass ingested. When significant differences were obtained, multiple *post hoc* comparisons were performed using a Tukey Honestly Significant Difference (HSD) test (Gotelli & Ellison 2004).

Fish diet data were pooled into a unique data set for two reasons. Firstly, no difference in the contribution of pelagic and benthic organisms consumed was recorded between fish populations (Table 2). Secondly, the assemblage of zooplankton and zoobenthos in the gut contents of fish from both lakes was the same.

Table 1. Prey availability and mean contribution (as percent) to the total assemblage in each lake zone of lakes Nahuel Rucá and Hinojales. Habitat association according to Thorp & Covich (1991) and González Sagrario & Balseiro (2010): B: benthic prey, Pt: plant associated prey, Pe: pelagic, open water prey; -: not found; nd: not determined; total contribution of each group in bold.

	Nahuel Rucá	Hinojales	Habitat
Littoral zone			
Gastropoda	31.77	32.84	
<i>Heleobia parchappii</i>	31.03	24.51	B
<i>Physa acuta</i>	0.20	–	Pt
<i>Uncancylus</i> sp.	0.45	2.59	Pt
<i>Biomphalaria peregrina</i>	0.05	5.74	Pt
<i>Pomacea canaliculata</i>	0.04	–	Pt/B
Crustacea	65.85	54.12	
<i>Palaemonetes argentinus</i>	20.86	1.48	Pt/B
<i>Hyallolella</i> sp.	6.91	24.98	Pt
<i>Chlamydotheca incisa</i>	37.43	27.66	Pt
Chydoridae (<i>Leydigia louisii</i>)	0.65	–	B
Insecta	2.23	13.04	
<i>Cyanallagma bonariense</i>	0.16	0.56	Pt
Anisoptera	0.02	–	Pt
Tabanidae	–	0.09	Pt/B
Chironomidae	1.36	11.56	Pt
Corixidae	0.22	0.09	Pt
<i>Belostoma</i> sp.	0.02	–	Pt
Tricoptera	0.07	0.37	Pt/B
Ephemeroptera	0.29	0.28	Pt
Coleoptera	0.09	0.09	Pt
Annelida	0.14	0.83	
Hirudinea	0.14	0.83	Pt/B
Pelagic zone			
Crustacea			
Calanoida			
<i>Notodiaptomus incompositus</i>	8.15	–	Pe
Cyclopoida	35.05	19.74	Pe
Cladocera			
<i>Moina micrura</i>	26.49	–	Pe
<i>Ceriodaphnia dubia</i>	24.60	5.64	Pe
<i>Bosmina (Neobosmina) huaronensis</i>	5.71	74.62	Pe
Lake bottom in open waters			
Insecta			
Chironomidae	0.93	nd	B
Crustacea			
Ostracoda (<i>Cyprideis salebrosa hartmanni</i> , <i>Limnocythere staplini</i>)	35.19	nd	B
Chydoridae (<i>Leydigia louisii</i>)	28.70	nd	B
<i>Bosmina (Neobosmina) huaronensis</i>	35.19	nd	Pe

Linear regression analyses were carried out to assess if changes in the ratio of benthic/pelagic prey consumed and in the total proportion of prey ingested were related to fish standard length (Gotelli & Ellison 2004).

Strauss' linear electivity index (L) (Strauss 1979) was calculated for each lake zone (pelagic, lake bottom and littoral area) to assess prey preference in each potential foraging area. Strauss' index ranges from -1 to $+1$, with positive values indicating preference and negative values avoidance or inaccessibility. The expected value for random feeding is zero (Strauss 1979).

For all analyses, data were transformed (using log, arc sine or square root transformations) when necessary to achieve normality and/or homocedasticity. All statistical analyses were carried out in R statistical package, version 2.12.1 (R Development Core Team, 2009).

Results

Availability and distribution of potential invertebrate prey across lake areas

The composition of the benthic, littoral and pelagic invertebrate assemblages was the same in lakes Nahuel Rucá (NR) and Hinojales (H) and each lake zone was characterized by specific organisms (Table 1). Lake zooplankton was dominated by small-bodied species in both lakes. For example, *M. micrura* and the cyclopoid copepods (150 and 193 individuals L^{-1} , respectively) dominated the community in summer in

Lake Nahuel Rucá, while the cladocerans *B. huaronensis* (H: 74 individuals L^{-1}) or *Ceriodaphnia dubia* (NR: 104 individuals L^{-1}) predominated in winter.

The littoral assemblage was composed of gastropods (G) (*Heleobia parchappii* (d'Orbigny 1835), *Pomacea canaliculata* (Lamarck 1822), *Uncancylus* sp. and *Physa acuta* Draparnaud, 1805), crustaceans (C) (*Palaemonetes argentinus* (Nobili 1901), *Hyalolella* sp., chydorid cladocerans and ostracods), and insects (I). The species composition did not differ between lakes and showed the same pattern of occurrence ($C > G > I$) (Table 1). In the littoral zone of both lakes, the insect assemblage was dominated by chironomid larvae (contributing 40–90%), the dominant gastropod was *H. parchappii* (66–98%) and the ostracod assemblage was dominated by a large-bodied species, *Chlamydotheca incisa* (Claus 1892), which comprised the 100% of the total ostracods recorded.

In the lake bottom of Nahuel Rucá, only cladocerans, ostracods and chironomid larvae were recorded (Table 1). The ostracod assemblage was composed of small bodied species such as *Limnocythere* and *Cyprideis* which represented the 80% of the total ostracods found. The occurrence of the planktonic species *B. huaronensis* in the bottom samples could be an artifact of the sampler that captured the *Bosmina* individuals that were hidden close to the lake bottom.

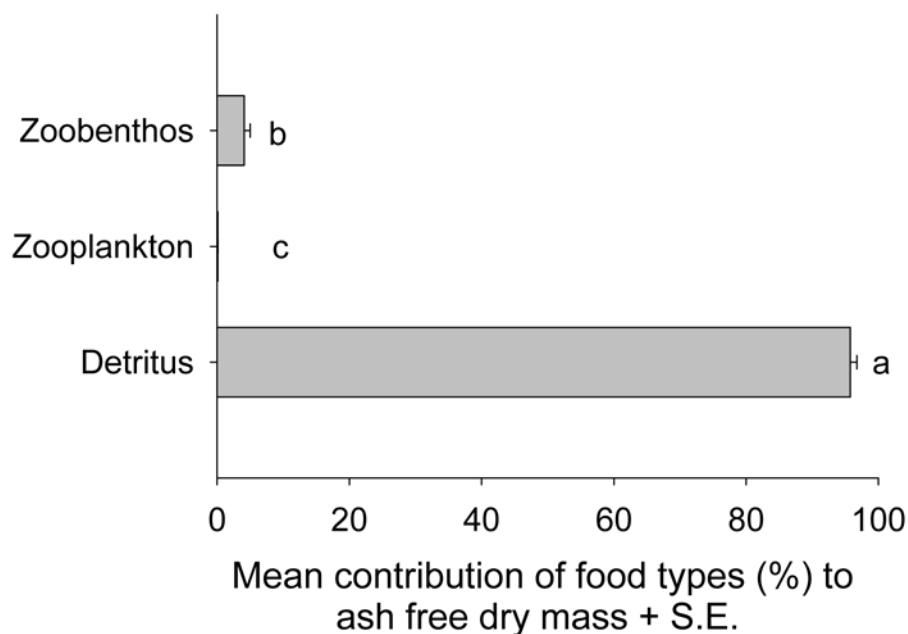


Fig. 1. Mean percent contribution of detritus, benthic invertebrates and zooplankton to the ash free dry mass ingested by *C. voga*. Error bars represent 1 S.E. Letters indicate significant differences among means according to multiple *post hoc* comparisons performed with Tukey HSD test. Significance level was fixed at 0.05.

Contribution of detritus and benthic and pelagic organisms to the total mass ingested

All fish caught, had the whole digestive tract full of food and sediment. Indeed, detritus (95.77%) accounted for the major fraction of the ash-free dry mass in the diet of *C. voga* (One-way ANOVA: $F_{2, 123} = 4458$, $p \ll 0.0001$). Aquatic invertebrates represented a minor fraction and benthic organisms showed a higher contribution to the total mass ingested than zooplankton (4.11% and 0.12%, respectively) (Tukey HSD: $p = 0.0020$) (Fig. 1).

The predominance of benthic versus pelagic prey items was also confirmed when the percentage of abundance was analyzed for each fish population (Table 2). Moreover, no difference in the contribution of benthic or pelagic prey was detected between populations of both lakes or in the composition of the prey assemblage ingested. On the one hand, benthic prey were represented by harpacticoid copepods, chydorid Cladocera, chironomid larvae and several ostracod species in both lakes. The chydorid assemblage was composed of a dominant species, *Leydigia louisii* Jenkins 1934,

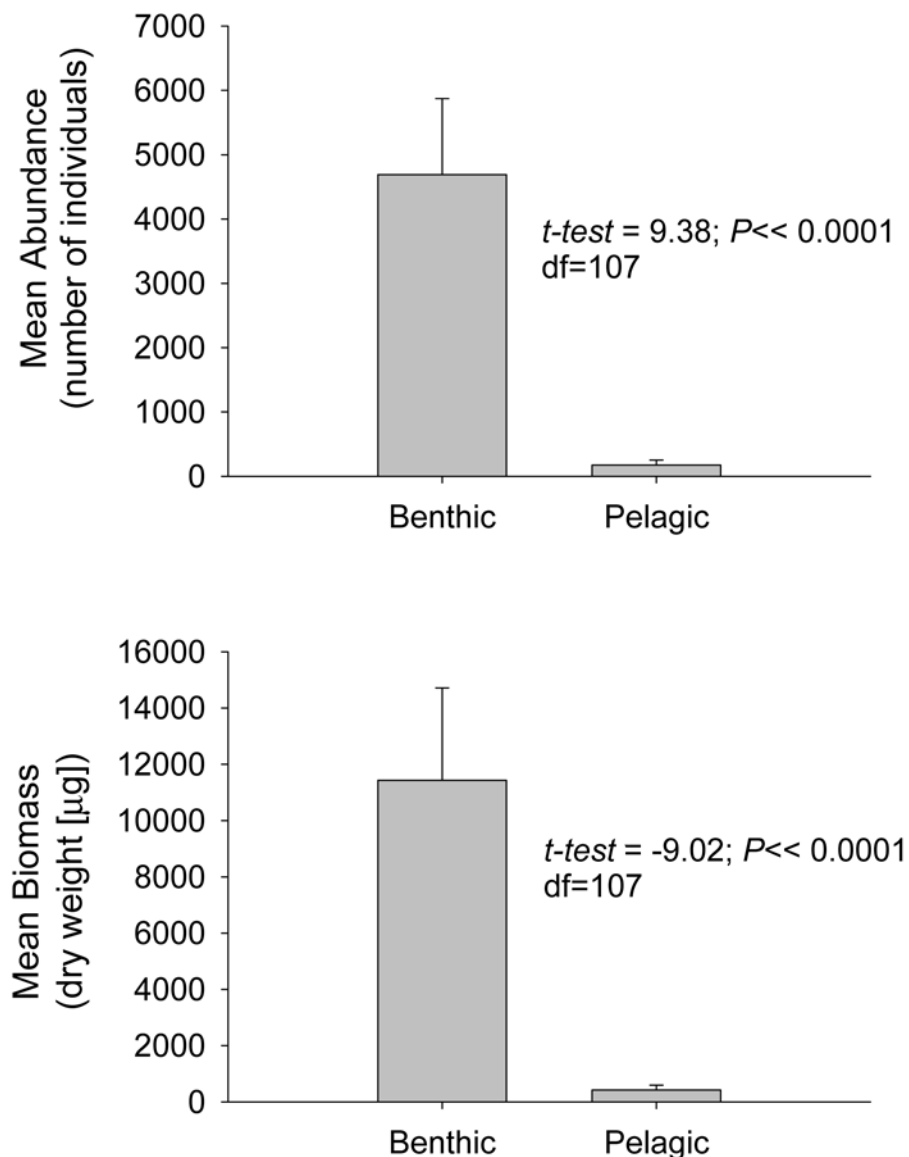
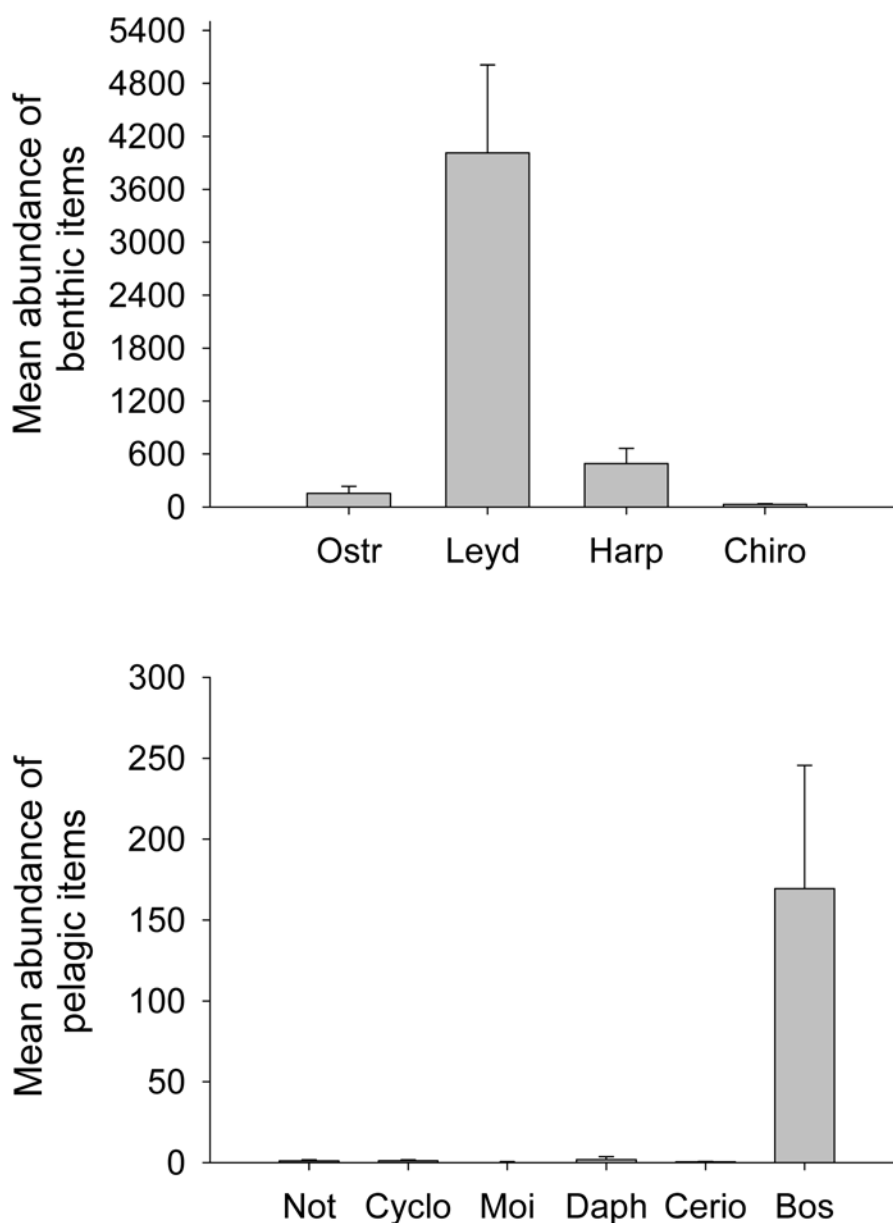


Fig. 2. Mean total abundance (number of individuals) (top) and biomass (as micrograms of dry weight) (bottom) of pelagic and benthic organisms occurring in fish (*C. voga*) digestive tracts. Error bars represent 1 S.E. Significant t- and p-values are shown for the comparison between pelagic and benthic means.

Table 2. Results of *t*-test comparing mean percentage abundances of benthic and/or pelagic items in fish diet within and between lakes Nahuel Rucá and Hinojales. Significant *p*-values are shown in bold.

Comparison	Lake	t-test	df	<i>p</i>
pelagic-pelagic	Nahuel Rucá-Hinojales	0.12	53	0.91
benthic-benthic	Nahuel Rucá-Hinojales	-0.17	53	0.88
benthic-pelagic	Nahuel Rucá	29	82	≤ 0.00001
benthic-pelagic	Hinojales	26.6	24	≤ 0.00001

**Fig. 3.** Mean abundance (number of individuals) of benthic (top) and pelagic (bottom) prey found in *C. voga* digestive tracts. Error bars represent 1 S.E. Bos: *Bosmina (Neobosmina) huaronensis*, Cerio: *Ceriodaphnia dubia*, Chiro: Chironomidae, Cyclo: Cyclopoida, Daph: *Daphnia (Ctenodaphnia) spinulata*, Harp: Harpacticoida, Leyd: *Leydigia louisii*, Moi: *Moina micrura*, Not: *Notodiptomus incompositus*, Ostr: Ostracoda.

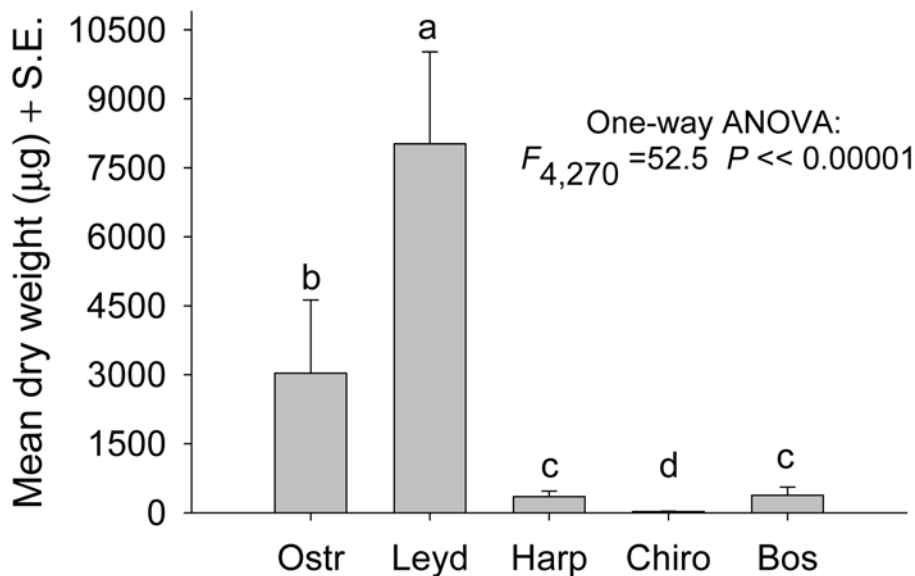


Fig. 4. Mean biomass (as micrograms of dry weight) of pelagic (*Bosmina*) and benthic items occurring in fish (*C. voga*) digestive tracts. Error bars represent 1 S.E. Letters indicate significant differences among means according to multiple *post hoc* comparisons performed with Tukey HSD test. Significance level was fixed at 0.05 in all cases. Bos: *Bosmina* (*Neobosmina*) *huaronensis*, Chiro: Chironomidae, Harp: Harpacticoida, Leyd: *Leydigia lousi*, Ostr: Ostracoda.

and rare species like *Alona* sp. and *Leberis davidi* Richards 1895, which were excluded from the analysis because of their low occurrence. Five species of ostracods were consumed, but *Cyprideis salebrosa hartmanni* Ramírez 1967 and *Limnocythere staplini* Gutentag & Benson 1962 contributed with more than the 80% to the total ostracod prey ingested. On the other hand, the zooplankton assemblage was composed of cyclopod copepods, the calanoid copepod *Notodiaptomus incompositus* (Brian 1925), and the cladocerans *Bosmina* (*Neobosmina*) *huaronensis* Dellachaux 1918, *Ceriodaphnia dubia* Richard 1894, *Daphnia* (*Ctenodaphnia*) *spinulata* Biraben 1917, and *Moina micrura* Kurz 1874. Zooplankton species except *Bosmina* appeared sporadically in the fish tracts and as a consequence the ingested zooplankton was dominated by small-bodied species (*Bosmina* mean size: 0.45 mm).

Total mean abundance and biomass of zoobenthos were several times higher than the contribution of zooplankton (Fig. 2). In both cases, benthic organisms contributed 27 times more to the fish diet than pelagic zooplankton. In particular, the benthic Cladocera *L. lousi* was the most abundant species found in the fish tracts (One-way ANOVA: $F_{4, 270} = 41.4$, $p \ll 0.0001$; Tukey HSD: $p \ll 0.0001$ for all comparisons) (Fig. 3). Moreover, mean abundance of *Leydigia* was at least more than 4 times higher than the rest of the benthic or pelagic items (*Bosmina*) considered in the analysis. Mean abundance of ostracods, harpacticoid

copepods and *B. huaronensis* were similar (Tukey HSD: $p > 0.05$), ranging from 150–460 individuals, and higher than the abundance of chironomid larvae (Tukey HSD: $p \ll 0.05$) (Fig. 3).

Furthermore, mean biomass of the items ingested followed a similar pattern than to mean abundance. The organism that accounted the highest mean biomass was *L. lousi*, followed by the ostracod assemblage (Fig. 4). *Bosmina* (zooplankton) and harpacticoid copepods (zoobenthos) did not differ in biomass contribution, and both were higher than the chironomid larvae biomass (Fig. 4). The same pattern was found for the percentage of biomass ingested by fish in each lake (One-way ANOVA: NR: $F_{4, 205} = 132.9$, $p \ll 0.0001$; H: $F_{4, 60} = 74.5$, $p \ll 0.0001$), again *Leydigia* was the dominant food item, followed by ostracods, *Bosmina* and harpacticoids with intermediate values and chironomids with the lowest contribution.

The study covered wide ranges of fish size (SL: 10–25 cm) and weight (24–551.3 g). Even so, no relationship was found between the biomass and abundance ratio of benthic to pelagic prey ingested and the fish standard length (biomass: $r^2 = 0.05$, $p > 0.11$; abundance: $r^2 = 0.03$, $p = 0.19$). Moreover, the ratio was always higher than 1 and did not change with the fish length (SL), implying that benthic prey were consumed over pelagic ones at all size classes (Fig. 5A). In contrast, the proportion of prey

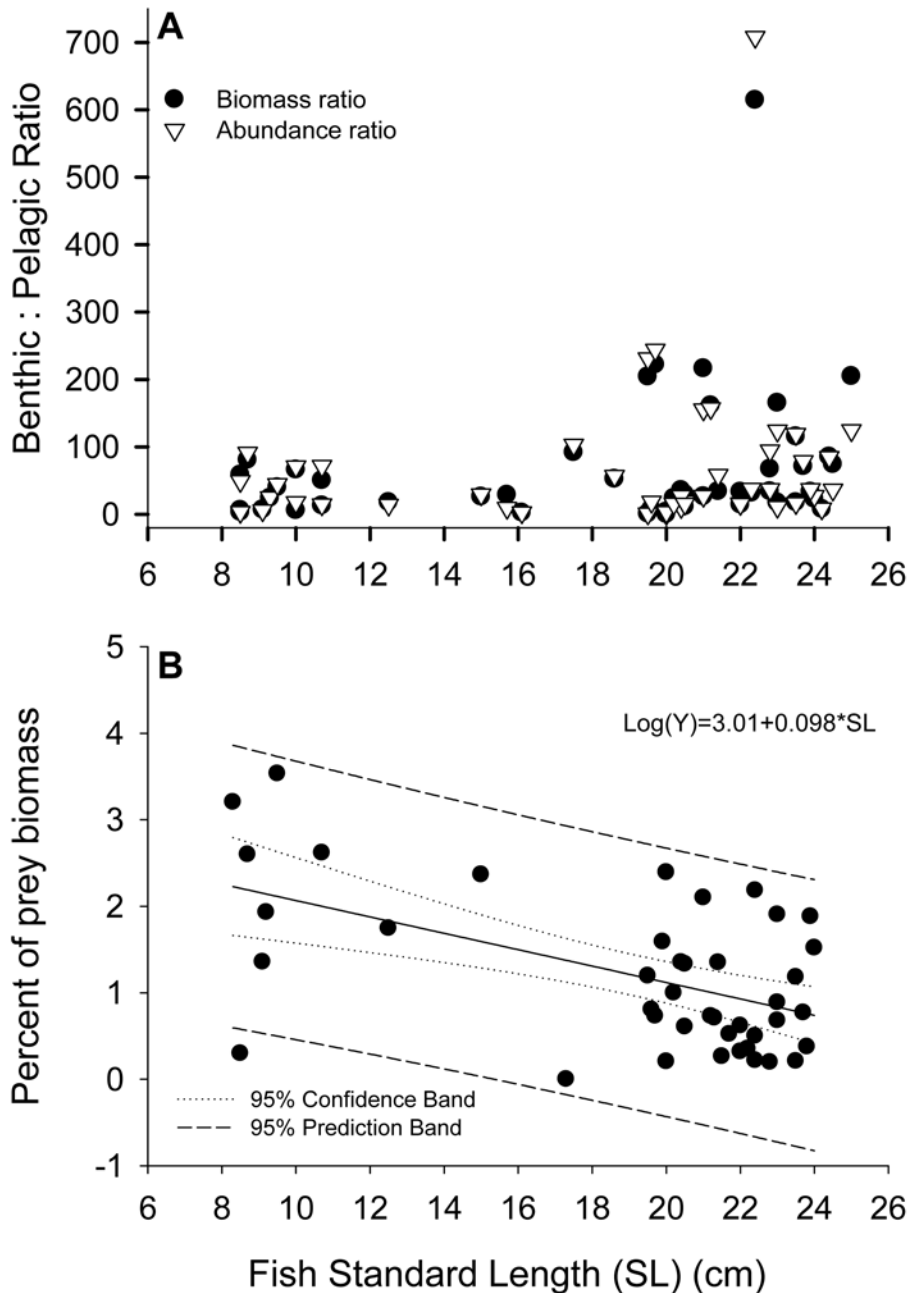


Fig. 5. Ratio of benthic to pelagic biomass and abundance (A) and contribution of total prey consumed (B) in digestive tracts of adults of *C. voga* along the fish size range analyzed (8.5–25 cm of standard length).

ingested decreased as fish became larger (Fig. 5B) ($r^2 = 0.29$, $p = 0.0002$).

Foraging area

Cyphocharax voga had sediment in the digestive tract in all the cases analyzed, accounting for the 56% of the total material ingested. Furthermore, diatoms and plant debris were also recorded, both having low fre-

quency of occurrence. The former, were alive when ingested by fish. The latter, corresponded to decaying macrophyte tissue (*Ceratophyllum demersum* L. spines or seeds, oogonia of charophytes, roots of *Ricciocarpus natans* L.). Alive plants and/or portions of fresh macrophyte tissue were not found in the digestive tracts.

All of the inhabitants of the lake bottom (chytrids, ostracods, chironomids) were recorded in the

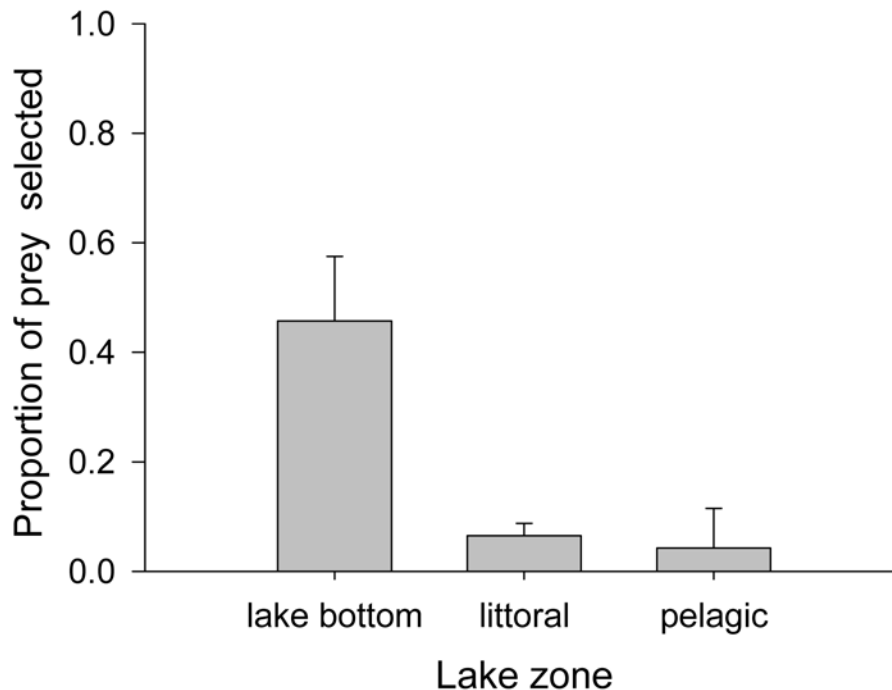


Fig. 6. Mean proportion of selected prey by *C. voga* in the different lake zones (lake bottom, littoral area and open waters) according to Strauss' Linear index.

digestive tracts of *C. voga*. Moreover, the ostracod assemblage eaten by this fish, consisting of *Limnocythere* and *Cyprideis* species, matched with the one recorded in the lake bottom of open water and differed from the littoral ostracod assemblage dominated by *Chlamydotheca* (Table 1).

In addition, Strauss' electivity index (L) showed only positive values (i.e. prey selection) for benthic prey. For example, mean L for *Leydigia* and the harpacticoid copepods occurring in the lake bottom were 0.47 and 0.11, respectively. Electivity values for pelagic preys were negative in all the cases. For prey occurring in the littoral area, all L values were negative except in the case of the benthic *Leydigia* (mean L: 0.74). In accordance with the Strauss' index, the proportion of prey selected in each lake zone was higher in the lake bottom area than in the littoral or the pelagic area (Fig. 6).

Discussion

This study presents evidence showing that adults of *C. voga* depend largely on benthic resources in turbid hypereutrophic shallow lakes. Fish tracts contain high proportions of sediment and detritus and zoobenthos from the lake bottom are selected preferentially. In addition, the similarity of the benthic prey assemblage

in *C. voga* tracts to the one occurring at the lake bottom also supports the dependence of this curimatid on benthic resources. As a consequence, *C. voga* in these hypereutrophic shallow lakes behaves as a detritivorous fish species. Several studies showed the relevance of detritivory as a feeding strategy in the neotropical fish fauna. For example, curimatid related species like *C. nageli* and *C. modestus* have been identified as iliophagous-detritivorous (Vaz et al. 1999, Peretti & Andrian 2004, Roquetti Velludo 2007, Lopes et al. 2009) and previous studies have classified *C. voga* as a detritivorous-iliophagous fish associated with periphyton and phytoplankton consumption (Grossman et al. 1996, Corrêa & Noguez Piedras 2008). In addition, many fish species belonging to the families Prochilodontidae, Curimatidae and Characidae combine the consumption of inorganic sediment and detritus with benthic associated algae and invertebrates (Flecker 1992, Winemiller et al. 2006, Corrêa & Noguez Piedras 2008, Schneider et al. 2011). It has been suggested that detritus alone could not sustain fish growth; whereas the combination of detritus and invertebrates can (Ahlgren 1990, Kim et al. 2007). Many detritivorous species combine the exploitation of detritus, a low quality and abundant resource (in the case of *C. voga* accounting the 95.77% of AFDM), with a less abundant and high quality resource; in this

case, zoobenthos and zooplankton (4.11 % and 0.12 % of AFDM, respectively). Invertebrate prey clearly provide the highest food quality in terms of both protein and energy compared to primary food resources like detritus, macrophytes or algae (Bowen et al. 1995). For example, the elemental composition of zooplankton and chironomids in carbon (C: ~48 % of dry mass) is similar (Sterner & Elser 2002, Frost et al. 2003) and higher than detritus (C: 7–9 % of dry mass in pampean lakes; Córdoba 2012). Thus, the sum of invertebrate prey might represent 19–23 % of the total C consumed by *C. voga* according to the percent of AFDM represented by zooplankton and benthic microinvertebrates. However, the relevance of benthic and pelagic prey could be greater because the efficiency of assimilation for C is higher for invertebrate prey than for detritus (Bowen et al. 1995).

The pattern of species contribution and composition found in the fish diet was the same in both lakes. Benthic organisms (the crustaceans *Leydigia*, ostracods and harpacticoid copepods) and pelagic *Bosmina* accounted in abundance and biomass for 93 % and 7 %, respectively, of the total prey ingested by *C. voga*. Previous studies have related *C. voga* diet with zooplankton consumption (Destefanis & Freyre 1972). Nevertheless, our results clearly indicate that *C. voga* exploits the lake bottom of these shallow lakes. This fact is supported by the high contribution of detritus in the diet, the selection of benthic species, the similarity of the ingested crustacean assemblage (particularly the ostracods) with the lake bottom assemblage and the consumption of zooplankton species associated with the lake bottom (*Bosmina*). Moreover, the prevalence of benthic prey over pelagic ones along the fish size range analyzed (Fig. 5A) also supports the strong preference and association of this fish with the lake bottom. Most fish species experience ontogenetic diet changes that can include shifts in prey preference and also in the foraging area (Rezsú & Specziár 2006). In particular, *C. voga* showed a decline in invertebrate consumption at larger sizes (Fig. 5B), but not in the foraging habitat (lake bottom) neither in its main resource as detritus predominates at all size classes. The reduction in the animal matter consumed and the increment in the detrital material have been documented in other neotropical detritivorous fish species. For instance, *Prochilodus lineatus* (Valenciennes 1837) shifts from zooplankton and phytoplankton, at the juvenile stage, to detritus consumption, at the adult state. This has been related to histological and morphological adaptation of the digestive tract and also with resource availability (Bayo & Cordiviola de Yuan 1996).

Regardless of fish habitat, a wide variety of fish are functionally multi-chain omnivores, deriving energy from both the benthic/littoral periphyton- and phytoplankton-based food webs (Vander Zanden & Vadeboncoeur 2002, Vadeboncoeur et al. 2005). Indeed, *C. voga* should be deriving energy from the benthic food web to a greater extent than from the pelagic food webs. In the first case, energy is obtained through the consumption of detritus and invertebrates and in the last case, through the ingestion of zooplankton species that seek refuge close to the lake bottom (in this study *Bosmina*). Empirical (Jeppesen et al. 2003) and modeling studies showed that top-down control by a 4th trophic level (piscivores) is stronger and more common in mesotrophic lakes, where littoral-benthic and pelagic food webs are coupled and both contribute to the production of higher trophic levels (Vadeboncoeur et al. 2005). As the productivity increases, the top-down control is exerted by the 3rd level (planktivorous fish) due to reduced visibility (Vadeboncoeur et al. 2005). Turbid lakes are a common feature of the Pampa Plain (Quirós et al. 2002, Kosten et al. 2012) and the zooplankton is dominated by medium to small sized species (Quirós et al. 2002, González Sagrario & Balseiro 2010). In lakes having a Secchi disc depth of 20–30 cm prey detection for fish is difficult. Despite this, *C. voga* preyed on a very small species like *B. huaronensis* (0.45 mm) and *Leydigia louisii* (0.74 mm), which constitute high quality prey in terms of C:P ratios (Sterner & Elser 2002). Indeed, *C. voga* consumes small herbivores and detritus, and avoids fast-moving copepods like other benthic filter feeders in turbid lakes (Clupeids and Cyprinids) or in the tropics (Chiclids) (Drenner & McComas 1980). Recently, it has been emphasized that predator foraging type has strong effects on food webs and is the major controlling factor of food web topology (Lazzaro et al. 2009). In particular, it has been demonstrated that the detritivorous *D. cepedianum* induced more richness of edible phytoplankton, and higher connectance and omnivory in the food web than the visual feeder *Leponis macrochirus* Rafinesque 1819 (Lazzaro et al. 2009).

New evidence has demonstrated that fish detritivory and omnivory is more widespread at lower latitudes and in warmer ecosystems (Lazzaro et al. 2003, Teixeira de Mello et al. 2009, González-Bergonzoni et al. 2012). For instance, detritivorous fish can comprise over 50 % of the fish community in subtropical and tropical lotic system in South America (Araujo-Lima et al. 1986, Fugi et al. 1996, Lopes et al. 2009), influencing ecosystem processes and functioning (Flecker 1996, Winemiller et al. 2006). In addition, fish spe-

cies replacement has been reported along a productivity gradient; for example, shifting from Centrarchids (visual feeder) to Clupeids (benthic filter feeders) in lakes of Central and Southeastern USA (Vanni et al. 2005). In agreement with these patterns, obligate piscivores and planktivores are less frequent in eutrophic pampean lakes and most of the fish species showed links between the pelagic and littoral (*O. bonariensis* and *O. jenynsii*, *R. quelen*) or the benthic (*C. voga*, *R. quelen*) food webs, suggesting that omnivory and detritivory is widely extended (La Sala 2012, Rodríguez Golpe 2012).

Fish effects on ecosystem functioning are not only related to prey consumption. Fish can forage in one habitat and excrete in another, thus translocate nutrients and affect the phytoplankton community structure by altering the supply rates and ratios of limiting nutrients (Attayde & Hansson 2001, Sereda et al. 2008). In particular, detritivorous fish can translocate nutrients from the benthos to the pelagic zone, and may play a large role in driving food web dynamics. For example, when gizzard shad relies on detritus it can sustain an important proportion of the primary production in reservoirs of Midwestern USA (Higgins et al. 2006, Vanni et al. 2006). Similarly, phytoplankton biomass in Brazilian reservoirs was related to fish guild structure more than fish species (Lazzaro et al. 2003). It has been demonstrated that chlorophyll concentration increased with the relative biomass of fish, showing that the predominance of omnivorous and detritivorous fish regulates algae (Lazzaro et al. 2003). Consequently, the detritus pathway 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). Indeed, detritivorous fish are theorized to increase ecosystem resilience, especially in productive systems, because they can stabilize or enhance productivity by relying on the detrital subsidy (Schaus et al. 2002). *C. voga* depends on detritus plus invertebrates, reaching a high biomass in warm temperate turbid lakes; thus, we hypothesize that this fish could have a high impact on ecosystem functioning, contributing to the dissolved nutrient pool of the water column and enhancing phytoplankton development. Therefore, the dominance of *C. voga* in turbid lakes might change food web topology by coupling lake habitats mainly through the consumption of the benthic pathway and the translocation of nutrients to the pelagic zone. In conclusion, shallow lakes are com-

plex systems where interactions among the pelagic, benthic and littoral areas are strong. The inclusion of the benthic pathway and detritivorous fish in food web analysis will provide a more realistic energy flow template for understanding lake ecosystem functioning. Therefore, future studies focused on the translocation of benthic-borne nutrients by *C. voga* and its contribution to phytoplankton promotion are encouraged because it is necessary to understand the impact of this fish in warm temperate lakes and to compare its relevance with other detritivorous fish species.

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