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Impact of fish introduction on planktonic food webs in lakes of the Patagonian Plateau

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ABSTRACT

Patagonia fishless ponds have been stocked with fishes for recreational purposes since early in the 20th century. We carried out a summer plankton sampling in 18 Patagonian lakes; 12 fishless, 5 with introduced fishes and 1 with endemic fish fauna. The lakes are situated on a latitudinal gradient from 39° to 49°S. Zooplankton and phytoplankton composition, phytoplankton relative abundance, and zooplankton body size and mouthpart morphology were analyzed. Results showed differences between lakes with and without fishes; in the presence of fish zooplankton size spectrum tended to be narrower because of the disappearance of *Daphnia* and large centropagid copepods. Zooplankton composition changed: centropagid species richness decreased and rotifers dominated. Contrarily, in fishless lakes 3 or 4 centropagid species, differing markedly in body size and exploiting different food niches, were observed co-occurring. These changes in zooplankton seemed to cascade down to phytoplankton. Fish introduction increased the phytoplankton similarity in lakes even belonging to different basins in a latitudinal gradient. Indeed, cyanobacteria dominated only in lakes with introduced fishes. Probably the elimination of *Daphnia* favored cyanobacteria proliferation due to nutrient rebalance. As a consequence, water quality decreases and the value of sport fisheries is reduced. Fish introduction in Patagonia is a practice that should be re-evaluated by governments and NGOs due to its potentially negative impact on lakes and local economies.

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1. Introduction

Biological invasions have long been recognized as a threat to the biodiversity since invaders may alter both direct and indirect interactions among populations and even induce trophic cascades (Simon and Townsend, 2003). The understanding of population biology of invaders and the effect of introduced species is necessary for constructing a robust theory of invasion biology that would provide a basis for rational decisions

about species introduction and eradication efforts (Townsend, 1996; Simberloff, 2003).

The introduction of salmonids in lakes and rivers of Patagonia, the southernmost region of South America, started early in the 20th century (Macchi et al., 1999). In Argentinean Patagonia, rainbow trout (*Oncorhynchus mykiss*) is the most widely distributed salmonid species (Pascual et al., 2002). In addition, during the 60s, native fishes (*Percichthys trucha* and *Odonthestes bonariensis*) were also introduced to fishless lakes

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(Marcolín et al., 1968; Quirós and Baigún, 1986; Quirós, 1990). Unfortunately, very few data were available on food web structure before these practices began. The Patagonian Plateau region is unfavorable for lake development (Iriando, 1989); thus the few existing lakes belong to isolated basins.

Visual planktivores can change size structure and species composition of freshwater zooplankton communities (Gliwicz and Pijanowska, 1989). Predation on native fauna by introduced trout frequently causes ecological changes, including the elimination of amphibian and reptile populations (Tyler et al., 1998; Knapp, 2005) and changes in zooplankton and benthic macroinvertebrate species composition and size structure (Anderson, 1980; Knapp et al., 2001). Previous studies in Patagonian lakes have referred to a strong effect on zooplankton body size, with a narrower spectrum in lakes with fish introductions (Modenutti and Balseiro, 1994). Also fishes may compete for food with avian fauna, thus flamingos are usually absent or scarce in Andean lakes with fish (Hurlbert et al., 1986). Recently, negative effects on swan and coot populations were observed in a Patagonian lake with introduced fishes (Ortubay et al., 2006). On the other hand, fish predation can exert a trophic cascade down to lower trophic levels as they can indirectly increase phytoplankton biomass by reducing zooplankton grazing pressure (Carpenter and Kitchell, 1993; Attayde and Hansson, 2001; Khan et al., 2003).

Zooplankton assemblages in Patagonian Plateau lakes are dominated by endemic calanoid copepods, particularly centropagids of the genera *Boeckella* and *Parabrotheas* (Modenutti and Balseiro, 1994; Diéguez and Balseiro, 1998; Menu-Marque et al., 2000). Twelve species of *Boeckella* are reported in these shallow lakes that represent reservoirs of the biodiversity of this assemblage (Menu-Marque et al., 2000). The regional distinctiveness of biological communities reflects historical factors that have restricted species ranges via physical isolation, ecological interactions and evolutionary diversification (Huston, 1994). Biotic exchange with the introduction of non-indigenous species has been dramatically accelerated by humans in historical times being an important mechanism of biotic homogenization (Olden and Poff, 2004). Biotic homogenization is an increase in species similarity among a set of communities through time (Beissner et al., 2003). Based on these ideas we hypothesize that fish introduction in Patagonia leads to increase plankton similarity as a consequence of the loss of large species due to the introduction of visual predators. Thus, the main objective of the present study is to analyze Patagonian planktonic food web structure of fishless lakes and lakes with introduced fishes along a latitudinal gradient from 39° to 49°S.

2. Study area

The study was carried out in 18 Patagonian lakes located between 38°58'–48°51'S and 68°20'–71°03'W. The climate is dry and cold with strong westerly winds, resulting in severe aeolian erosion (Iriando, 1989). The lakes belong to 4 areas: [1] Northern area of Laguna Blanca and surroundings (39°S and 70°W), [2] Central area of the *Nothofagus* forest-Patagonian steppe ecotone (41°S and 71°W), [3] Central steppe area (41°S and 68°W) and [4] Southern area in Santa Cruz province

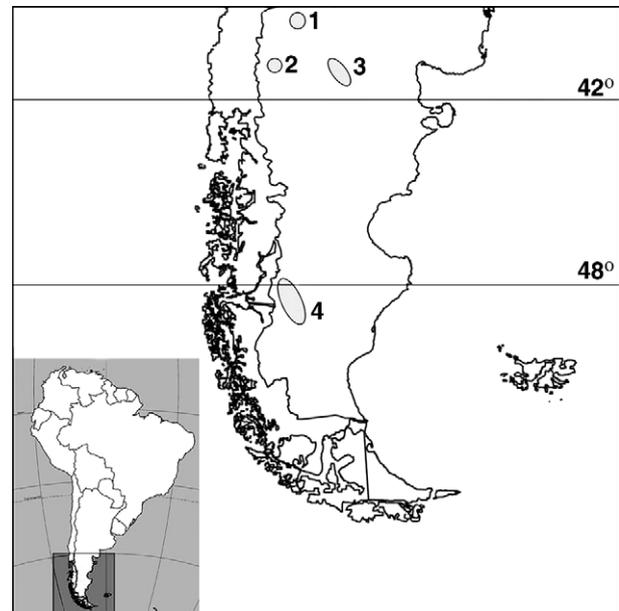


Fig. 1 – Map of the Patagonian Region. 1–4 represent the sampling areas (39°–49°S): [1] Northern area of Laguna Blanca and surroundings (lakes: Blanca, Jabón and El Burro), [2] Central area of the *Nothofagus* forest-Patagonian steppe ecotone (lakes: El Chanco and Los Juncos), [3] Central steppe area (lakes: Ñe Luan, Carrilauquen Chica, Carrilauquen Grande and NF1) and [4] Southern area in Santa Cruz province (lakes: Cardiel, Del Mie, Volcán 2, Volcán 3, Volcán 4, P. Moreno 1, P. Moreno 2, P. Moreno 3 and P. Moreno 4). Lakes with fish are indicated in bold letters.

(49°S and 72°W) (Fig. 1). The region is a steppe with small-leaved shrubs and the mean annual precipitation varies between 400 mm in [2], 200 mm in [1] and [4] and less than 150 mm in [3] (Paruelo et al., 1998). The lakes are shallow, and in most cases the maximum depths are less than 12 m. Carrilauquen Chica has a maximum depth of 8 m, Carrilauquen Grande 8.5 m, Ñe-Luan 10 m, Del Mie 2 m, Laguna Blanca 12 m, Jabón 4 m and El Chanco and El Burro 2 m; the other lakes lack bathymetric maps. On the contrary, Lake Cardiel is a deep lake with a maximum depth of 76 m. Twelve of the studied lakes are fishless. The other six lakes have fishes, Lake Del Mie has *Galaxias platei*, a native fish species (Milano, 2003), and the other five lakes contain introduced fish species. Carrilauquen Grande, Carrilauquen Chica, Ñe Luan and Cardiel lakes were stocked with salmonids, mainly *O. mykiss* during the first half of 20th century (Pascual et al., 2002). Laguna Blanca was a fishless lake until the 60s when the indigenous fishes *Percichthys colhuapiensis*, *P. trucha* and exotic salmonids were introduced. Lakes with fish will hereafter be indicated in bold letters.

3. Methods

Fieldwork was carried out during summers (February) 2001–2004, and the lakes were sampled at midday. All lakes were sampled in at least two different summer seasons. Zooplankton samples were collected with a 25 cm diameter and 55 µm-mesh-plankton net and two or more horizontal tows of 10 m

were made in the central area of the lake. The tows were pooled into one sample and preserved in 4% formalin solution. Water samples for phytoplankton quantification were collected subsuperficially (0.5 m depth) with a Ruttner bottle from 10 lakes, five with fishes (Blanca, Carrilauquen Grande, Carrilauquen Chica, Ñe Luan and Del Mie lakes) and five without fish (El Burro, Jabón, Volcán 2, 3 and 4). Unfortunately, in the case of Lake Cardiel the phytoplankton sample was collected with a net mesh of 55 μm , thus we only obtained net phytoplankton. Phytoplankton samples were preserved in acid Lugol solution, and were quantified under an inverted microscope following Utermöhl (1958). Algal cells were identified to the lowest possible taxonomic category (genus or species), then were assigned to the following groups: Cyanophyceae, Chlorophyceae (Chlorococcales), Cryptophyceae + flagellated Chrysophyceae (<20 μm), and others (mainly Bacillariophyceae, Chlorophyceae Zygnematales and

Euglenophyceae). Biovolumes were calculated applying Sun and Liu (2003) geometric models based on measurements of at least 30 algal cells of each species. In the analysis of phytoplankton biovolume the order Zygnematales was considered separately (Chlorophyceae Zygnematales) due to their high relative contribution to total biovolume.

In the laboratory, zooplankton species were identified and measured. Crustaceans were quantified under stereomicroscope in 5 ml Bogorov chambers, and rotifers in 1 ml Sedgwick–Rafter chambers under a direct microscope. At least 60 individuals of each abundant species and all individuals of rare species were measured under an Olympus SZX9 stereomicroscope at 12–50 \times magnification. Body size was considered as follows: for cladocerans, linear dimension from the top of the head shield to the base of the caudal spine; for copepods, the total body length from the anterior extremity of cephalothorax to the tips of the furcal rami (without setae);

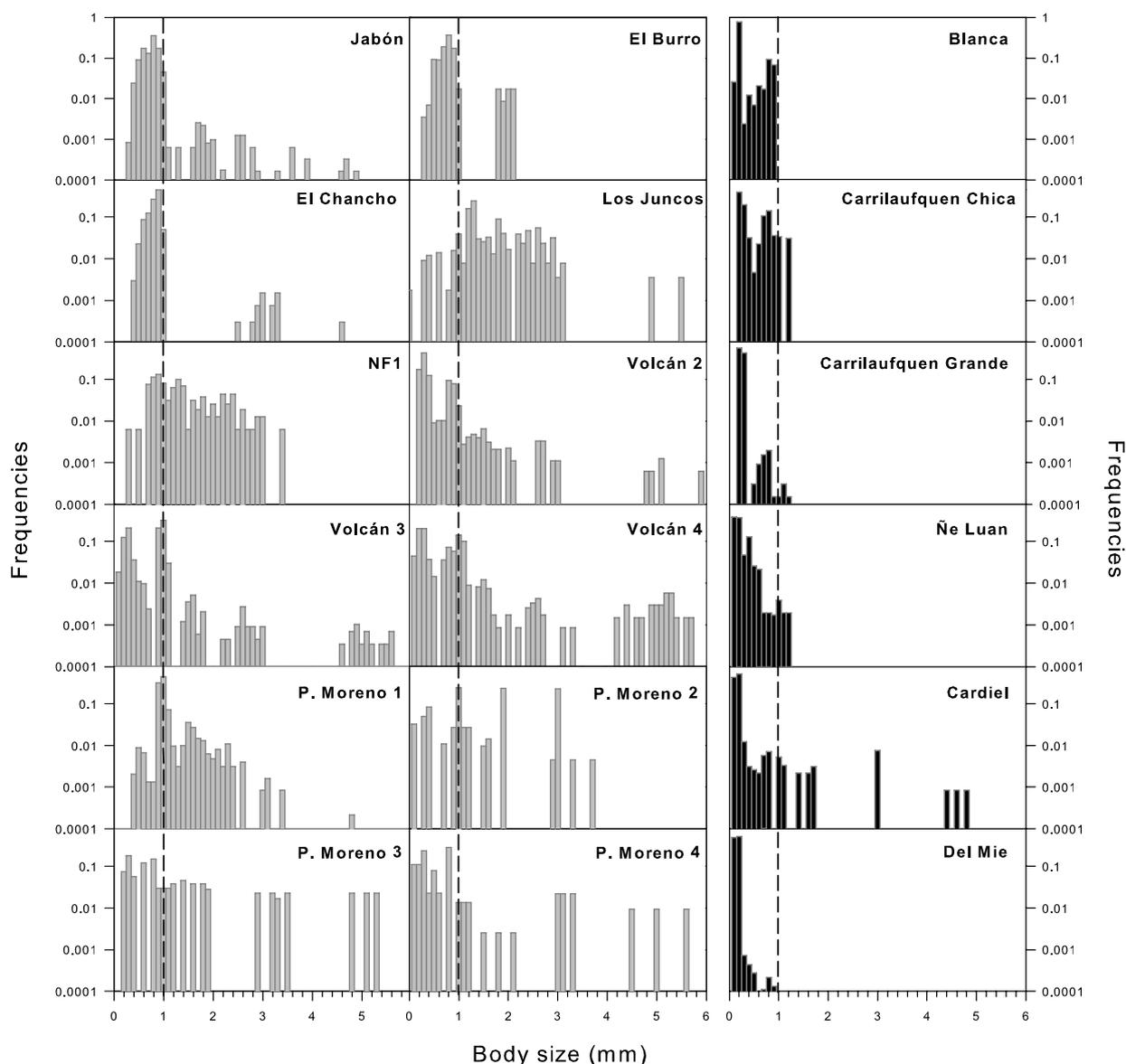


Fig. 2 – Zooplankton size spectrum obtained for lakes without fish (grey bars) and lakes with fishes (black bars). Vertical dashed lines indicate 1 mm body size.

and for rotifers, the total body of lorica length without spines. The proportion of each species or size within species (different instars of copepods) was estimated for each sample.

In order to study the relationship between centropagid mouthpart structure and feeding mode, several adult females and males of each species were analyzed. Mandibles and maxillipeds were dissected and observed under a direct microscope Olympus BX50 and images were digitalized using an image analyzer (Image Pro, Media Cybernetics). Mandible (Md) as the total length of the cutting edge, and total length of maxillipeds (Mxp), were measured.

Levels of significance of differences were tested with parametric and non-parametric tests (ANOVA, and Mann–Whitney test). Homoscedasticity and normality were tested when required. All statistical analyses were performed with SigmaStat 3.01 statistical package. The similarity between different lakes was estimated through a hierarchical cluster analysis based on binary data (presence–absence) in the case of crustacean zooplankton species. In the case of phytoplankton, the relative abundance of the different groups was estimated in the same way. Biota distance was estimated through Euclidean distances and clusters were constructed with an unweighted pair-group average (UPGMA). Analyses were performed with Statistica.

4. Results

In the whole data set of 18 Patagonian lakes we recorded a broad spectrum of zooplankton sizes, ranging from 0.1 mm

for the rotifer *Keratella cochlearis* and copepod nauplii, to 6.3 mm for the centropagid copepod *Parabroteas sarsi* adults. The complete spectrum was attained only in fishless lakes (Fig. 2). Lakes with fishes showed a narrower size distribution, with the dominance of small-sized zooplankton (less than 1 mm). We observed significant differences between fish and fishless lakes in the number of classes over 1 mm with values larger than 0 (Mann–Whitney, $P < 0.001$). Among lakes with fish, **Del Mie** is the only lake with endemic fish fauna, whereas the others were stocked with a mixed assemblage including exotic and native fishes with different success (Table 1). Considering the time of introduction, Lake **Laguna Blanca** represents the most recently manipulated lake, while both **Carrilauquen** lakes represent the least recently manipulated ones. Regarding fish fauna and time of introduction in each lake (Table 1), no remarkable differences in size spectra were observed between shallow lakes with native (**Del Mie**) and introduced fishes (Fig. 2).

Zooplankton community structure differed markedly between lakes with and without fishes. Fishless lakes were dominated by crustaceans, in particular calanoid copepods. A total of 8 centropagid species were recorded including the large *P. sarsi* and 7 *Boeckella*. All fishless lakes, except NF1, contained at least two or more species of co-existing centropagid copepods (Fig. 3, see numbers at the bottom of the figure). Most of these lakes contained the largest copepod, *P. sarsi*, since it was present in 8 of the 13 fishless environments sampled. On the contrary, each lake with fishes contained only one species of *Boeckella*, and no centropagid copepods were

Table 1 – Fish fauna and zooplankton and phytoplankton dominant species in the six lakes with fishes

	Fish species	Year of introduction	Zooplankton dominant species	Phytoplankton dominant species
<i>Lakes with introduced fishes</i>				
Blanca	* <i>Percichthys colhuapiensis</i> <i>Percichthys trucha</i> <i>Salmo trutta</i> <i>Oncorhynchus mykiss</i> ⁽²⁾	1968/70	<i>B. caudatus</i> <i>Pompholix sulcata</i>	<i>Aphanocapsa delicatissima</i> West, W. and G.S.
Ñe Luan	* <i>Oncorhynchus mykiss</i> <i>Odontheistes bonariensis</i> <i>O. hatcheri</i> ⁽¹⁾	1940s 1978/79	<i>B. angularis</i>	<i>Microcystis aeruginosa</i> Kütz.
Carrilauquen Grande	* <i>Oncorhynchus mykiss</i> <i>Odontheistes bonariensis</i> <i>O. hatcheri</i> ⁽¹⁾	1905 1978/79	<i>Keratella tropica</i> <i>Pompholix sulcata</i> <i>B. calyciflorus</i>	<i>Oscillatoria tenuis</i> Ag.
Carrilauquen Chica	* <i>Oncorhynchus mykiss</i> <i>Odontheistes bonariensis</i> <i>O. hatcheri</i> ⁽¹⁾	1905 1978/79	<i>Brachionus calyciflorus</i> <i>B. caudatus</i> <i>Asplanchna brightwelli</i>	<i>Oscillatoria tenuis</i> Ag.
Cardiel	<i>Oncorhynchus mykiss</i> <i>Salvelinus fontinalis</i> ⁽³⁾	1947	<i>Keratella cochlearis</i> <i>Colurella</i> sp. <i>Lecane</i> (L.) sp.	<i>Anabaena flos-aquae</i> (Lyngb.) Bréb. <i>Oscillatoria</i> spp.
<i>Lake with native fish</i>				
Del Mie	<i>Galaxias platei</i> ⁽⁴⁾	Native	<i>K. cochlearis</i> <i>Notholca acuminata</i> <i>Filinia longiseta</i> <i>Polyarthra vulgaris</i>	<i>Pediastrum boryanum</i> (Turp.) Menegh.

References: * indicates the dominant fish species in each lake. Literature source: (1) Quirós and Baigún (1986); (2) Ortubay et al. (2006); (3) Pascual et al. (2002); (4) Milano (2003).

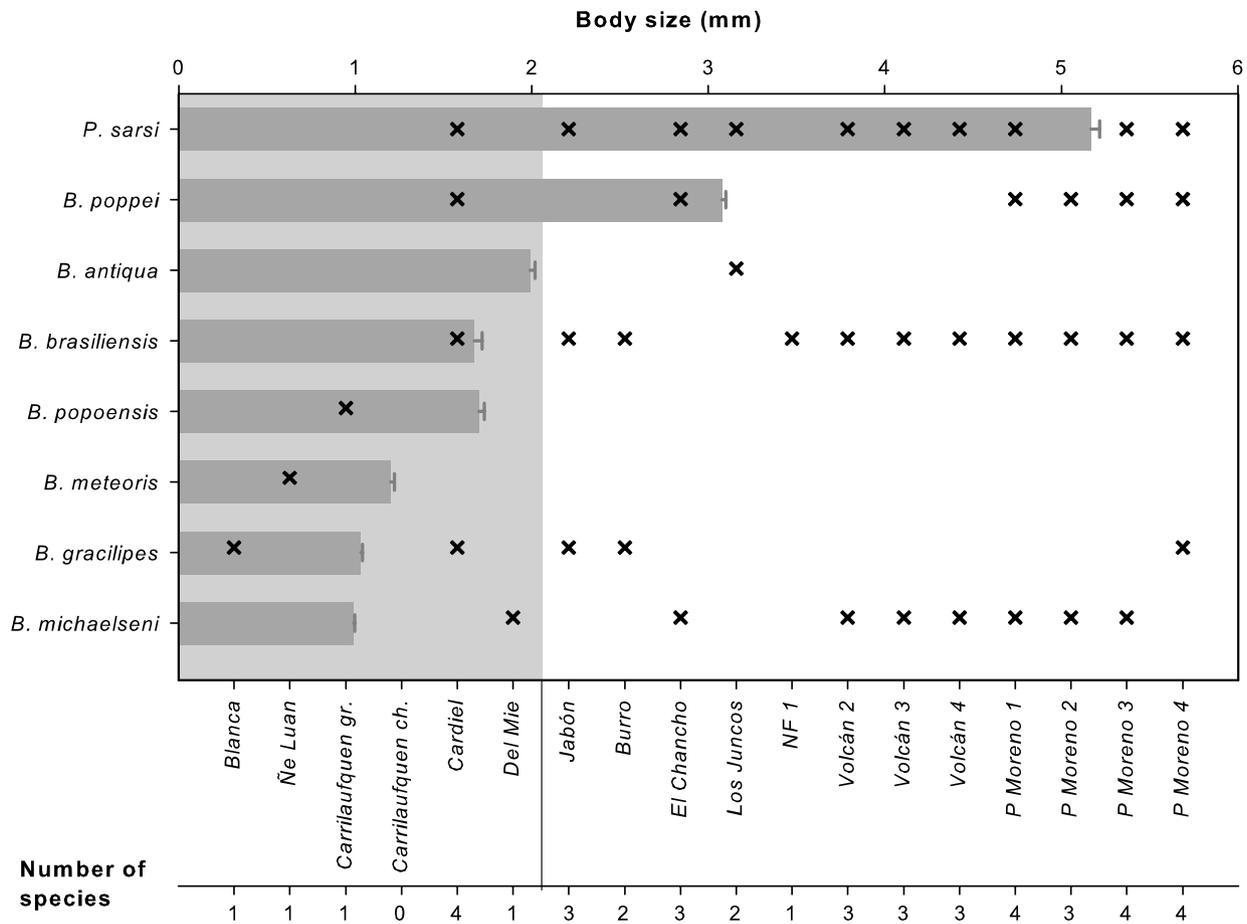


Fig. 3 – Presence (x) of the different centropagid species in lakes. Shaded area indicates lakes with fishes. Grey horizontal bars indicate species body size (upper scale, mean ± standard error). Numbers at the bottom indicate centropagid species richness in each lake.

recorded in Lake Carrilauquen Chica. A particular case was the deep Lake Cardiel which presented 4 centropagid copepods (3 *Boeckella* species and *P. sarsi*) though in very low relative abundances (pooled copepod relative abundances <15% of total zooplankton abundances). Centropagid copepods constitute a size gradient (Fig. 3, grey bars). In lakes with fish, copepods hardly exceeded 1 mm, with the exception of Lake Cardiel (Fig. 4a). On the other hand, copepod sizes in fishless lakes ranged from <1 mm up to values >5 mm (Fig. 4a). The difference in maximum copepod sizes between fish and fishless lakes was significant (Mann–Whitney, $P = 0.005$). The variation observed in copepod size may imply the coexistence of different feeding groups within this assemblage. We observed significant differences in mandible and maxilliped sizes (one way ANOVA, $P < 0.001$). The small *Boeckella gracilipes* and *B. michaelseni* exhibited a very small size of the mandibles and maxillipeds constituting a homogenous group (Fig. 4b, Tukey test, $P > 0.05$). These two species feed on particles <50 μm (Balseiro et al., 2001; Modenutti et al., 2003) and were never found together, but almost all lakes contained one of them (Fig. 3). The other centropagid species all displayed significant differences amongst themselves and with the *B. gracilipes*–*B. michaelseni* group (Fig. 4b, Tukey test, $P < 0.001$). *P. sarsi* is carnivorous preying on rotifers and small copepods and cladocerans (<1.6 mm) (Heywood, 1970; Balseiro and Vega, 1994;

Diéguez and Balseiro, 1998). Finally, *B. poppei*, *B. antiqua* and *B. brasiliensis*, although herbivores, can access large food items like diatoms and chlorophytes (50–150 μm) (Weller, 1977, and own observations). In addition, differences in their mouthpart sizes (Fig. 4b) may indicate that these species would exploit a different fraction of this resource, *B. poppei* being the species which accesses with larger food items.

Difference in maximum cladoceran body size between fish and fishless lakes was significant (Mann–Whitney, $P = 0.017$). In fishless lakes, three large *Daphnia* species were recorded (*D. dadayana*, *D. commutata* (*D. obtusa* group sensu Benzie, 2005), and *Daphnia* sp.) driving the size spectra of cladocera to sizes that ranged between ~2 mm and 3.5 mm (Fig. 5). These cladocerans were completely absent in all lakes with fishes and in two fishless lakes (El Burro and P. Moreno 4). In these lakes, the presence of smaller cladocerans such as *Ceriodaphnia dubia* and *Bosmina longirostris* were observed, and cladocera size spectra dropped down to less than 1 mm (around 0.5 mm) (Fig. 5).

We observed that shallow lakes with introduced fishes were very similar in the crustacean assemblage with the loss of large-sized species. Cluster analysis showed three groups: one (I) corresponded to shallow lakes with introduced fishes (Carrilauquen Grande, Carrilauquen Chica, Ñe Luan and Blanca), a second one (II) includes two fishless lakes: El Burro

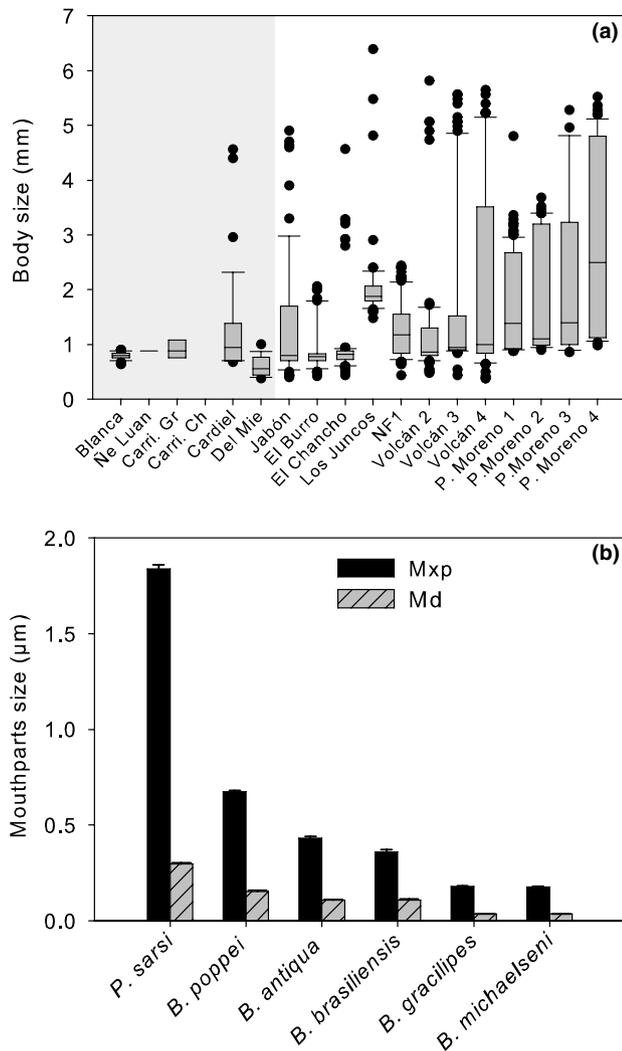


Fig. 4 – Centropagid assemblages in Patagonian lakes: a. Body size (mm) in lakes with fishes (shaded area) and fishless lakes. Median, quartiles and data outside the 10th and 90th percentiles are indicated. b. Mandible (Md) and maxilliped (Mxp) sizes (µm, mean ± standard error).

and NF1, and finally, the third group (III) included ten fishless lakes and two lakes with fish: the deep lake Cardiel and the lake with endemic fish fauna (Del Mie) (Fig. 6).

Smaller zooplankton, like rotifers, showed an opposite trend to that of crustaceans. In lakes with fish, rotifers dominated the zooplankton (Table 1) and showed an increase in species number (2–3 species in fishless lakes up to 9 in fish lakes) and in relative abundance (10% of total abundance in fishless lakes up to 90% in lakes with fish). In environments with fish the rotifer assemblage was represented mainly by filter-feeders Brachionidae such as *K. cochlearis*, *Notholca acuminata*, *Brachionus angularis*, *B. caudatus* and *B. calyciflorus*, while Lake Carrillaufquen Chica was the only environment where the predaceous rotifer *Asplanchna brightwelli* was recorded (Table 1).

Contrasting phytoplankton abundance and structure was observed between lakes with and without fish (Fig. 7a and b). Lakes with fish showed higher abundances of the net phytoplankton fraction while fishless lakes exhibited a compara-

tively greater relative importance of nanoplankton (Table 2). Lakes with fishes exhibited nano:net ratios less than 0.5 (Table 2) and the difference, when comparing with fishless lakes, was significant (one way ANOVA, $P = 0.001$). In addition, we found some important differences in phytoplankton composition among lakes. In lakes with introduced fishes phytoplankton was monopolized by cyanobacteria (Cyanophyceae) both in terms of abundance (>90% of total cell abundance, Fig. 7a) and biovolume (>45% of total biovolume, Fig. 7b). Three fish lakes (Carrillaufquen Grande, Carrillaufquen Chica and Cardiel) were dominated by filamentous species (Table 1). In Lake Del Mie, the one with native fish (*Galaxias platei*), net phytoplankton also prevailed (Fig. 7a and b), but chlorophyceans (Chlorococcales) instead of cyanobacteria dominated the assemblage (Table 1). In fishless lakes cyanobacteria never dominated (Fig. 7a and b). This result was confirmed by the hierarchical cluster analysis based on relative abundances of the different phytoplankton groups. Dendrogram showed two groups: one (I) corresponds to lakes with introduced fishes (Carrillaufquen Grande, Carrillaufquen Chica, Ñe Luan, Blanca and Cardiel) and the other (II) included fishless lakes and the lake with endemic fish fauna (Del Mie) (Fig. 8). This result indicates that fish introduction may increase the phytoplankton similarity in lakes even belonging to different basins on a latitudinal gradient.

5. Discussion

Size-selective predators have been shown to favor small-bodied zooplankton through suppression of competitors or intermediate predators (Brooks and Dodson, 1965; Dodson, 1974; Hall et al., 1976; Vanni, 1988; Carpenter and Kitchell, 1993). In Patagonian shallow lakes, the zooplankton community may change dramatically when fish are present, in that rotifers dominated both in species number and abundance. The absence of invertebrate predators (*P. sarsi*) and large competitors such as *Daphnia* may account for the success of this small filter-feeder group. Although we have not carried out manipulative experiments the few data on zooplankton structure previous to fish introduction support our observations. Marcolín et al. (1968) indicated the presence of large centropagids such as *P. sarsi* and *Boeckella brasiliensis* in Laguna Blanca before fish introduction. Nowadays, these two species no longer exist in Laguna Blanca, though they remain in the nearby ponds Jabón and El Burro.

In fishless lakes co-occurring centropagid species differed markedly in body and mouthpart sizes; allowing the coexistence of species that may exploit different food items. Coexistence of similar species will occur only if they are of sufficiently different sizes such that there is no overlap in their diets (Hutchinson, 1951). This assumption is reliable for the centropagid assemblages of Patagonia, since only species with different size were observed in the same environment (Fig. 3). On the contrary, the coexistence of large *Daphnia* with this assemblage (Fig. 5) would be consistent with a weak competition for food resources since large *Daphnia* and *Boeckella* species have a low food niche overlap (Modenutti et al., 2003).

The loss of distinctive crustacean assemblages and the increase in similarity within shallow lakes with fish seemed

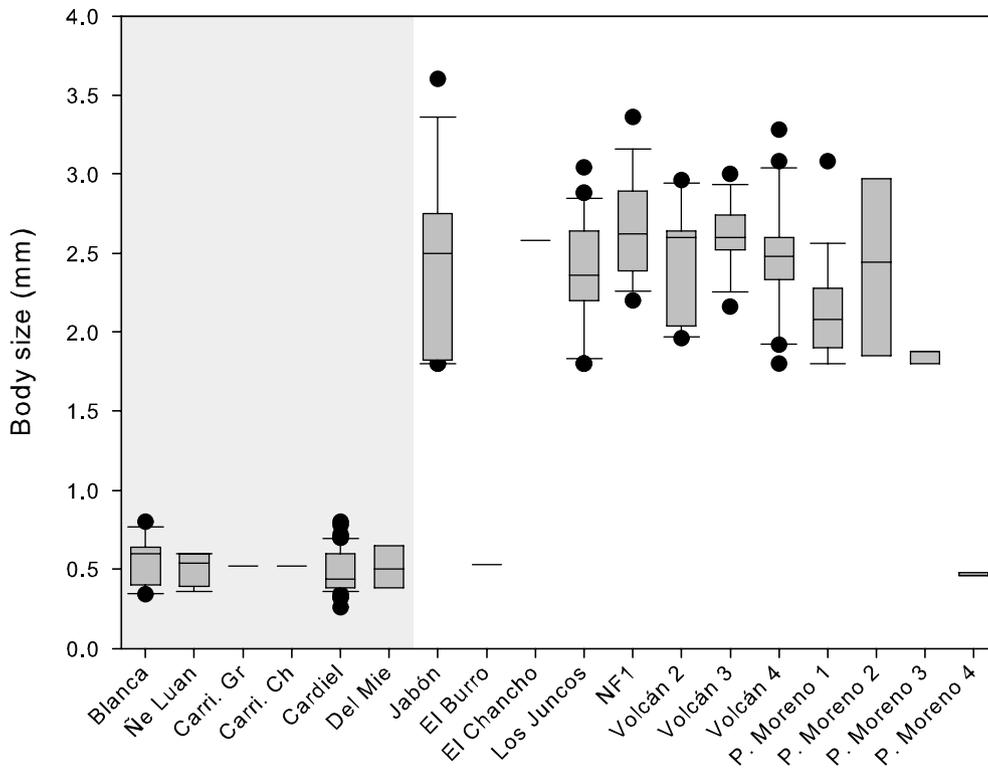


Fig. 5 – Body size (mm) of the dominant cladoceran species in lakes with fishes (shaded area) and fishless lakes. Median, quartiles and data outside the 10th and 90th percentiles are indicated.

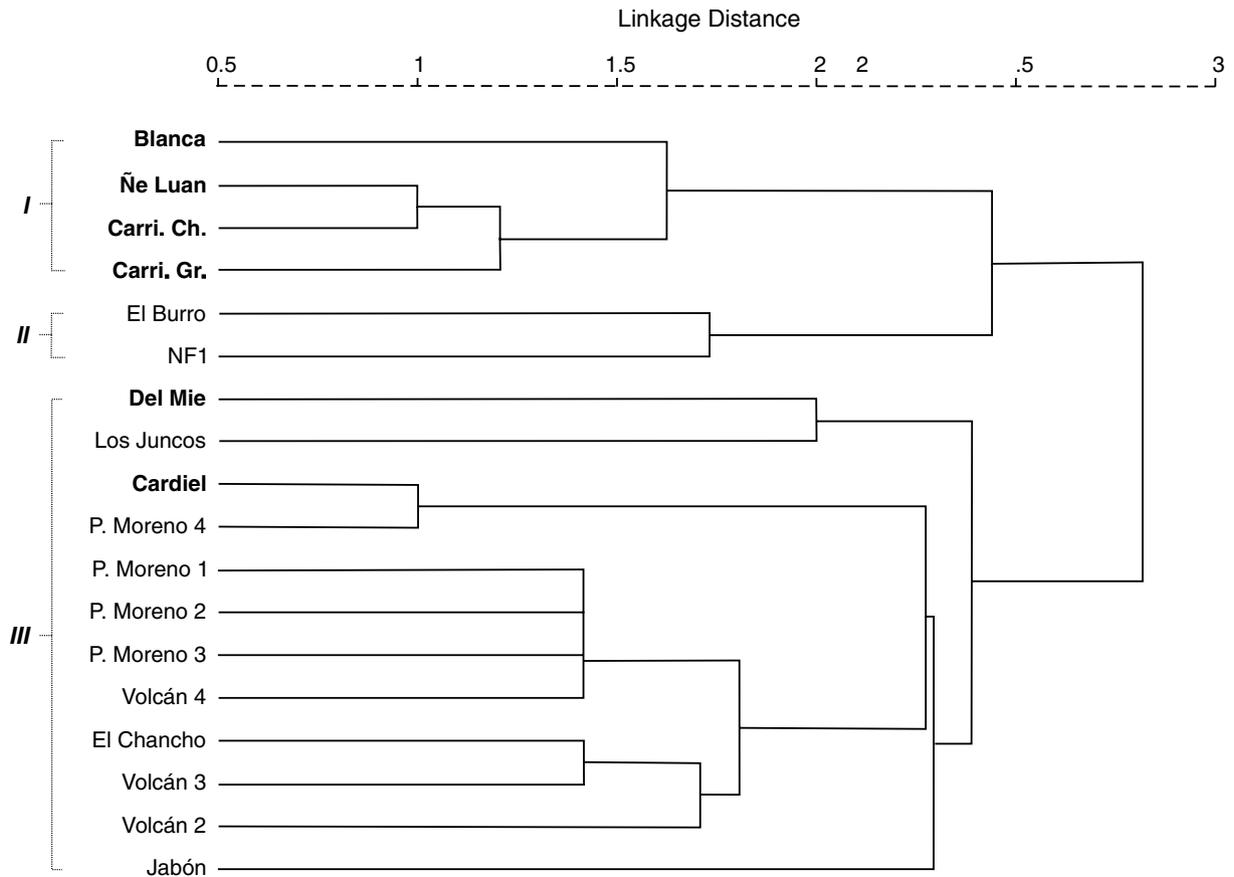


Fig. 6 – Crustacean dendrogram comparing all lakes, obtained by analysis of a presence-absence matrix by Euclidean distances and UPGMA. References: lakes with fish are noted in bold type.

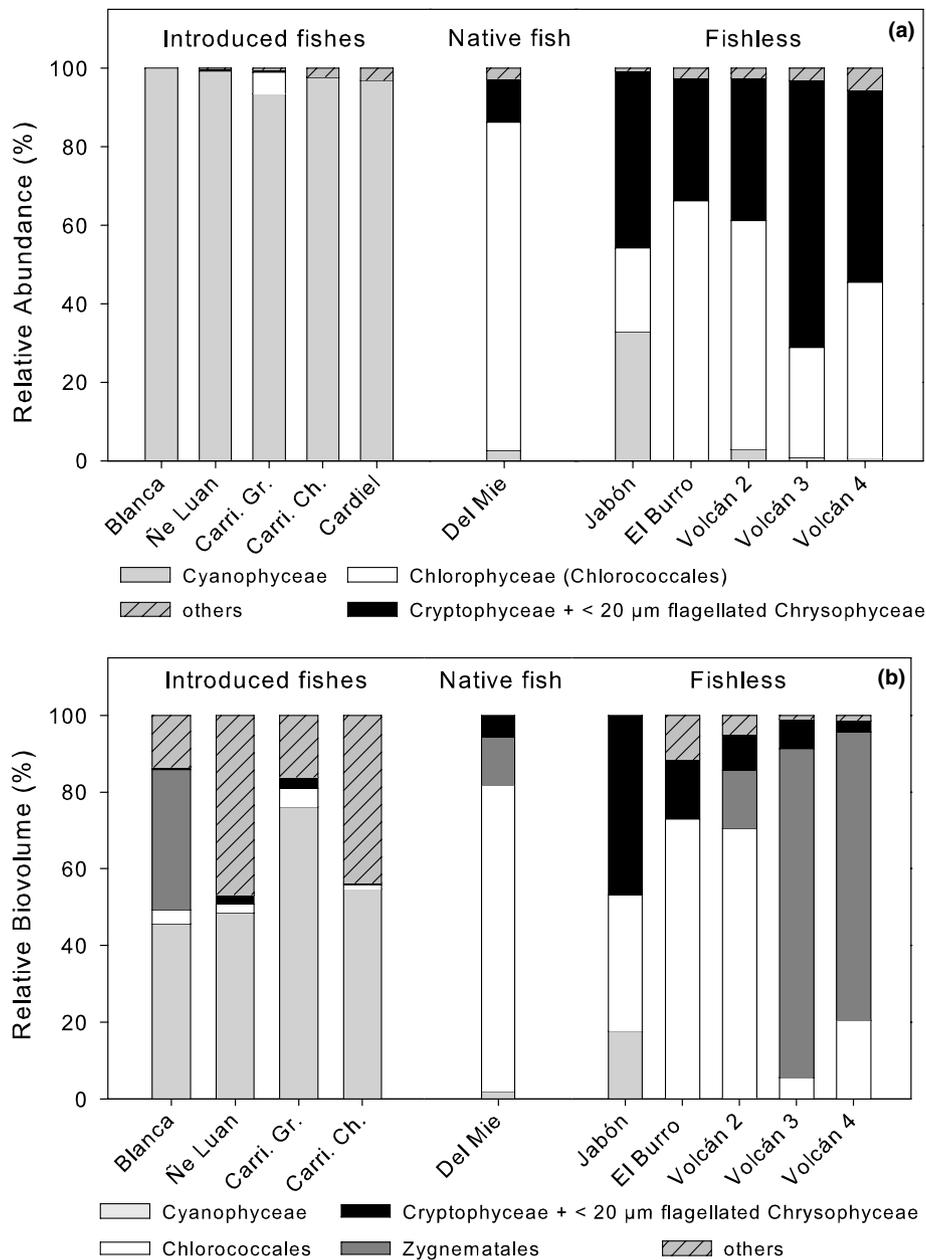


Fig. 7 – Phytoplankton taxonomic composition in Patagonian lakes: a. relative abundance and b. relative biovolume.

to cascade down to phytoplankton, as significant differences were also found in phytoplankton composition. Fishless lakes showed a more heterogeneous phytoplankton community while cyanobacteria were dominant in lakes with introduced fishes. In an experimental study comparing enclosures with and without fishes, Kurmayer and Wanzböck (1996) also observed a more heterogeneous algal community structure in the absence of fishes. Remarkably, Lake Del Mie, the only lake with native fish, did not show this pattern of cyanobacteria prevalence though net phytoplankton dominated (Fig. 7a and b, Table 1). The introduction of invasive species threatens native biodiversity and ecosystem functioning (Simon and Townsend, 2003). The prevalence of cyanobacteria may indicate that nutrient recycling changed in the presence of fish (Elser, 1999). Probably, the

elimination of *Daphnia*, a species with high phosphorus requirements (DeMott et al., 2004), may favor cyanobacteria proliferation, as *Daphnia* tends to sink phosphorus and as such prevents the outbreak of cyanobacteria (Elser, 1999). In addition, chemical, structural, and nutritional defenses of cyanobacteria can act as a feedback that favors their dominance (Christoffersen, 1996; Sukenik et al., 2002; Jang et al., 2003). Finally, cyanobacteria may have negative effects on zooplankton and fish assemblages (Laurenmaatta et al., 1995; DeMott, 1999; Wiegand and Pflugmacher, 2005). Cyanobacteria, mainly the filamentous ones, interfere with large zooplankton filtering process, thus a smaller size range of zooplankton in the lakes with fish could be favored (DeMott et al., 2001). Despite the different mechanisms involved, we observed that fish introduction in fishless lakes, is always

Table 2 – Total phytoplankton abundance: nano (<20 µm) and net (>20 µm) phytoplankton fractions, and the nano:net ratios in five lakes with fishes and five fishless lakes

	Phytoplankton abundance (cells ml ⁻¹)			Nano:Net
	Total	Nanoplankton	Net phytoplankton	
<i>Lakes with introduced fishes</i>				
Laguna Blanca	5,493,620	1733	5,491,887	0.0003
Ñe Luan	1,002,690	7555	995,135	0.0076
Carrillaufquen Grande	102,642	3352	99,291	0.0338
Carrillaufquen Chica	321,365	3067	318,398	0.0097
<i>Lakes with native fish</i>				
Del Mie	4816	1634	3182	0.5135
<i>Lakes without fishes</i>				
Jabón	7603	4230	3374	1.2536
El Burro	226	93	133	0.6964
Volcán 2	519	327	192	1.7004
Volcán 3	1220	851	369	2.3037
Volcán 4	923	581	343	1.6957

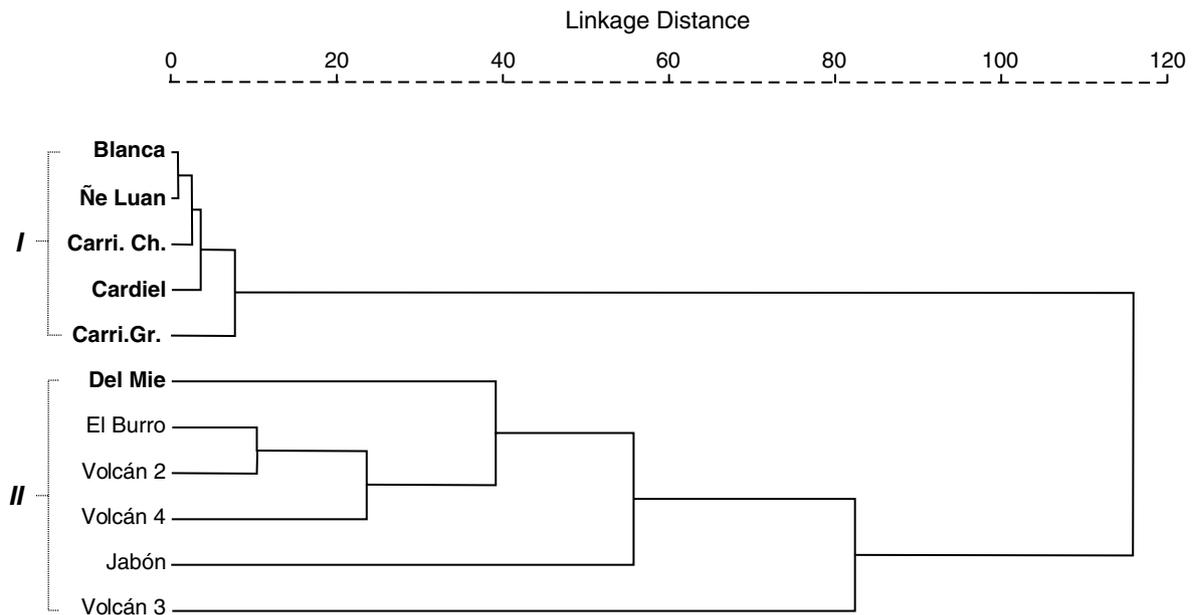


Fig. 8 – Phytoplankton dendrogram comparing 5 lakes with fish and 5 fishless lakes, obtained by analysis of the relative abundances of phytoplankton taxonomic groups by Euclidean distances and UPGMA. References: lakes with fish are noted in bold type.

related with the increase in similarity of crustacean and phytoplankton composition of lakes (Figs. 6 and 8).

The observed differences in phytoplankton composition between lakes with introduced fishes and those with native fish (Lake Del Mie) may be also related with the time of introduction or colonization. Fish introduction by man started nearly one century ago, and their effect on food webs and nutrient recycling seemed to favor cyanobacteria. On the other hand, fish colonization in Lake Del Mie was post-glacial (Cussac et al., 2004) hence the positive effect on cyanobacteria may have occurred early in the colonization. Trophic cascades and nutrient recycling may have favored non-cyanobacteria net phytoplankton dominance (e.g. chlo-

rophytes) because nutrient rebalance may have occurred during succession.

Invasion of predators such as fish may reduce prey diversity in the short term. However, colonization by species from nearby fish ponds may compensate for the initial loss of species and result in a long term positive effect if there is sufficient dispersal among local habitats (Shurin, 2001). The Patagonian steppe is an unfavorable region for lake development (Iriondo, 1989); thus the few existing lakes belong to different basins. Therefore, it is possible to assume an inadequate dispersion among local habitats. Shurin (2001) suggested that small zooplankton coexist regionally with larger species because of their ability to coexist locally with

size-selective predators such as fish. In this sense the presence of fish would increase regional biodiversity. Some Patagonian Plateau lakes have native fishes (e.g. Lake Del Mie), thus small zooplankton coexisted with larger species prior to fish introductions. Nevertheless, the outcome of other types of local interactions may also depend on spatial heterogeneity and movement of species along broad regional scales (Shurin, 2001). In that sense, the ponds and lakes in the Patagonian steppe extended difficulties to species dispersion. In addition, fish introduction in fishless lakes causes dramatic changes that cascade down to phytoplankton. As a consequence, water quality decreases and the value of sport fisheries would be reduced. Thus, fish introduction in Patagonia is a practice that should be reevaluated by governments and NGOs due to its potentially negative impact on lakes and local economies.

6. Conclusion

Our study showed clear differences in plankton composition and zooplankton size spectrum in lakes with and without fishes. Large and medium-sized centropagids including the predaceous copepod *P. sarsi* and the large cladoceran *Daphnia* were present in most of the fishless lakes while they were absent in lakes with fishes. The few available data on copepod assemblage structure prior to the introduction of fishes confirm our findings that fish caused a loss in the biodiversity of centropagid copepods.

We observed that fish introduction homogenizes crustacean plankton composition causing an increase in the relative abundance of rotifers. We also found dramatic changes in phytoplankton community. Cyanobacteria monopolized phytoplankton in lakes with introduced fishes, but not in fishless lakes or lakes with endemic fish fauna. Probably the elimination of *Daphnia*, a species with high phosphorus requirements, favored cyanobacteria proliferation due to nutrient rebalance.

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