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Differential piscivory of the native *Percichthys trucha* and exotic salmonids upon the native forage fish *Galaxias maculatus* in Patagonian Andean lakes

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Abstract

The present paper analyses predation patterns, of *Percichthys trucha* and salmonid fish upon *Galaxias maculatus* in five lakes of northern Patagonia with differing community and environmental characteristics. Tank experiments were performed to evaluate relative efficiency of native and exotic predators of *G. maculatus* under treatments with and without cover (aquatic vegetation). Important differences were found between predators with regards to distribution and consumption of *G. maculatus*. Salmonids are more efficient than *P. trucha* in consuming *G. maculatus* in deep environments with scarcely vegetation; in contrast to native species they frequently use the pelagic environment. Although pelagic habitat might have served in the past as a refuge from native predators in the past, *G maculatus* now experiences intense predation in the pelagic zone by exotic salmonids. It is suggested that the widespread distribution of *G. maculatus* in Patagonian lakes may have facilitated the success of salmonids throughout Patagonia.
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Introduction

Among the many impacts that man imposes upon natural systems introductions of exotic species are among the most important and difficult to evaluate (Lodge, 1993; Meador, Brown, & Short, 2003; Moyle, 1997; Rainbow, 1998). Predation and decline of native species within their natural habitat often is one of the most noticeable negative effects (Ogutu-Ohwayo, 1990; Townsend & Crowl, 1991; Zaret & Paine, 1973). Regarding this problem, piscivorous fish should have a bigger impact upon native fish communities than other functional groups (Moyle & Light, 1996).

The introduction of salmonids into Argentine Northern Patagonia started in 1904 (Marini, 1936). *Salvelinus fontinalis* and *Salmo salar* adapted rapidly (Ormsby, 1908a, b) dispersing both naturally and artificially throughout the region (Marini, 1942; Valette, 1924). From 1931 onwards, *Oncorhynchus mykiss* and *Salmo trutta* were also stocked and dispersed intensively (Macchi, 2004). Stocking policies, dispersal capabilities of each species and interactions among them produced throughout the last 100 years changes in the local and regional abundance and distribution of salmonids.

Today *O. mykiss*, *S. trutta* and *S. fontinalis* are the most common salmonid species (Pascual et. al., 2002; Vigliano & Darrigran, 2002). Whereas *S. fontinalis* was dominant until the mid-1940s (Bruno Videla, 1944; Gonzáles Regalado, 1945), *O. mykiss* became the most important salmonid species in the 1950s (Fuster de Plaza, 1950).

Among the native galaxiids, *Galaxias maculatus* shows the most extended distribution worldwide, inhabiting Australia, New Zealand, Tasmania, Malvinas Islands, Chile and Argentina (Campos, 1970). In South America this species presents diadromous and land-locked life cycles (McDowall, 1971). In North-eastern Patagonian lakes *G. maculatus* possesses landlocked life cycle. Adult specimens spawn in the littoral area and larvae hatch after approximately 28 days migrating to the pelagic zone. Larval metamorphosis occurs after 6 months forming schools that migrate towards the benthic and littoral areas of the lake where juveniles and adults spend most of their life (Barriga, Battini, Macchi, Milano, & Cussac, 2002; Battini, 1997; Cussac, Cervellini, & Battini, 1992).

Due to the common biogeographic origin New Zealand and Australia possess similar fish communities to those of Patagonia including both native and salmonid species. Salmonids seem to have had significant negative impact on native fish populations in New Zealand (McDowall, 1990), though controversy exists about the causes of such effects (McDowall, 2003). Competition for space coupled with competition for food has been proposed as the cause for the decline of *G. vulgaris* populations in New Zealand streams (McIntosh, Townsend, & Crowl, 1992). However, the same authors concluded that the predation pressure by *S. trutta* might be the forcing mechanism that could explain the patchy distribution of *G. vulgaris* in New Zealand streams (McIntosh, 2000). Based on historical data Cadwallader and Eden (1982) proposed that the predation by *O. mykiss* could be responsible for the decline of *G. maculatus* in Australia's Purrumbete Lake. Glova (2003) found that both competition and predation are important for the relationship between *S. trutta* and *G. maculatus* in rivers in New Zealand.

In fish communities of North-eastern Patagonia, *G. maculatus* is highly vulnerable to predation not only by exotic salmonids, but also by native species (Macchi, Cussac, Alonso, & Denegri, 1999; Milano et al., 2002). In all studied environments, the highest predation on *G. maculatus* by native species was produced by *Percichthys* species (Macchi et al., 1999). Meanwhile, galaxiids in New Zealand evolved in environments lacking predatory fish, a situation that according to McDowall (1990) would make them particularly vulnerable to exotic species. Thus ecological comparisons between the fish fauna of Australasia and South America would be particularly interesting because of these differences in the functional groups of the native species. For instance, is *G. maculatus* in Patagonia "preadapted" to some degree to the predation pressure by exotic salmonids compared to its predation–naïve relatives of Australasia or not?

In any case, the wide distribution of this species and the high incidence in the diet of the predator species indicate that it plays a key role in the trophic structure of Patagonian lakes. Therefore, the characterization of predation by native and exotic species on *G. maculatus* constitutes a key background information for understanding the impact by salmonids. Generally speaking, the native *Percichthys* spp. and salmonids have similar feeding patterns (Macchi, 2004; Macchi et al., 1999). This needs to be carefully analyzed in order to detect subtle differences with regards to their predation pressure on *G. maculatus* (Herbold & Moyle, 1986).

The present study focuses on predation in terms of similarities and differences in relation to predator habitat use and consumption of *G. maculatus* by *P. trucha*, *O. mykiss*, *S. fontinalis* and *S. trutta* through field work and tank experiments.

Materials and methods

Study area

The study was conducted in five lakes of the Nahuel Huapi National Park located in North-eastern Patagonia (Fig. 1). The area is characterized by a great diversity of lakes ranging from large and deep glacially originated lakes to small and shallow ones. The climate is temperate with mean annual precipitations of up to 1000 mm (Pedrozo, Chillrud, Temporetti, & Díaz, 1993). The vegetation is characterized by dense *Nothophagus* sp. and *Astrocedrus chilensis* forest (Dimitri, 1972).

Chosen lakes belong to different drainage basins (Fig. 1). Lakes Moreno, Morenito and Gutiérrez are directly connected to the larger Nahuel Huapi Lake, all draining to the Atlantic Ocean. Lake Guillelmo belongs to the Manso river basin which flows into the Pacific Ocean. Escondido Lake is a small water body that does not communicate effectively with other water bodies. The main physical characteristics and the plant cover of the lakes are summarized in Table 1.

Like typical Patagonian Andean Lakes, they all have low fish diversity and low fish biomass (Quiros, 1990), but have abundant *G. maculatus* populations. Lakes Morenito, Moreno and Escondido have significant populations of *P. trucha*. *Odontesthes hatcheri* is found only in the former two lakes but not in the latter one. *Diplomystes viedmensis* and *G. platei* are found in Gutiérrez and Moreno lakes. However, they differ in the composition of exotic fish (Table 1). *O. mykiss* and *S. fontinalis* are abundant in lakes Moreno, Gutiérrez
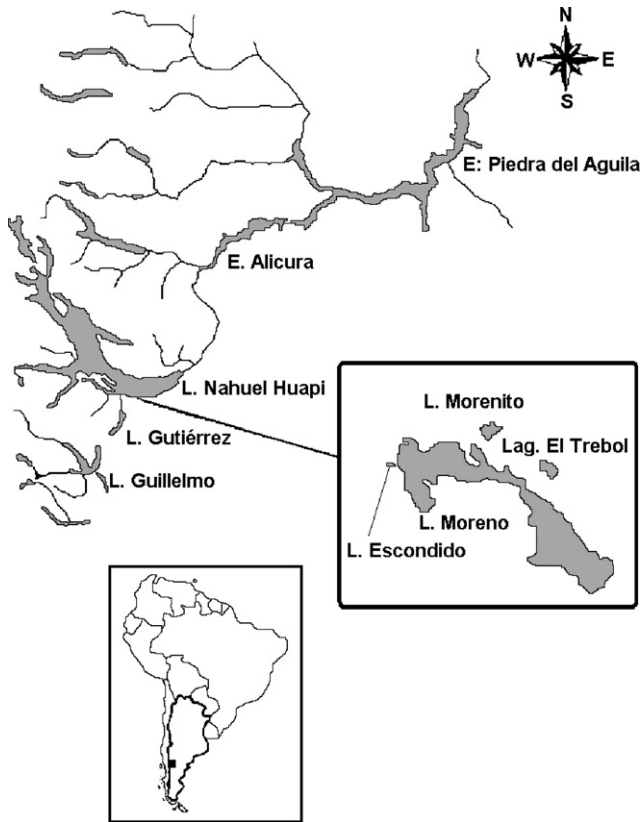
Fig. 1. Study area.

and Guillelmo. Both species were occasionally caught in Morenito Lake. *O. mykiss* is also caught in Lake Escondido in small numbers, whereas *S. trutta* is important in Lake Gutiérrez and occasionally was caught in Lake Moreno.

Field sampling and data analysis

Fish data came from fish surveys using gill nets; sampling design and gill net deployment was related to each lake morphometric characteristics (Table 1). In Lake Escondido, fish sampling was accomplished through the use of 25 m long gill nets of 15, 20, 30 and 50 mm bar mesh sizes and 2 m in height. On all other water bodies fish were caught using gill net gangs formed by 15, 20, 30, 50, 60 and 70 mm bar mesh size panels, 10 m in length and 2 m in height each. In Lakes Guillelmo, Moreno and Gutiérrez gill net gangs were set at 2, 10, 30 and 50 m depths upon the epibenthic habitat and at 0, 15, 20, 30, 40, 50 and 60 m in the pelagic habitat following the methodology described by Vigliano et al. (1999). In Lakes Morenito and Escondido gill nets were set at 2 and 10 m depths in the epibenthic habitat.

Meanwhile Lake Gutiérrez, Lake Guillelmo and Lakes Moreno and Morenito were sampled every 3 months between 1995–1997, 1997–1999 and 1999–2000,

Table 1. Studied lake characteristics and catches per unit of effort (CPUE) of different predator species in 5 lakes of Nahuel Huapi National Park, CPUEN

Lake	Altitude (m.a.s.l.)	Area (km²)	Maximum depth (m)	Conductivity (µS cm⁻¹)	Summer temperature (°C)	Secchi disk (m)	Plant coverage (%)[a]	CPUE (100 m² per 12 h fishing)			
								P. trucha	O. mykiss	S. fontinalis	S. trutta
Escondido	764	0.8	8	52.2	21.5	6.7	90.0	3.06	—	—	—
Moreno	765	10.6	112	37.1	18.2	17.0	28.4	1.56	1.24	0.39	0.01
Morenito	766	0.82	15	37.1	20.8	6.5	83.1	7.89	—	—	—
Gutiérrez	790	16.4	111	58.1	18.3	18.0	6.8	—	0.93	0.26	0.24
Guillelmo	826	5.4	107.2	54.8	16.2	12.5	13.4	—	1.93	5.97	—

[a]Macchi (2004).

respectively, Lake Escondido was sampled bimonthly between 1996 and 1998.

All specimens of predator fish caught were identified to the species level, their standard lengths (Stl mm) and total weight (Wt gr) were recorded, and their digestive tract was removed and preserved in 4% formalin for later diet analysis. Prey items and food categories were identified under a dissecting microscope (Wallace, 1981). Prey fishes were identified to the species level and separated into three categories: (1) *G. maculatus* juveniles and adults, (2) galaxiid larvae and (3) other fish. In this work only categories 1 and 2 were used. Galaxiid stages were defined through their standard lengths following Barriga et al. (2002) defining those specimens larger than 28.3 mm as juveniles and adults and the rest as larvae. Because larvae of *G. maculatus* cannot be differentiated externally from those of *G. platei* and because *G. maculatus* is either the only galaxiid present (Lakes Guillelmo, Morenito and Escondido) or is much more frequent than *G. platei* (Lakes Moreno and Gutierréz) (Milano et al., 2002; Barriga et al., 2002), all galaxiid larvae found were assigned to *G. maculatus*.

The volume of each prey type was measured by recording water volume displacement. Fish prey length was measured from the tip of the head up to the urostile. When the degree of digestion prevented the correct length measurement, the fish length was estimated from regressions between length and different body part sizes, such as head, mandible and vertebrae (Macchi unpublished data) following the methodology described by Scharf, Yetter, Summers, and Juanes (1998).

Due to the gill net selectivity sampled predator populations were defined by fishes larger than Stl ≥ 95 mm. The size distributions of *P. trucha*, *O. mykiss*, *S. fontinalis* and *S. trutta* between lakes were tested by a pairwise Kolmogorov–Smirnov test, and Kruskal–Wallis (K–W) test for more than two samples or the Mann–Whitney (M–W) test for two samples (Sokal & Rohlf, 1981).

Catch per unit of effort (CPUE) data are presented as the number of fish caught of each species per $100 \, m^2$ of net and 24 h of soak time. Average CPUEs data of Lakes Moreno, Gutiérrez and Guillermo were used to analyze benthic and pelagic habitat use by each predator species through the M–W test. Catch variation by depth strata within each habitat was evaluated through K–W: shallow benthic (2 m–10 m), deep benthic (30 m–50 m), shallow pelagic (0 m–10 m) and deep pelagic (>10 m).

Analysis of the frequency of piscivory between lakes for each predator species and between species was done through the comparison of the average volume of galaxiids per stomach including empty stomachs, thus obtaining a piscivory index for each predator species and lake. Comparison between lakes was done using the

K–W test for more than two samples or the M–W test for two independent samples.

Size frequencies of predators that consumed galaxiids were compared to those that did not through a homogeneity test (L'Abée-Lund, Langeland, & Saegrov, 1992; Sokal & Rohlf, 1981) after grouping fish in 200 mm size intervals. This test was also applied to compare the size distribution of predators of larvae and predators of juveniles + adult within each species.

Relative specialization of the different predator species in relation to larvae versus juveniles + adults categories was tested through a χ^2 test (Sokal & Rohlf, 1981) applied to the frequency of stomachs containing each prey-type category within each predator species.

Sizes of *G. maculatus* consumed in each lake by each predator species was compared trough analysis of variance (ANOVA) when data fulfilled the assumptions of normality and variance homogeneity or with a K–W test for more than two samples or the M–W test when they did not.

Seasonal consumption variations of *G. maculatus* in Lakes Gutiérrez and Moreno were analyzed through a K–W test for more than two samples.

Mean volume of larvae and of juvenile + adults per stomach per predator species in the benthic and pelagic habitats were compared through the M–W test for two independent samples.

Predation experiments

Experiments were carried out to evaluate the consumption of *G. maculatus* by each predator species (*P. trucha*, *O. mykiss* and *S. fontinalis*) and to assess prey size selection in relation to habitat complexity. Experiments were performed in four circular 55 cm radius PVC outdoor tanks (volume: 500 l). Tanks located at the University of Comahue hatchery were set in line experiencing the same light, temperature and weather conditions. Water supply to each tank was continuously supplied from the main water hatchery channel. During the experiment water in- and outflow was interrupted so as to avoid internal currents that could affect both prey and predator behavior with regards to what could be expected on a lenthic environment.

A refuge experiment tank situation was simulated by adding six shredded nylon ropes of 26.5 cm in length that were anchored with stones on the middle of the tank. Average refuge volume was approximately $10,600 \, cm^3$ per tank. For the no refuge experimental tank situation prey were put into the tanks with out any type of refuge against predators.

Experiments were conducted between April 10, 2003 and May 20, 2003. Daily temperature records showed that the temperature variations (9.5–10 °C) were too small to produce significant variations in the metabolism

Table 2. Predation experiment design: numbers of *G. maculatus* used per experiment below 50 mm Stl. $N = 20$ and above 50 mm Stl.; $N = 3$

	Treatments			
	Without predator	*P. trucha*	*O. mykiss*	*S. fontinalis*
With refuge				
Number of replicates	4	4	4	4
Mean Stl mm	—	338.8	290.0	265.0
Size range mm (Stl.)	—	325–360	250–325	230–300
Start day	04/04/03	10/04/03	23/04/03	29/04/03
End day	06/04/03	12/04/03	25/04/03	01/05/03
Without refuge				
Number of replicates	4	4	4	4
Mean Stl mm	—	328.0	265.5	281.3
Size range mm (Stl.)	—	300-360	200–310	250–315
Start day	07/05/03	22/05/03	20/05/03	09/05/03
End day	09/05/03	24/05/03	22/05/03	11/05/03

or the behavior of the fishes. All refuge experiments were performed first, followed by the no refuge experiments. Galaxiids were caught during March until May 2003, transported to the laboratory in order to determine their standard lengths and to separate them into two groups: specimens smaller and larger than 50 mm for their use after a week adaptation period.

Predator specimens were caught in Moreno, Gutiérrez and Guillelmo Lakes during March until May 2003. To avoid fungal proliferation, the fishes were disinfected with malachite green and stored in separate circular tanks according to species and covered with a sunscreen mesh to reduce solar exposure and diminish stress. Fish recovered rapidly from this treatment and were used in the experiments after an adaptation period of 2 days.

Each experiment (with or without refuge) were done with four replicates for each treatment (no predator, with *P. trucha*, with *O. mykiss*, with *S. fontinalis*) (Table 2).

In each circular tank 20 individuals of *G. maculatus* of less than 50 mm Stl (Stl mean: 40.61, range: 20–50) and 3 specimens bigger than 50 mm Stl (Stl mean: 58.45, range: 51–65) were placed. This prey size range was chosen because it corresponds with the one naturally found in Lake Moreno (unpublished data). Prey smaller than 30 mm Stl could not be used because they died when manipulated.

The prey fishes were left alone for 30 min after being put into the experimental tanks, after which a predator was introduced in each of the four tanks (Table 2). All tanks were covered with sunscreen nets (mesh size: 1 mm) and reposed during 48 h. Afterwards, the predators were extracted and the remaining *G. maculatus* were counted and measured.

The variation in the consumption rate of *G. maculatus* between predators was examined using a two-way paired ANOVA analysis. To validate paired contrasts α was adjusted using the Dunn–Šidák equation:

$$\alpha'' = 1 - (1 - \alpha)^{1/k},$$

where α'' is the adjusted α value, α is the original value $= 0.05$ and $k =$ numbered of contrasts ($k = 4$). Relative vulnerability of different size prey was analyzed using the G_H test for homogeneity (Sokal & Rohlf, 1981).

Results

Predator catches and size distributions

The native *P. trucha* was the dominant species in all lakes where it was present. Their, catches were more important in shallow environments with higher summer temperatures and higher aquatic vegetation cover. In contrast salmonids were abundant in deeper lakes with lower temperature with less submerged vegetation (Table 1).

The size distributions of *P. trucha* differed between all paired studied lakes (Escondido vs. Moreno K–S, $Z = 5.67$; Escondido vs. Morenito K–S, $Z = 5.12$; Moreno vs. Morenito K–S, $Z = 1.41$, $p < 0.05$). The distribution of *O. mykiss* differed between both Gutiérrez and Guillelmo Lakes with regards to Moreno Lake (Moreno vs. Guillelmo: K–S, $Z = 1.95$, $p < 0.05$; Moreno vs. Gutiérrez: K–S, $Z = 2.07$, $p < 0.0001$). *S. fontinalis* distribution differed between both Gutiérrez and Moreno Lake with regards to Guillelmo Lake (Guillemo vs. Gutiérrez: K–S, $Z = 2.57$, $p < 0.0001$; Guillelmo vs. Moreno: K–S, $Z = 3.03$, $p < 0.0001$). The size distribution of *S. trutta* was different between the two lakes were it was caught (Gutiérrez vs. Moreno:

Table 3. Standard length (mean, median and range in mm), variation coefficient (VC %) of *P. trucha, O. mykiss, S. fontinalis* y *S. trutta* in 5 lakes of Nahuel Huapi National Park

	LAKE				
	Escondido	Morenito	Moreno	Gutiérrez	Guillelmo
P. trucha					
N	179	59	209	—	—
Mean (Stl mm)	237.5	334.0	308.1	—	—
Median (Stl mm)	227	338	330	—	—
Range (Stl mm)	125–410	215–395	118–435	—	—
VC	26.0	10.8	22.7	—	—
O. mykiss					
N	—	—	175	202	51
Mean (Stl mm)	—	—	318.1	270.3	289.0
Median (Stl mm)	—	—	300	257	305
Range (Stl mm)	—	—	105–578	97–489	130–455
VC %	—	—	32.3	33.5	22.4
S. fontinalis					
N	—	—	71	63	273
Mean (Stl mm)	—	—	289.5	274.1	232.1
Median (Stl mm)	—	—	305	320	235
Range (Stl mm)	—	—	110–420	100–420	95–420
VC %	—	—	26.0	24.9	29.3
S. trutta					
N	—	—	5	45	—
Mean (Stl mm)	—	—	553.0	395.4	—
Median (Stl mm)	—	—	550	420	—
Range (Stl mm)	—	—	485–630	105–510	—
VC %	—	—	12.1	24.8	—

K–S, $Z = 1.74$, $p < 0.05$). The mean sizes of all predator species were significantly different between lakes: *P trucha*: K–W: $\chi^2 = 120.4$, d.f. $= 2$, $n = 447$, $p < 0.0001$; *O. mykiss*: K–W: $\chi^2 = 20.5$, d.f. $= 2$ $n = 361$, $p < 0.0001$; *S. fontinalis*: K–W: $\chi^2 = 44.5$, d.f. $= 2$, $n = 287$, $p < 0.0001$; *S. trutta*: M–W: $Z = -3.25$, $n = 50$, $p < 0.001$ (Table 3).

Predator spatial-temporal distribution

All predator species were caught in all habitats of the sampled lakes. No seasonal trends in catch were apparent. Catches were generally more abundant in the shallower depth strata of all habitats (Figs. 2 and 3). *P. trucha* was more abundant in the shallower benthic habitat of Moreno lake (K–W: $\chi^2 = 17.2$, d.f. $= 3$, $n = 40$, $p < 0.001$). *O. mykiss* also preferentially used shallower benthic strata of the three lakes where it was captured (Moreno lake: K–W: $\chi^2 = 13.4$, d.f. $= 3$, $n = 40$, $p < 0.004$; Gutiérrez lake: K–W: $\chi^2 = 15.2$, d.f. $= 3$, $n = 40$, $p < 0.002$; Guillelmo lake: K–W: $\chi^2 = 19.8$, d.f. $= 3$, $n = 32$, $p < 0.0001$). This species

appears constantly in the pelagic habitat of all lakes. CPUE of *O. mykiss* in Gutiérrez, Moreno and Guillelmo Lakes catches were higher in shallow pelagic waters.

S. fontinalis was more abundant in shallow benthic habitat of Moreno and Guillelmo Lakes (Moreno Lake: K–W: $\chi^2 = 10.2$, d.f. $= 3$, $n = 40$, $p < 0.05$; Guillelmo Lake: K–W: $\chi^2 = 27.2$, d.f. $= 3$, $n = 32$, $p < 0.055$). In Gutiérrez Lake the highest catch values corresponded to deep benthic strata (Gutiérrez Lake: K–W: $\chi^2 = 11.1$, d.f. $= 3$, $n = 40$; $p < 0.05$), whereas *S. trutta* showed higher catch values in deep benthic habitat of this lakes (K–W: $\chi^2 = 7.8$, d.f. $= 3$, $n = 40$, $p < 0.05$). The small numbers of specimens of this species caught in Moreno Lake did not allow for the corresponding analysis.

Predation upon *G. maculatus*

Only *O. mykiss* and *S. fontinalis* showed significant differences in relation to the numbers of *G. maculatus* consumed in the sampled lakes (K–W: $\chi^2 = 26.7$, d.f. $= 2$, $n = 432$, K–W: $\chi^2 = 148.5$, d.f. $= 2$, $n = 409$, $p < 0.05$, *O. mykiss* and *S. fontinalis*, respectively; Fig. 4).
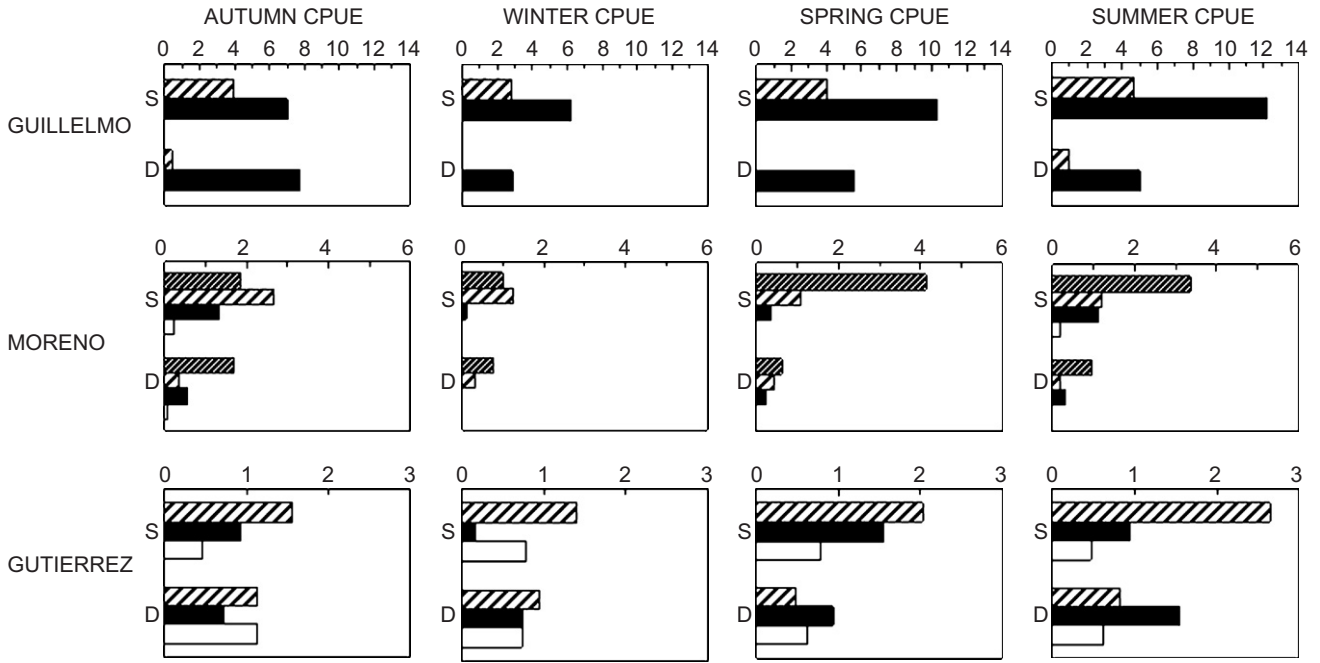
Fig. 2. Catch (CPUE) for each lake benthic habitat of *G. maculatus* predators (fish >95 mm Stl.) and depth strata. S: shallow, D: deep. *P.trucha*, ▨ ; *O. mykiss*, ▨ ; *S. fontinalis*, ■ ; *S. trutta*, ☐ .
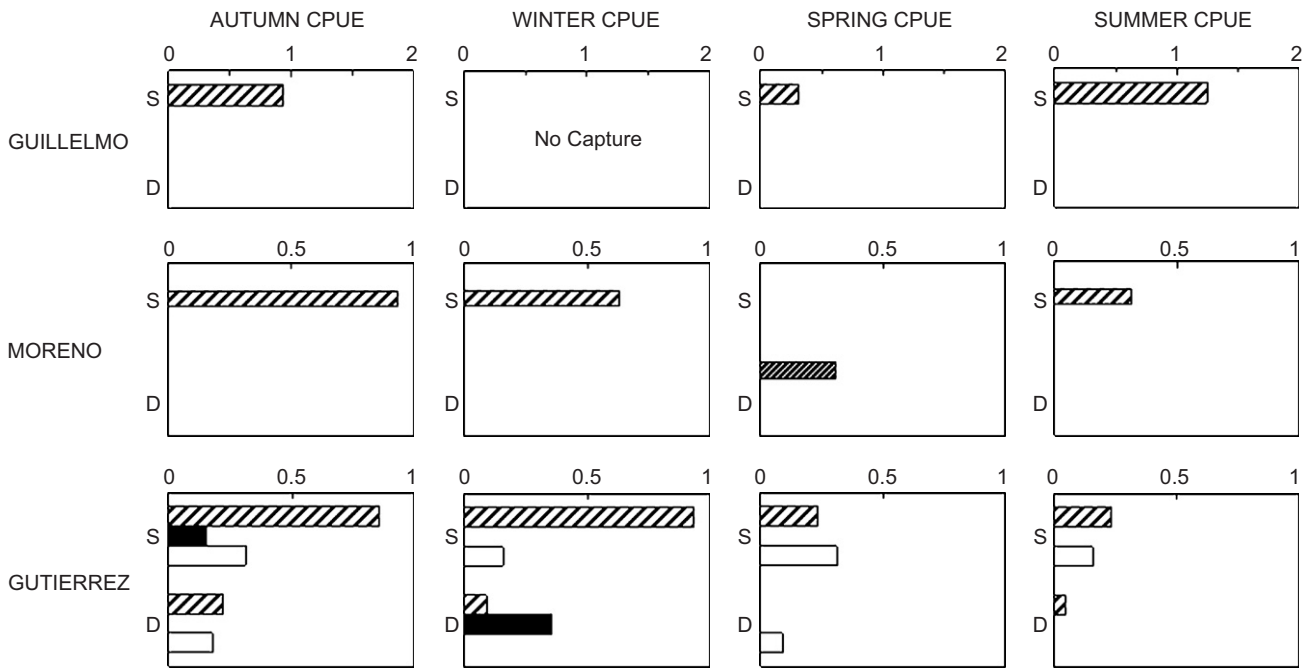
Fig. 3. Catch (CPUE) for each lake pelagic habitat of *G. maculatus* predators (fish >95 mm Stl.) and depth strata. S: shallow, D: deep. *P.trucha*, ▨ ; *O. mykiss*, ▨ ; *S. fontinalis*, ■ ; *S. trutta*, ☐ .

In Moreno Lake *P. trucha* ate less galaxiids than any of the three salmonid species. Meanwhile *O. mykiss* was the salmonid that consumed more *G. maculatus* in this lake (K–W: $\chi^2 = 53.1$, d.f. $= 3$ $n = 460$, $p < 0.0001$). On the contrary in Gutiérrez lake this species was the one that consumed the least galaxiids and *S. trutta* the one that consumed the most (K–W: $\chi^2 = 35.5$, d.f. $= 2$, $n = 310$, $p < 0.0001$). No differences were found between
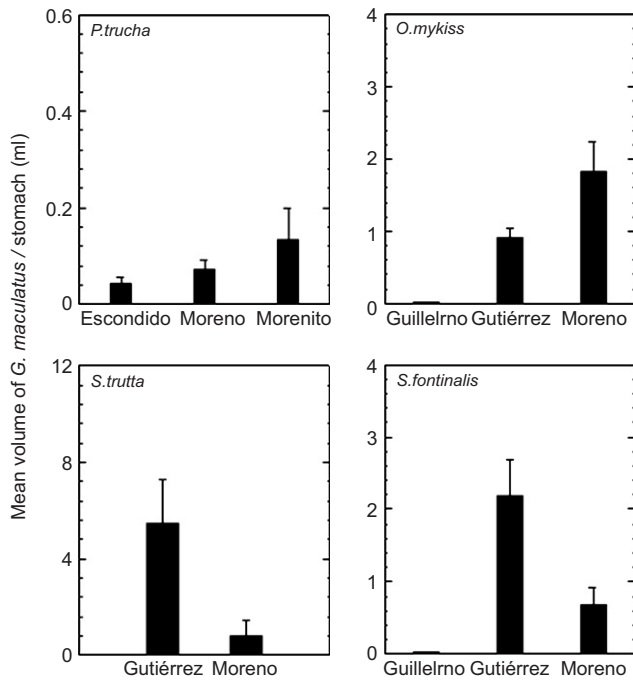
Fig. 4. Rate of consumption ($\pm$SE), measure as mean volume of *G. maculatus* by *P. trucha*, *S. trutta*, *O. mykiss* and *S. fontinalis* per stomach.

the volume of galaxiids consumed by the two salmonid species caught in Guillelmo Lake (M–W: $Z = 0.83$, $n = 330$, $p > 0.05$).

No significant differences were found between the size of fish that consumed galaxiids and those that did not for any of the predator species (*P. trucha*: GH = 17.5, d.f. = 13, $n = 376$, $p > 0.05$; *O. mykiss*: GH = 23.4, d.f. = 19, $n = 361$, $p > 0.05$; *S. fontinalis*: GH = 14.5, d.f. = 15, $n = 299$, $p > 0.05$; *S. trutta*: GH = 0.1, d.f. = 2, $n = 50$, $p > 0.05$, for the grouped data of all lakes). Also, no significant differences were found for the size distributions of the fish that consumed larvae and of the ones that consumed juveniles + adults of *G. maculatus* (*P. trucha*: GH = 1.9, d.f. = 6, $n = 50$, $p > 0.05$; *O. mykiss*: GH = 6.5, d.f. 17, $n = 175$, $p > 0.05$; *S. fontinalis*: GH = 17.4, d.f. = 9, $n = 86$, $p > 0.05$; *S. trutta*: GH = 4.2, d.f. = 3, $n = 43$, $p > 0.05$). Both facts suggest that the observed differences in the galaxiid consumption rate were not related to predator size in each lake.

In Lakes Moreno and Gutiérrez the consumption of galaxiids by predators was subject to seasonal influence. In Gutiérrez Lake the three salmonids species consumed more *G. maculatus* during winter than during other seasons (*O. mykiss*: K–W: $\chi^2 = 15.9$, d.f. = 3, $n = 202$; $p < 0.0001$; *S. fontinalis*: K–W: $\chi^2 = 10.7$, d.f. = 3, $n = 63$, $p < 0.05$; *S. trutta*: K–W: $\chi^2 = 20.4$, d.f. = 3 $n = 45$, $p < 0.0001$). In Lake Moreno *P. trucha* and *O. mykiss* increased significantly their consumption on galaxiids during summer; meanwhile *S. fontinalis* did so

in spring. (K–W: $\chi^2 = 8.1$, d.f. = 3, $n = 209$;K–W: $\chi^2 = 10.2$, d.f. = 3, $n = 125$, $n = 73$, $p < 0.05$ for *P. trucha*, *O. mykiss* and *S. fontinalis*, respectively).

Galaxiids of all categories were eaten in all habitats, even though the relative consumption of larvae was higher than that of juveniles + adults in the pelagic habitat (Table 4). In Lake Moreno, only those *P. trucha* caught in the benthic habitat had food in their stomachs (Table 4). *O. mykiss* consumed them in both habitats of Gutiérrez and Moreno Lakes. In Lake Guillelmo specimens in pelagic strata did not feed on galaxiids. For Lake Gutiérrez we observed differences in the mean volume per stomach of juveniles and adults of *G. maculatus* eaten in each habitat. Differences in larvae consumption by this species were found between both habitats of Moreno Lake (Table 4). In Gutiérrez Lake *S. fontinalis* and *S. trutta* were caught in both the benthic and pelagic habitats not showing differences in galaxiid consumption between habitats.

A relative specialization with regards to the larvae and juveniles + adults categories was evident between the different predator species. *P. trucha* consumed more frequently juveniles + adults than larvae ($\chi^2 = 13.5$, d.f. = 1, $n = 50$, $p < 0.0001$). Meanwhile *O. mykiss* and *S. trutta* ate larvae more frequently than juveniles + adults (*O. mykiss*: $\chi^2 = 9.6$, d.f. = 1, $n = 175$, $p < 0.05$; *S. trutta*: $\chi^2 = 22.4$, d.f. = 1, $n = 43$, $p < 0.001$). On the other hand *S. fontinalis* ate both categories with equal frequency ($\chi^2 = 2.3$, d.f. = 1, $n = 86$, $p > 0.05$).

No relationships were found between the mean size of fish consumed and lake of origin for *P. trucha* (ANOVA, $F = 3.3$, d.f. = 2, $n = 69$, $p > 0.05$), or *S. trutta* (M–W: $Z = -4.2$ $n = 50$, $p < 0.05$). The size of consumed prey differed for *O. mykiss* and *S. fontinalis* between some of the lakes (*O. mykiss*: K–W: $\chi^2 = 8.4$, d.f. = 2, $n = 278$, $p < 0.05$; *S. fontinalis*: K–W: $\chi^2 = 9.6$, d.f. = 2, $n = 105$, $p < 0.05$). For both species the consumed prey size was smaller in Guillelmo Lake, intermediate in Gutiérrez Lake and bigger in Moreno Lake.

Piscivory experiments

No *G. maculatus* of the control tanks (with and without refuge) died during the experiments. For both conditions, the three predator species consumed galaxiids showing important differences (Fig. 5). The complete model includes two independent variables "species and refuge" (ANOVA, $n = 24$; $R^2 = 0.71$; R^2 adjusted = 0.67; $p < 0.002$). Consumption of *G. maculatus* differed among predator species, with a predation for all species lower in the refuge experiment. The average number of galaxiids consumed was lowest for *P. trucha*, with significantly lower rate than those of *O. mykiss* ($F = 26.11$, $p < 0.0001$) and of *S. fontinalis*

Table 4. Mean volume ($\pm$ standard errors) of galaxiids per stomach (ml) of caught predators in the benthic and pelagic habitats of lakes Moreno and Gutiérrez; N = number of fish with food in their stomachs

	Gutiérrez		Moreno	
	Benthonic	Pelagic	Benthonic	Pelagic
P. trucha				
N	—	—	155	—
Larvae	—	—	0.02 ± 0.01	—
Juveniles + adults	—	—	0.07 ± 0.02	—
Total	—	—	0.09 ± 0.002	—
O. mykiss				
N	149	32	141	3
Larvae	0.83 ± 0.16	1.09 ± 0.50	1.45 ± 0.39	14.54 ± 14.53*
Juveniles + adults	0.15 ± 0.02	0.01 ± 0.02*	0.50 ± 0.14	0.23 ± 0.23
Total	0.98 ± 0.17	1.10 ± 0.5	1.95 ± 0.41	14.77 ± 14.42*
S. fontinalis				
N	59	4	56	—
Larvae	1.95 ± 0.54	1.73 ± 0.71	0.52 ± 0.25	—
Juveniles + adults	0.26 ± 0.08	0	0.34 ± 0.08	—
Total	2.21 ± 0.54	1.73 ± 0.71	0.86 ± 0.30	—
S. trutta				
N	39	6	5	—
Larvae	5.58 ± 2.08	4.52 ± 2.24	0.67 ± 0.67	—
Juveniles + adults	0.05 ± 0.02	0.12 ± 0.12	0.10 ± 0.10	—
Total	5.63 ± 2.07	4.64 ± 2.33	0.77 ± 0.65	—

Mann–Whitney (M–W), significant difference between habitats *$p < 0.05$.

($F = 10.51$, $p < 0.05$). The average numbers consumed by the last two species did not differ significantly ($F = 3.49$, $p > 0.05$).

On both experimental situations no prey size selection was detected, prey was eaten proportionally to their abundance (with refuge: $G_H = 0.11$, d.f. = 3, $p > 0.05$; without refuge: $G_H = 0.21$, d.f. = 3, $p > 0.05$).

Discussion

P. trucha was dominant in the three lakes where it was present, with higher catches in shallower environments, with higher temperatures and aquatic vegetation cover. On the other hand salmonids were abundant in deeper, cooler lakes with less aquatic vegetation. Vigliano et al. (2001) found that *P. trucha* were more abundant in vegetated areas of Moreno Lake. Salmonids were more abundant in less structured areas of this water body; this could reflect a higher capacity of the native species to use some of the resources of vegetated areas (Olson, Mittelbach, & Osenberg, 1995).

All species were caught in both benthic and pelagic habitats. *O. mykiss* had the highest presence with regards to the other predator species in the pelagic habitat in all lakes. Space use by fish is determined by a great variety of both abiotic and biotic factors (Jackson, Peres-Neto, & Olden, 2001; Wootton, 1998) being resource competition, food availability and predation the most important factors determining species distribution in lakes (Grossman, Ratajczak, Crawford, & Freeman, 1998; Krueger & May, 1991). The highest abundance of *O. mykiss* in the pelagic habitat could be due to a higher capacity to exploit existing resources in it, giving this species an additional advantage over the other components of the fish community in those situations where benthic resources are limited.

The four studied species are facultative predators (Keast, 1985; Mittelbach & Persson, 1998). According to previous studies the piscivory is strongly related to the characteristics of the water body, the prey and the predator behavior (Macchi et al., 1999). Our results showed a differential consumption pattern of the predator species on *G. maculatus*. *P. trucha* ate more juvenile and adult galaxiids irrespectively of lake of origin, did not use the pelagic habitat for feeding and contrary to what it was expected were more efficient eating *G. maculatus* in less vegetated habitats. *G. maculatus* seems to be a secondary food item for *P. trucha* (Macchi, 2004; Macchi et al., 1999) having galaxiid abundance more influence than the inhibitory effects of vegetation on predation rate.
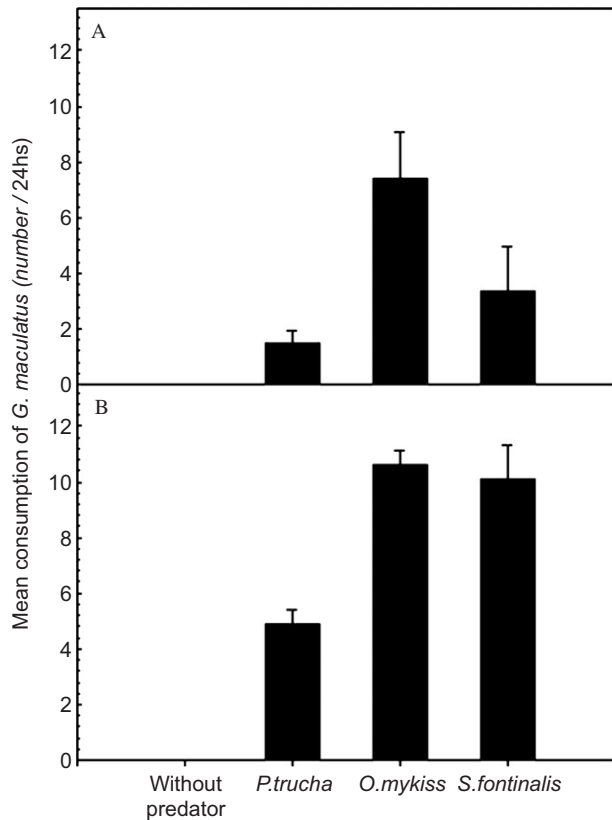
Fig. 5. Mean consumption rate (±SE) of *G. maculatus* by *P. trucha*, *O. mykiss* and *S. fontinalis* in experimental tanks with refuge (A), and without refuge (B) compared to a control tank without predator.

S. trutta are larger than the other species and pray more frequently on large size fish such as *P. trucha* (Macchi, 2004), which would yield more energy per prey. When *P. trucha* are absent such as in Gutiérrez Lake, *S. trutta* replaces big sized fish with great quantities of *G. maculatus* through out the year. Contrary to what would be expected they prey mainly on smaller size *G. maculatus*, which are very abundant in this lake (Barriga et al., 2002).

A third pattern found corresponds to *O. mykiss*, which is the main galaxiid predator in Andean lakes (Arenas, 1978; Macchi, 2004). This species tends to consume great quantities of larval galaxiids in the pelagic habitat. Galaxiids can be a major part of the diet for this species during most of the year such as in Moreno Lake, or it can combine galaxiid consumption with other types of prey broadening its trophic niche. This makes them more efficient as predators in less structured lakes, such as Gutiérrez Lake. Low consumption of *G. maculatus* in Guillelmo Lake could be due to its low densities in this water body (Macchi, 2004).

S. fontinalis has a feeding behaviour somewhat in between that of *P. trucha* and *O. mykiss*. No differences were found for this species with regards to larvae or juvenile + adults consumption. Our experiments showed less consumption efficiency in more structured environments with more vegetation cover. Also it was observed that their presence in the pelagic habitat was circumstantial, which is contrary to what has been observed in lakes from their native range (Magnan, 1988; Magnan & FitzGerald, 1982). This species also showed great variations in consumption between lakes. In Gutiérrez Lake it is the second most important predator, possibly because in this lake it inhabits deeper benthic habitat (Vigliano et al., 1999) were galaxiids are more abundant (Barriga et al., 2002). The relatively low numbers of galaxiids in the stomachs of *S. fontinalis* in Moreno Lake could possibly be due to the higher amount of vegetation cover in this water body. Relative low abundance of galaxiids could be once again the cause for the low selection for this fish prey species in Guillelmo Lake. In lakes of the United States where *S. fontinalis* has been introduced it tends to incorporate a higher amount of fish into its diet (Adams, Frissell, & Rieman, 2001). In Patagonia *S. fontinalis* consumption of galaxiids could be limited by competition with *O. mykiss*.

Despite the differential piscivory patterns among salmonids, they differ as predators of *G. maculatus* from *P. trucha* because they exert a higher overall predation pressure, consume smaller sizes and exert significant predation rates in the pelagic habitat. We cannot assert that the predation behavior observed nowadays of *P. trucha* upon *G. maculatus* observed today is representative of historic habits before the introduction of salmonids, because no studies exist prior to the fish introductions. We can only speculate that it is the result of behavioral changes in response to competition with exotic predators.

We should consider that historic data indicate that the Patagonian silverside (*Odontesthes hatcheri*) was very abundant prior to salmonid introductions. Bruno Videla (1938) reported great abundances of both *P. trucha* and *O. hatcheri* in lakes of Los Alerces National Park before salmonids. Gonzáles Regalado (1945) sustains that salmonids have been the main factor for *O. hatcheri* decline through out their original distribution range. Today *O. hatcheri* occupies marginal habitats of the water bodies originally studied by Bruno Videla (1938), with very low catches in the deep glacial lakes of Northeastern Patagonia (Alonso et al., 1997). It has recently being verified that the silverside feeds upon *G. maculatus* larvae (Macchi et al., 1999), and might have been a significant predator in the past when it was more abundant.

From the point of view of conservation the most dramatic scenario would be that the piscivorous behavior of salmonids would be a new development for galaxiids. Undoubtedly predation intensity by salmonids, starting

with the extensive initial introduction of *S. fontinalis* was high from the beginning (Macchi et al., in press). However, lower predation intensities by this species in vegetated environments may have diminished the impact upon *G. maculatus*.

O. mykiss is by far a more efficient predator of galaxiids than *P. trucha* and possibly also than *S. fontinalis*. This capacity together with the widespread existence of *G. maculatus* in Patagonian lakes may have facilitated the widespread success of *O. mykiss* throughout Patagonia.

Acknowledgments

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