Niche segregation facilitates coexistence between native and introduced fishes in a deep Patagonian lake

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Niche segregation facilitates coexistence between native and introduced fishes in a deep Patagonian lake

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Abstract Species introductions force sympatry between species that did not coevolve. Introduced salmonids have coexisted with native fish since the early 20th century in Patagonian water bodies, thus generating questions about the mechanisms that facilitate their coexistence. We analyzed the trophic and spatial intra- and inter-specific relationships established among native and salmonid species in a deep oligotrophic lake of Patagonia in order to determine niche partitioning patterns as strategies for their coexistence. Salmonids were more generalist feeders, while native species had narrower trophic niches. Native fish and introduced salmonids partitioned food, mainly through the consumption of the crayfish *Samastacus* sp. and the native galaxiid *Galaxias maculatus*, respectively. The diet of most species changed with body size, shifting from insects/amphipods to the larger *G. maculatus* and crayfish. Trophic interactions varied with season, in association with prey seasonality. In general, fishes feeding on the same prey were captured in the same depth strata, indicating common use of food and space. Our results provide new evidence on the trophic ecology of a mixed fish community (exotic-native), supporting the idea that native and non-native fishes could be avoiding negative interactions (e.g., competition) through trophic and spatial resource partitioning.

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Introduction

Species introductions force sympatry between species that did not coevolve, which can result in the coexistence or exclusion of species and consequent modification of the community and ecosystem (Bøhn et al., 2008). A long-standing debate in ecology centers on identification of the processes that determine which species coexist in a local community. Empirical approaches to the problem generally find that species coexistence is favored by differences in resource use (Garrison, 2000), with sympatric species usually presenting a high level of separation along at least one of three niche dimensions: food, habitat, or time (Ross, 1986).

Fish introductions into freshwater constitute an important threat to the structure and functioning of ecosystems, as introduced species may interfere with the use of resources by native species, altering food web functioning, and leading to a decline in native fish populations due to predation and competition for food and habitat (Vander Zanden et al., 1999; Hayden et al., 2013). The ecological strategies of native and introduced species are important in terms of the invader's success in becoming established in the novel environment and the impact of that invasion (Marchetti et al., 2004). Among introduced species, generalists are more likely to become successfully established (Clavel et al., 2010), since an introduced generalist may be able to use a variety of resources in the invaded habitat, thus alleviating direct competition with native taxa (Hayden et al., 2013). Conversely, an introduced specialist may be able to dominate its preferred resource and exclude native competitors (Bøhn et al., 2008). Furthermore, the introduction and establishment of top predators can drastically alter the food web structure and ecosystem functioning of native communities, through predation and consequent trophic cascade top-down effects (Eby et al., 2006).

Rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and brook trout (*Salvelinus fontinalis*) are opportunistic top predators that have been widely introduced into cool-water environments around the world (Crawford & Muir, 2008). They have been identified as responsible for several negative impacts in freshwater ecosystems, including taxonomic diversity reduction (McDowall, 2003) and native food web disruption (Benjamin et al., 2013). These species were introduced into Patagonian water bodies at the beginning of the 20th century where they were able to establish self-sustaining populations (Macchi et al., 2008). Many works have demonstrated their negative ecological consequences in Patagonian freshwater communities, either directly, through predation and competition (Penaluna et al., 2009; Vigliano et al., 2009) or indirectly, by altering the behavior and abundance of prey, thus causing changes in native fish abundance and distribution (Habit et al., 2012; Correa & Hendry, 2012; Correa et al., 2012). The successful establishment of salmonids in Patagonian lakes could be attributed to their biological characteristics and to the characteristics of the recipient systems (i.e., biotic resistance and habitat suitability). In Patagonian lakes, salmonids found appropriate environmental conditions, adequate trophic resources, and few potential competitors. Morphological differences between salmonids and native fish may have favored the invasion process and subsequent coexistence. Salmonids have a more streamlined body, characteristic of open water foragers, and search for widely distributed and conspicuous prey (e.g., fish prey). Native species, in contrast, are morphologically better adapted to foraging in structurally complex habitats such as the vegetated littoral zone, and search for more cryptic prey (Svanbäck & Eklöv, 2004).

In Argentine Patagonia, the lack of studies prior to salmonid introductions and the absence of freshwater bodies without salmonids have historically made it very difficult to determine how native species may have reacted to the introductions, or identify the mechanisms that shaped the present communities. In recent years, progress has been made in relation to the current state of fish communities and salmonid–native interactions in the region. Literature ranges from descriptions of fish assemblage composition and salmonid distribution (Pascual et al., 2007; Aigo et al., 2008; Macchi et al., 2008) to studies of current trophic relationships between some of the species (Macchi et al., 1999, 2007; Lattuca et al., 2008; Vigliano et al.; 2009; Juncos et al., 2011, 2013). Hydroacoustic surveys and complementary gillnetting data have shown that salmonids and native fish are

found predominantly in the nearshore areas of the lakes (Rechencq et al., 2011), thus interactions occur mainly in the littoral zone (Macchi et al., 1999; Milano et al., 2002, 2006). Some segregation of habitat between salmonids and native fish, and similarities in their diets have been shown (Lattuca et al., 2008; Juncos et al., 2011, 2013). Moreover, evidence has been found that salmonids, unlike native fish, are also able to use the superficial pelagic habitat (Macchi et al., 2007; Rechencq et al., 2011; Juncos et al., 2013). However, all the studies mentioned address partial issues in relation to the overall trophic ecology of salmonid–native interactions in scenarios of low-to-medium fish assemblage and lake structural complexity, knowledge which is often mistakenly extrapolated to lakes of higher complexity. The present work attempts to elucidate and integrate varying aspects of salmonid–native interactions in Lake Nahuel Huapi, the largest and most biologically and structurally complex water body of Northern Patagonia.

The Lake Nahuel Huapi fish community is formed by five native species: creole perch (*Percichthys trucha*), velvet catfish (*Olivaichthys viedmensis*), big puyen (*Galaxias platei*), Patagonian silverside (*Odontesthes hatcheri*), and small puyen (*Galaxias maculatus*), plus the three aforementioned salmonid species. Salmonid introduction into this lake began in 1904 with the stocking of *S. fontinalis*, followed by *O. mykiss* in 1928, and *S. trutta* in 1931; all three species establishing self-sustaining populations (Macchi et al., 2008). The current scenario in Lake Nahuel Huapi, a large ultra-oligotrophic lake with a simple food web, includes three exotic predators (i.e., salmonids) coexisting with five native fishes that are ecologically different to salmonids. Theoretically, for species to coexist some degree of niche segregation between species must be expected. Moreover, the degree of niche overlap between two species may also vary ontogenetically and can be affected by seasonal changes in food availability (Werner & Gilliam, 1984). Therefore, we hypothesized that native fishes and introduced salmonids in Lake Nahuel Huapi (1) show marked niche (i.e., diet and habitat) segregation throughout the seasons, and also (2) undergo ontogenetic niche shifts (i.e., from small invertebrates to larger prey). To test these hypotheses, we analyzed the trophic and spatial intra- and inter-specific relationships established between natives and salmonid species in this lake. The specific objectives of the study

were (1) to determine seasonal- and size-related feeding habits of the species and (2) to determine seasonal intra- and inter-specific niche interactions (trophic and spatial) between fishes. This work thus summarizes and provides new information on niche partitioning patterns as strategies for native and non-native fish coexistence in large Patagonian Lakes.

Methods

Study area

Lake Nahuel Huapi (40°55′S, 71°30′W; Fig. 1), located at 765 masl within the Nahuel Huapi National Park, is Northern Patagonia's largest natural lake, with a surface area of 557 km² and a maximum depth of 464 m (Díaz et al., 2007). Lake Nahuel Huapi can be classified as monomictic and ultraoligotrophic to oligotrophic, with mean total phosphorous concentrations of 5.0 μg l⁻¹, mean chlorophyll a concentrations of 0.5 μg l⁻¹, and a mean Secchi disk of 14.4 m (Díaz et al., 2007). The basin is composed of seven branching arms with 357 km of shoreline and is drained by the Limay River into the Atlantic Ocean. The climate in the region is cold temperate. As the prevailing westerly winds cross the Andes, they create a strong climatic gradient across the lake basin, with higher precipitation and moisture in the west and arid conditions toward the east. Fall and winter precipitation on Lake Nahuel Huapi ranges from 2,700 to 500 mm year⁻¹, following the West to East climatic
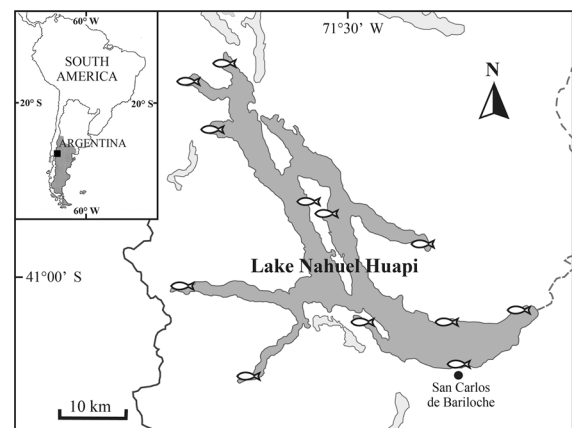

Fig. 1 Map of the study area in Northern Patagonia, Argentina, indicating the 12 sampling sites (fish symbols)

gradient characteristic of the region (Fig. 1). Shoreline and upland vegetation reflects this gradient, thus dense southern beech (*Nothofagus* spp.) forests inhabit the western end and steppe shrubs prevail at the eastern end of the basin.

The lake fish community is formed by five native fish and three introduced salmonids. *Oncorhynchus mykiss* and the native *P. trucha* are currently the most abundant species, salmonids representing almost 60% of the total CPUE (experimental gill net catch per unit effort; Juncos et al., 2011).

Data collection

Fishes were sampled between 2005 and 2009 using gill nets set once in summer, autumn, winter, and spring at 4 different sites each year, totaling 12 sampling sites (Fig. 1). At each site, sinking horizontal gill nets (70 m long, 2 m high, each consisting of seven 10-m-long panels with randomly located bar mesh sizes of 15, 20, 30, 40, 50, 60, and 70 mm) were set at sunset, parallel to the shore at depths of 2, 10, 20, 30, 40, and 50 m. The nets were picked up at dawn, thus averaging 10 h of soak time. Specimens with total lengths (TL) of at least 210 mm are completely recruited to this net configuration, but fishes smaller than 210 mm are considered to be underrepresented in catches. Pelagic zones were not sampled because previous studies in the region showed that fish densities in these habitats are very low (Vigliano et al., 1999, 2009) except for larval galaxiids too small to be vulnerable to gill nets, which would require unfeasibly high fishing effort to obtain meaningful catch data. Each fish was identified to species level; total and standard lengths (TL and SL) were measured to the nearest millimeter and total weight (WT) to the nearest gram. Stomachs were removed and preserved for the examination of food contents under a stereomicroscope.

A total of 1,781 individuals belonging to the seven species likely to be caught with gill nets (individuals >210 mm TL) were collected for diet analysis. The number of fish with food in their stomachs was 1,341: 541 *O. mykiss*, 347 *P. trucha*, 237 *S. trutta*, 107 *G. platei*, 54 *O. viedmensis*, 49 *S. fontinalis*, and 6 *O. hatcheri*. Empty guts (25 %) were not considered in subsequent analysis. Prey items were identified to the lowest possible taxonomic level, and wet weight was recorded in grams. Prey items were then grouped into nine major categories: (1) insect larvae and pupae/ nymphs, (2) adult insects, (3) molluscs (mostly *Chilina*

sp.), (4) crayfish *Samastacus* sp., (5) freshwater anomuran crab *Aegla* sp., (6) amphipod *Hyalella* sp., (7) galaxiid larvae and juveniles, (8) *G. maculatus* adults, and (9) other fish. Larval forms of *G. maculatus* and *G. platei* are difficult to differentiate at this stage and were thus grouped into the category "larval and juvenile galaxiids"; however, personal observations and studies in other lakes in the region showed that the *G. maculatus* represent almost all the larval galaxiids.

Data analysis

Data were analyzed in four steps, according to three levels of resolution, from the most general to the most specific: (1) general diet fish segregation patterns without considering size groups, season, or depth of catch; (2) size-related diet shifts of each species; (3) seasonal trophic overlaps between species-size units as determined in step 2; (4) seasonal habitat (i.e., depth strata) overlaps for the same species-size units used in step 3.

To determine the diet specialization of each species, niche breadth was quantified using Levins Index (1968) as $B = \left[\left(\sum p_i^2 \right) \right]^{-1}$, where p_i is the proportional contribution in numbers of prey i individuals to the total number of prey items. Levins Index results in values from 1 to n, with 1 equivalent to a single type of prey (specialist predator) and n indicating that all the different types of prey appear in equal proportion (generalist predator). The relative contribution of each prey category to fish diet was estimated using the index of relative importance (IRI; Pinkas et al., 1971) as $IRI = (N\% + W\%) \, O\%$, where N and W are the number and weight of food items of a given food type expressed as a percentage of all food items; O is the frequency of occurrence expressed as the number of stomachs containing one or more items of each food category, expressed as the percentage of all non-empty stomachs. To facilitate diet comparisons between species, IRI was standardized to IRI%, calculated as $IRI\% = 100 \, IRI (\Sigma IRI)^{-1}$.

A multivariate approach at two resolution levels was used to explore diet similarities between and within species, using the statistical package PRIMER (version 5.2.9; Clarke & Gorley, 2006). To determine whether fish stomach contents differed between all the sampled sites, the nonparametric one-way analysis of similarity (ANOSIM, $\alpha = 0.05$, 999 permutations in the matrix) was applied to a similarity matrix based on the square

root transformed values of IRI% (an appropriate transformation for percentage data, Platell & Potter, 2001) of each species. Because the relative importance of prey did not vary between sampling sites for any species (ANOSIM; $0.008 >$ Global $R > 0.19$; $P > 0.05$), subsequent analyses were carried out without considering sampling site influence. To elucidate size-related groups and ontogenetic changes in fish diet, fish samples were grouped into 10- to 40-mm length classes on the basis of the available size range, and IRI% was calculated for each one. A hierarchical agglomerative cluster analysis based on the square root IRI% values for each length class was performed to define size groups of similar diet, using the Bray–Curtis coefficient of similarity (multiplied by 100) based on a similarity matrix and the group-average linking method (Clarke & Warwick, 2001). The similarity profile (SIMPROF) test ($\alpha = 0.05$; 999 permutations) was applied to distinguish significant groups in the cluster analysis, to test the null hypothesis of no meaningful structure within samples (Clarke et al., 2008). The results were used to define new length groups based on diet similarities. These new size groups were then used as units of comparison for describing seasonal diet and depth overlapping patterns. Pairwise Bray–Curtis similarity was used as a measure of dietary overlap (Marshall & Elliott, 1997). For depth overlap analysis, relative abundances for each species/size class by depth-strata cell were computed as the mean catch per unit effort (CPUE), where effort is defined as the product of soak time multiplied by the total area of each gill net used, and standardized to 15 h and 100 m^2 of gill net. Bray–Curtis similarity matrices were calculated

separately for diet and depth analysis, using the square root transformed IRI% and CPUE%, respectively, then presented seasonally through hierarchical agglomerative clustering (group-average linkage). Similarity levels higher than 60 % were considered significant overlaps (Nunn et al., 2007). We also described "moderate overlaps" as those with similarities between 50 and 60 %. The features underlying the overlapping patterns were interpreted using the correspondence analysis (CA) ordination technique. The CA was computed using the XLSAT 7.5 package, between the species-size (rows) and prey categories, or depth strata (columns), to simultaneously visualize the relationships between fish and food source (or depth use) data in the same low-dimensional vector space. This analysis allowed us to distinguish the prey categories responsible for the overlapping patterns and the depth strata in which species were most related in each season. Correspondence analysis is a very robust approach, widely used for analyzing compositional data, as is frequently the case with diet data (Chipps & Garvey, 2007).

A significance level of a minimum of 5 % was considered in all statistical analyses.

Results

General dietary patterns

Trophic diversity varied between species on an annual basis, with salmonids having a more diverse diet than native fish (Table 1). Among salmonids, *O. mykiss*

Table 1 Annual trophic diversity (expressed as Levins Index, B) and diet composition (expressed as percentage index of relative importance, IRI%) of the seven fish species caught in Lake Nahuel Huapi

	Odontesthes hatcheri	*Percichthys trucha*	*Galaxias platei*	*Olivaichthys viedmensis*	*Oncorhynchus mykiss*	*Salmo trutta*	*Salvelinus fontinalis*
B	1	1.6	1.9	2.1	5	3.7	4.3
Insect larvae and pupae/nymphs	3.73	19.86	0.47	24.48	15.66	0.14	0.09
Adult insects	0.00	0.00	0.00	0.06	3.20	0.01	0.38
Molluscs	96.27	0.00	0.05	0.51	1.12	0.15	1.90
Samastacus sp.	0.00	66.51	71.15	66.01	7.13	19.84	9.33
Aegla sp.	0.00	0.29	0.00	1.71	5.45	0.74	14.00
Hyalella sp.	0.00	8.20	16.49	6.24	20.97	1.54	21.34
Galaxiid larvae and juveniles	0.00	2.05	10.70	0.68	32.38	50.74	21.62
Galaxias maculatus adults	0.00	3.07	1.11	0.31	14.08	26.17	31.33
Other fish	0.00	0.02	0.03	0.00	0.01	0.68	0.01

exhibited the highest trophic diversity ($B = 5$), the most piscivorous *S. trutta* the lowest ($B = 3.7$), and *S. fontinalis* had intermediate values ($B = 4.3$) (Table 1). *Odontesthes hatcheri* was at the opposite end of the trophic spectrum, with a very specialized diet ($B = 1$), feeding almost exclusively on molluscs (Table 1). However, this could be an artifact due to the small number of individuals captured ($n = 6$), and only in summer. Therefore, *O. hatcheri* was not included in subsequent size-related and diet overlap analyses. *Percichthys trucha*, *G. platei,* and *O. viedmensis* presented narrower trophic niches ($B = 1.6, 1.9, 2.1$, respectively) (Table 1), suggesting that native fish have more specialized diets than salmonids. The crayfish *Samastacus* sp. was the most important prey for natives, whereas larval and juvenile galaxiids and adults of *G. maculatus* were the most important prey for salmonids (Table 1). For the most generalist species, *O. mykiss*, the amphipods *Hyalella* sp., and insects (larvae and pupae) were important complementary prey. Larval insects also contributed greatly to the diets of *P. trucha* and *O. viedmensis*. *Samastacus* sp. and *Aegla* sp. were secondary prey for *S. trutta* and *S. fontinalis*, respectively (Table 1).
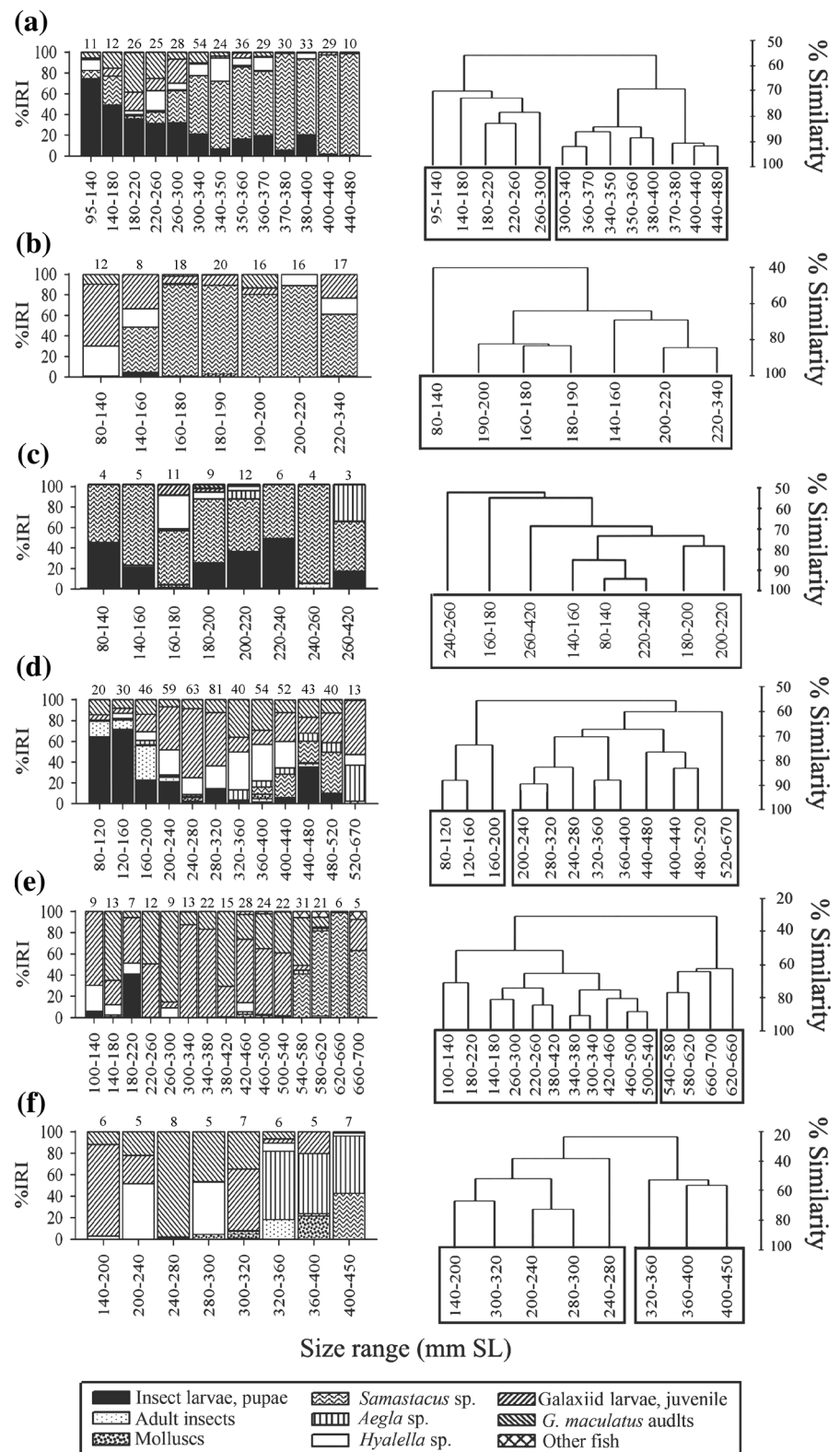
Size-related dietary patterns

Size-related diet shifts were observed only in *P. trucha, O. mykiss, S. trutta,* and *S. fontinalis* (Fig. 2). For these species, cluster analysis and the SIMPROF test led to the identification of two significant feeding groups (hereinafter size groups will be denominated "small" and "large"; Fig. 2a, d, e, f, right column). Small *P. trucha* fed mainly on larval insects and adult *G. maculatus*, whereas large individuals consumed *Samastacus* sp. crayfish (Fig. 2a, left column). Small *O. mykiss* fed mainly on insects and *G. maculatus* adults, while large *O. mykiss* consumed predominantly larval and juvenile galaxiids and to a lesser extent, *Samastacus* sp. (Fig. 2d, left column). The diet of small *S. trutta* was characterized by larval and juvenile galaxiids and adults of *G. maculatus*, while the diet of large individuals was determined by the consumption of *Samastacus* sp. (Fig. 2e, left column). Small *S. fontinalis* consumed mainly *G. maculatus* adults and lower proportions of larval and juvenile galaxiids. Unlike the large individuals of the other species analyzed, large individuals of *S. fontinalis* incorporated the crab *Aegla* sp., instead of the crayfish

Samastacus sp. (Figure 2f, left column). The diets of *G. platei* and *O. viedmensis* did not show a significant ontogenetic shift, *Samastacus* sp. being the preferred prey for most sizes of both species, as well as some galaxiids or larval insects, respectively (Fig. 2b, c).

Seasonal trophic overlaps

Diet inputs used for trophic analyses are in electronic supplementary material (ESM S1). The CA graphic representation shows the associations between fishes (proximity between points indicate their similarity), thus corroborating the groups evidenced through cluster analysis and also showing the relationship between fishes and prey categories (through the projections of the point "species" on the "variable" prey vectors). In spring, significant dietary overlaps (>60 % similarity) were found for small and large *S. fontinalis*, and also for small and large *P. trucha* and large *O. mykiss* (Fig. 3a). The great similarity between size-classes of *S. fontinalis* was given by the high consumption of the amphipod *Hyalella* sp., while the feeding group of *P. trucha* and large *O. mykiss* was highly associated with the consumption of insect larvae and pupae. Small *O. mykiss* overlapped moderately with the later group, also consuming adult insects (dotted line in figure). *Galaxias platei* and large *S. trutta* formed a feeding group with moderate similarity, consuming mainly *Samastacus* sp. and also *G. maculatu*s adults in the case of *S. trutta* (ESM S1). Small *Salmo trutta* presented low similarity to the other fishes because of the dominance of *G. maculatus* adults in its diet. *Olivaichthys viedmensis* had empty guts. In summer, there were three feeding groups with significant overlaps (Fig. 3b). Small individuals of *S. trutta* and *S. fontinalis* had higher diet overlap, feeding on *G. maculatus* adults. Small individuals of *P. trucha* and *O. mykiss* overlapped mainly due to the consumption of insect larvae and pupae, and they all overlapped moderately with large *O. mykiss,* which included adult insects in their diets. *Galaxias platei*, *O. viedmensis,* and large individuals of *P. trucha* and *S. trutta* formed a feeding group characterized by the consumption of *Samastacus* sp., while large *S. fontinalis* were differentiated by the consumption of *Aegla* sp. In autumn, the combination of the hierarchical cluster and CA evidenced two feeding groups with high similarity (Fig. 3c). One was formed by small individuals of *S. trutta*, *S. fontinalis*, *P. trucha,* and small and large *O. mykiss*, all characterized

Fig. 2 Diet composition (expressed as percentage index of relative importance, IRI%) separated by size ranges (*left column*), and dendrograms showing diet similarities of size ranges using group-average linking on Bray–Curtis similarities and significant groups defined by SIMPROF test (*right column*) for **a** *P. trucha*, **b** *G. platei*, **c** *O. viedmensis*, **d** *O. mykiss*, **e** *S. trutta*, and **f** *S. fontinalis*. *n* is indicated above the *bars* of each size range
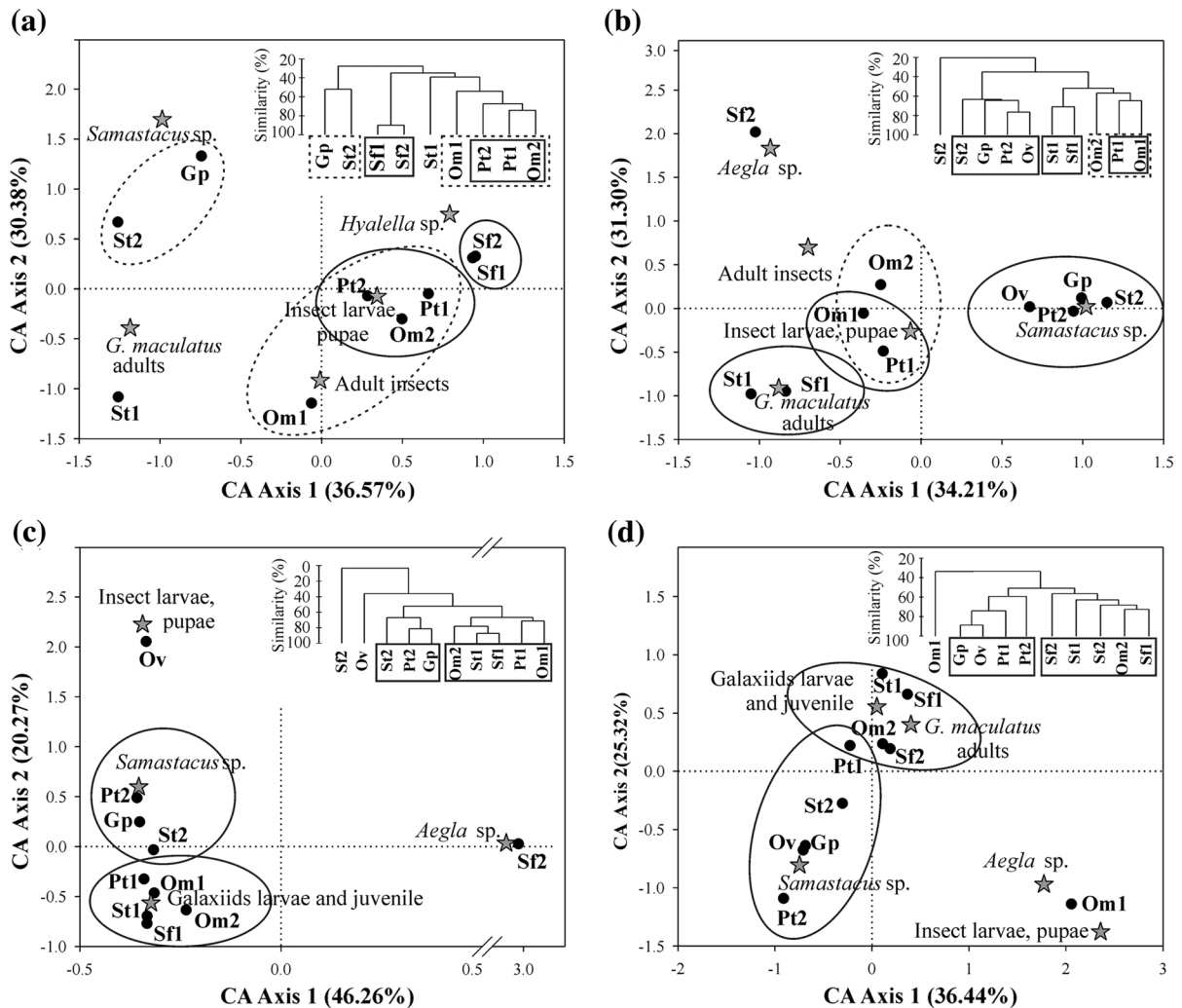

Size range (mm SL)

Legend:
- ■ Insect larvae, pupae
- ▨ *Samastacus* sp.
- ▨ Galaxiid larvae, juvenile
- ░ Adult insects
- ▥ *Aegla* sp.
- ▨ *G. maculatus* audlts
- ▦ Molluscs
- □ *Hyalella* sp.
- ▧ Other fish

(a)

(b)

(c)

(d)

Fig. 3 Diet similarity dendrogram and CA biplot representing fishes (*black points*) and prey (*gray stars*) for spring (**a**), summer (**b**), autumn (**c**), and winter (**d**) data. *Boxes* or *circles* in *solid line* indicate significant overlaps (similarity >60%), and *boxes* or *circles* in *dotted lines* indicate moderate overlaps (similarity between 50 and 60 %). Only scores of the most important prey categories are indicated in CA axes (prey contributing less than 2 % of inertia were excluded). Pt1: small *P. trucha* (95–300 mm SL); Pt2: large *P. trucha* (300–480 mm SL); Ov: *O. viedmensis*; Gp: *G. platei*; Om1: small *O. mykiss* (80–200 mm SL); Om2: large *O. mykiss* (200–670 mm SL); St1: small *S. trutta* (100–540 mm SL); St2: large *S. trutta* (540–700 mm SL); Sf1: small *S. fontinalis* (140–320 mm SL); St2: large *S. fontinalis* (320–450 mm SL)

by the consumption of larvae and juvenile galaxiids. A second group was formed by *G. platei* and large individuals of *P. trucha* and *S. trutta*, feeding mainly on *Samastacus* sp., and also eating galaxiids, explaining the proximity of the two groups in the CA graph. Large *S. fontinalis* were separate, consuming exclusively *Aegla.* sp., while *O. viedmensis* consumed mostly insects. In winter, significant overlaps occurred between salmonid fishes, which fed on galaxiid larvae, juvenile, and adults, while native fishes overlapped

because of the predominant consumption of *Samastacus* sp. Small *P. trutta* also fed mainly on galaxiids (ESM S1), which was reflected by its location in the CA graph (Fig. 3d). Small *O. mykiss* were differentiated by the consumption of *Aegla* sp. and insects.

Seasonal habitat overlaps

When looking at relations between fishes according to catch depths (Fig. 4), some important patterns can be

highlighted. In spring (Fig. 4a), *G. platei* and large *S. trutta* (eating *Samastacus* sp., see Fig. 3a) were mainly associated with deeper strata (30–50 m). Intermediate strata (10–30 m) were occupied by *O. viedmensis*, small *P. trucha*, large *O. mykiss* (eating insects), and small *S. trutta* (eating *G. maculatus*). Finally, superficial strata (2 m) were mainly used by *S. fontinalis* (consuming *Hyalella* sp.), small *O. mykiss*, and large *P. trucha* (both eating insects; see Fig. 3a). In summer, a great spatial overlap was observed, with

fish distributed throughout all depths (Fig. 4b). However, a gradient in catches by depth could be observed. *Salvelinus fontinalis* were restricted to superficial strata (2–10 m), *O. mykiss* and small *S. trutta* had slightly wider depth range distributions (2–30 m), *P. trucha* were more frequently captured at intermediate depths (20–40 m), and large *S. trutta* and *G. platei* in the deepest strata (30–50 m). In autumn (Fig. 4c), *O. viedmensis*, small and large *P. trucha*, small and large *S. trutta*, large *O. mykiss,* and *G. platei* shared the same
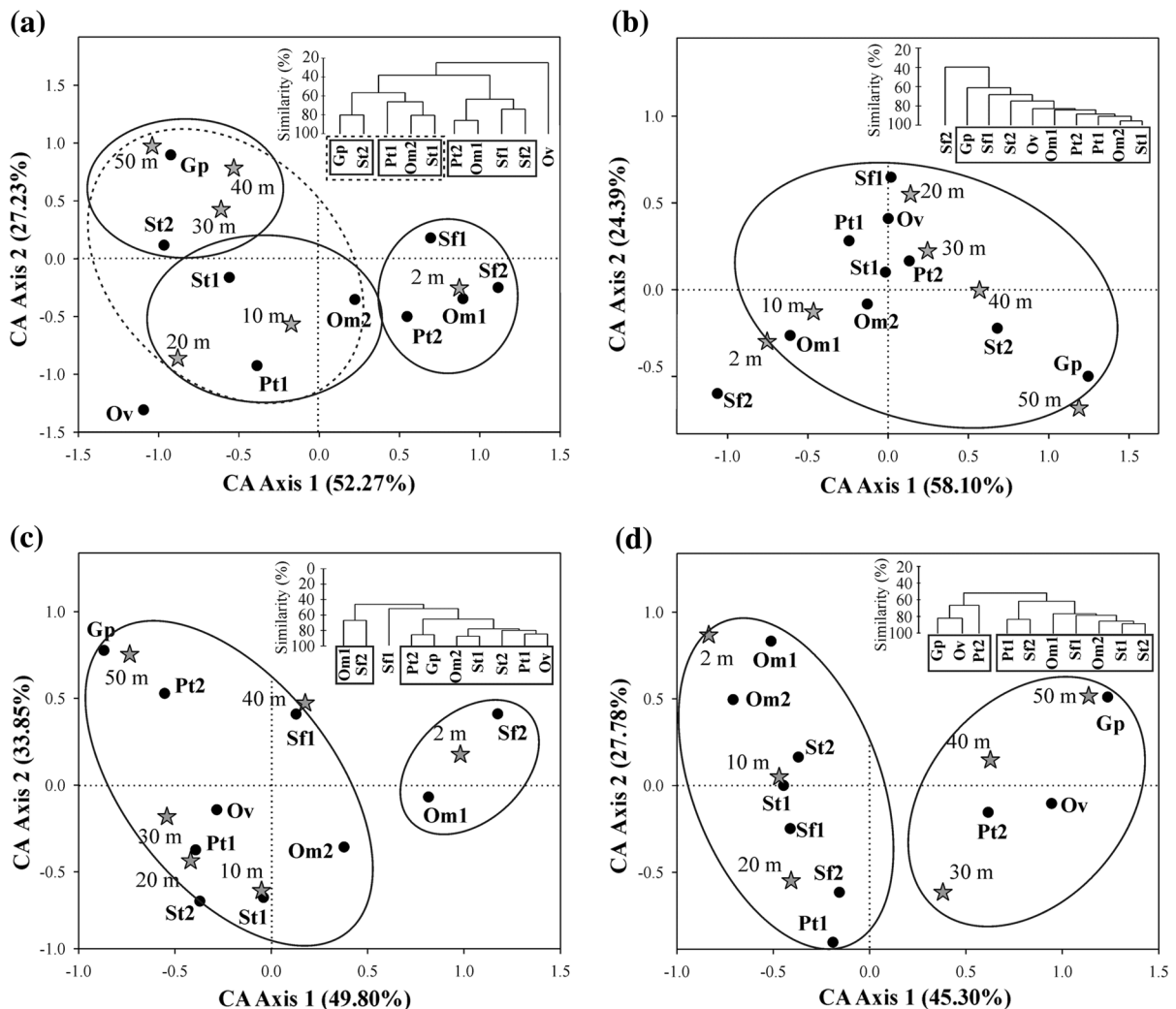

Fig. 4 Depth catch similarity dendrogram and CA biplot representing fishes (*black points*) and depth strata (*gray stars*) for spring (**a**), summer (**b**), autumn (**c**), and winter (**d**) data. *Boxes* or *circles* in *solid line* indicate significant overlaps (similarity >60%), and *boxes* or *circles* in *dotted lines* indicate moderate overlaps (similarity between 50 and 60 %). Pt1: small

P. trucha (95–300 mm SL); Pt2: large *P. trucha* (300–480 mm SL); Ov: *O. viedmensis*; Gp: *G. platei*; Om1: small *O. mykiss* (80–200 mm SL); Om2: large *O. mykiss* (200–670 mm SL); St1: small *S. trutta* (100–540 mm SL); St2: large *S. trutta* (540–700 mm SL); Sf1: small *S. fontinalis* (140–320 mm SL); St2: large *S. fontinalis* (320–450 mm SL)

depth strata (10–50 m), although higher catches of *G. platei* and large *P. trucha* occurred at 40 and 50 m (high similarity), where they ate *Samastacus* sp. (see Fig. 3c). Small *O. mykiss* and large *S. fontinalis* shared superficial strata. In winter, the fishes sharing prey resources also shared depth strata, with natives and salmonids clearly segregating in space. *Galaxias platei*, *O. viedmensis*, and large *P. trucha* were mainly captured between 30 and 50 m and were segregated from the fishes eating galaxiids located between 2 and 20 m depth (Fig. 4e).

Discussion

Our results demonstrated that there is resource partitioning between non-native salmonids and native fish in Lake Nahuel Huapi, mainly through the consumption of a native fish, the small puyen *G. maculatus*, and of the crayfish *Samastacus* sp., in agreement with previous studies in the region (Macchi et al., 1999; Vigliano et al., 2009; Juncos et al., 2011, 2013). However, a more detailed analysis showed that the trophic relationships of the lake's fish community are much more complex. The interactions within and between species are greatly influenced by fish size, season, and depth. In this sense, a few specific patterns can be summarized: (1) Size-related diet shifts were observed in salmonid fishes and in the native *P. trucha*, with the prey consumed varying from smaller to bigger sizes as consumer size increased. (2) *Galaxias platei,* together with large individuals of *P. trucha* and *S. trutta,* usually presented high diet similarities, feeding mainly on *Samastacus* sp. associated with deeper depth strata. (3) Smaller fishes, especially small individuals of *P. trucha* and *O. mykiss*, usually shared trophic resources, in each season apparently relying on easily available prey, and occupying intermediate and superficial depth strata. (4) *Salvelinus fontinalis* was usually differentiated from the other fish by the consumption of *Hyalella* sp. or *Aegla* sp., in superficial depth strata. (5) In general, fishes feeding on the same prey were captured in similar depths, indicating common use of food and space.

Through Levins index, we found that salmonids were more generalist feeders, especially rainbow trout, while native species had narrower trophic niches. Reviewing the literature on the feeding ecology of salmonids around the world, it is difficult to ignore the great trophic flexibility exhibited by these fishes, with diets varying according to the environment in which they are found (e.g., Wissinger et al., 2006; Browne & Rasmussen, 2009). Because of diet flexibility, generalists are often able to live in diverse habitats. Therefore, non-native generalist fishes have a better chance of finding necessary resources and appropriate environmental conditions (Clavel et al., 2010), as is the case of introduced salmonids in Northern Patagonian lakes. Furthermore, the morphological characteristics of salmonids, with streamlined bodies and great visual development (both characteristics found in open water foragers, Svanbäck & Eklöv, 2004), make them efficient predators of *G. maculatus* (Macchi et al., 2007). On the other hand, *P. trucha* is a benthic-littoral feeder in Patagonia, eating *G. maculatus* when they are in high abundance (Macchi et al., 2007), mainly in littoral habitats (Juncos et al., 2013). This in turn would have allowed salmonids to differentiate from the more specialist and benthivorous native fishes in Lake Nahuel Huapi, facilitating their coexistence. Therefore, the different food preferences and particular foraging strategies that characterize native (benthic feeders, e.g., *P. trucha*) and salmonid species (more efficient open water- fish feeders) might be important factors in minimizing negative interactions in this and other Patagonian lakes (Macchi et al., 1999, 2007).

We found diet shifts related to size in all species except *O. viedmensis* and *G. platei*. In general, the fish switched from small benthic invertebrates to larger fish and crayfish prey. Furthermore, small *O. mykiss* also fed on adult insects (mainly of terrestrial origin), highlighting their ability to take advantage of varying food and energy sources (e.g., allochthonous) throughout their lives. *Percichthys trucha*, especially at large sizes, relied mainly on *Samastacus* sp., whereas salmonids were more piscivorous at all sizes, feeding mainly on galaxiids, with the exception of large *S. fontinalis*, which consumed greater proportions of *Aegla* sp. The piscivory of *S. trutta* was predominant until they reached 540 mm SL (corresponding to age five according to Juncos et al., 2013), when they incorporated *Samastacus* sp. into their diet. Diet shift to larger prey presumably occurs as an attempt to eat more energetically profitable organisms as predators increase in size, followed by increased growth rates (Werner & Gilliam, 1984). However, as prey size increases, so do encounter probability and handling

time, while prey vulnerability decreases (Graeb et al., 2006). In the lake studied, size-related variations were observed in fish diet, especially regarding the most important prey items (i.e., galaxiids and crayfish). These two high-quality prey (see Vigliano et al., 2009) are the main source of energy for salmonids and *P. trucha* in Lake Nahuel Huapi throughout the year; their energy budgets being supplemented by other prey according to season and size. *Galaxias maculatus* has a reduced size spectrum, and lower energy densities than *Samastacus* sp. (Vigliano et al., 2009). In general, most of the larger predators seem to select the high-energy *Samastacus* sp. instead of *G. maculatus*. However, when galaxiid abundance is high (i.e., in autumn, when they recruit to the littoral zone, Barriga et al., 2002), most predators consume this small prey, thereby maximizing energy acquisition by targeting the most abundant, profitable, and easily captured prey, thus minimizing the energetic cost of food uptake. This could indicate that piscivory is more likely to be related to prey availability than to predator size in this ecosystem.

When combining seasonal variability, size-related diets, and fish depth distributions, variable and complex patterns of intra- and inter-specific diet overlaps between fish emerged. Consumer size and prey availability seem to be the most important variables in determining the observed trophic segregation (or trophic similarity) patterns. Fish belonging to the larger size groups generally formed a trophic group based on *Samastacus* sp. consumption (or the other decapod, *Aegla* sp., in the case of *S. fontinalis*), while smaller sized groups mainly overlapped due to the consumption of prey which were more readily available in each season (e.g., insects in spring, *G. maculatus* larvae and juveniles in autumn). Regarding fish depth distribution, in general, fishes feeding on the same prey were captured in the same depth strata. For instance, fishes consuming *Samastacus* sp. were caught mostly in deeper strata (40–50 m), while fishes eating *G. maculatus* or insects were caught mainly at depths less than 30 m, and fishes feeding on *Aegla* sp. (like *S. fontinalis*) were mostly restricted to superficial depth strata (2 m). These patterns could be linked to prey distribution. Although little is known about crayfish distribution and abundance in Patagonian lakes, an increase in their catches with increasing depth has been observed in Lake Nahuel Huapi (M. B. Lucci, unpublished data), which is in agreement with our

findings. Our results regarding diet and depth overlap indicate a common use of food and space rather than the complete niche segregation expected as a mechanism to avoid potential competition (Garrison, 2000). However, information on trophic and spatial overlap alone is insufficient to test the presence or severity of competition. To evaluate competition, besides substantial niche overlap, limited available resources have to be demonstrated (Wiens, 1993). Low diet overlap could result from past competition (i.e., ghost of competition past; Connell, 1980), or, conversely, significant overlap may occur with no competition if predators are sharing abundant prey resources, as could be the case of *G. maculatus* in Lake Nahuel Huapi. Stages of *G. maculatus* found in predators' stomachs include both metamorphic larvae (which are migrating from pelagic to littoral habitat in search of refuge and food), and littoral juveniles and adults (Juncos et al., 2013). It has recently been shown that juvenile and adults of *G. maculatus* perform diel horizontal migrations (Milano et al., 2013). Therefore, it is likely that predators take advantage of the high availability and increased vulnerability of *G. maculatus* not only during recruitment of metamorphic larvae to the littoral zone, but also during the diel movements of juveniles and adults outside the littoral area.

Bioenergetics model simulations of fish consumption have shown that non-native predatory fishes exert higher predation pressure on *G. maculatus* and other prey than the native predator *P. trucha* (Juncos et al., 2013), reflecting the impact of salmonid introductions on prey populations. Some authors have argued that elevated abundances of top predators, resulting from the stocking of predatory sport fishes, have often been associated with an imbalance between predator consumption and prey abundance, which is likely to be the greatest in less-productive lakes (Eby et al., 2006). However, other authors have stated that a preferred-prey species that is tolerant to predation (i.e., is able to maintain its abundance in the face of predation) can affect community structure by supporting the density of a predator, thus reducing the density of other prey (Holt, 1977) or allowing it to coexist (Noy-Meir, 1981), thus constituting a keystone prey species. In this context, we can consider *G. maculatus* as a keystone species, without which the ecosystem could have been severely impacted after salmonid introduction. The pre-adaptation of this fish to predation (Macchi et al., 1999), combined with its plastic-

generalist life cycle (Barriga et al., 2012) and its high annual production (Vigliano et al., 2009), could enable it to act as a buffer, thus alleviating the impact of introductions, despite the high predation pressures involved. *Galaxias maculatus* seems to represent a permanent food supply for both native and salmonid fish predators, limiting the negative interactions generated by fish introductions, and thus promoting the coexistence of native fish with exotic salmonids. Our work points out that differential feeding strategies and ontogenetic diet shifts combined with the differential use of depth strata also contribute to this coexistence, probably by maintaining relatively stable predator abundances and ensuring overall constant predation pressure on shared food resources. Moreover, the reproductive strategies of native fish, which mainly spawn in shallow habitats of the lake during spring months (Buria et al., 2007), in contrast with salmonids which mainly spawn in tributaries during autumn and spring (R. Juncos, unpublished data), with juveniles spending 1 or 2 years in tributary rivers, could help natives and salmonids to avoid negative interactions (e.g., competition or predation) during their early life stages. Finally, both the size and heterogeneity of the lake offer habitat diversity providing refuge from predators and also variable food sources, thus improving the capacity of the fish to maintain their populations and avoid negative interactions.

We have to consider *O. hatcheri* as a special case. In other Patagonian lakes, this species has been described as omnivorous, with a diet based on benthic and planktonic organisms (Grosman & Rudzik 1990; Bello et al., 1991; Macchi et al., 1999), and they can even be piscivorous as adults (Bello et al., 1991). In Lake Nahuel Huapi, the few specimens collected fed almost exclusively on the snail *Chilina* sp., which could simply be a consequence of the small sample or the outcome of negative interactions (e.g., resource competition, predation) with other species. Historical records show that *O. hatcheri* were very abundant in lakes before salmonid introductions (Macchi, 2004), probably playing an important role as planktivorous fish (together with *G. maculatus*, Cervellini et al., 1993). Extensive fishing between 1999 and 2005 in all lakes of the Nahuel Huapi drainage basin have shown that this species is only found in protected areas such as highly vegetated near shore habitats, and is absent from open waters in deep oligotrophic lakes (Vigliano

et al., 1999, 2009). These evidences led us to think that salmonids could be responsible for the decline of *O. hatcheri* in Lake Nahuel Huapi, directly affecting them through predation, or indirectly competing for pelagic prey (zooplankton and galaxiid larvae) or benthic prey (macrozoobenthos). Therefore, negative interactions with salmonids may have caused a reduction in *O. hatcheri* trophic and spatial niches. To test these assumptions, however, more detailed studies on the trophic interactions and population dynamics of this species should be carried out.

Regarding the big puyen *G. platei*, recent studies in invaded and non-invaded lakes in western Chilean Patagonia showed that salmonids are the primary drivers of changes in the food web position of this species (Correa & Hendry, 2012), and of their population decline, having them found refuge in low-order lakes unsuitable for salmonids (Correa et al., 2012). A different situation is found in Northern Argentine Patagonian lakes where the *G. platei* population has apparently not declined. The diet of this species consists of large and mobile benthic prey, such as *Hyallela* sp., *Samastacus* sp., and free-ranging larvae and juvenile galaxiids. For most Northern Patagonian lakes, *G. platei* is normally found at depths of under 30 m, below the summer thermocline and euphotic zone, in close association with the lake bottom (Milano et al., 2002, 2006), and also in the water column of the deep pelagic zone (M. Rechencq, unpublished data). It is a specialized bottom dweller and has a wide latitudinal distribution as a result of general adaptations to benthic life (Milano, 2003). Food and refuge can be found in the detritus of the benthic habitat, as well as in the darkness of the deep pelagic water column, and both habitats would probably serve as an antipredatory strategy in an environment which combines low trophic competition with high selection pressure (Cussac et al., 2004). Hence, *G. platei* resistance to salmonid introductions in Argentine Northern Patagonian lakes could be due to its ability to exploit a habitat that is unfavorable for salmonids (i.e., deep benthic habitat), where it finds refuge from predation and competition. Overall, the impact on more vulnerable native species, as could be the case of *O. hatcheri*, could be related to the lack of available refuges not used by salmonids.

To our knowledge, the present work is one of few to deal with different aspects of the feeding ecology of a fish community impacted by salmonids in a lake of

great dimensions (both surface and depth), attempting to disentangle the mechanisms that facilitate salmonid–native coexistence. Here we go deeper into the study of resource partitioning as a strategy for native and exotic fish coexistence in an understudied large deep ultraoligotrophic lake in Argentine Northern Patagonia, analyzing ontogenetic and seasonal trophic relationships and also habitat segregation patterns. Our research provides some new evidence on the trophic ecology of these mixed communities (exotic-native), supporting the idea that native and non-native fishes could be avoiding negative interactions (e.g., competition) through trophic and spatial resource partitioning. Future research should focus on assessing prey availability and prey traits to determine the capacity of the system to support this complex fish community and to establish the role of competition in community stability. Furthermore, stable-isotope analysis of nitrogen and carbon is a powerful tool for tracing food webs, widely applied in studies of fish ecology in lakes (Vander Zanden et al., 1999), so its use in this lake study could help confirm the observed trophic and spatial patterns, also providing time-integrated and energy-based descriptions of those relationships.

References

Aigo, J., V. Cussac, S. Peris, S. Ortubay, S. Gómez, H. López, M. Gross, J. Barriga & M. Battini, 2008. Distribution of introduced and native fish in Patagonia (Argentina): patterns and changes in fish assemblages. Reviews in Fish Biology and Fisheries 18: 387–408.

Barriga, J. P., M. A. Battini, P. J. Macchi, D. Milano & V. E. Cussac, 2002. Spatial and temporal distribution of landlocked *Galaxias maculatus* and *Galaxias platei* (Pisces, Galaxiidae) in a lake in the South American Andes. New Zealand Journal of Marine and Freshwater Research 36: 349–363.

Barriga, J. P., M. A. Battini, M. García-Asorey, C. Carrea, P. J. Macchi & V. E. Cussac, 2012. Intraspecific variation in diet, growth, and morphology of landlocked *Galaxias maculatus* during its larval period: the role of food availability and predation risk. Hydrobiologia 679: 27–41.

Bello, M. T., M. M. Bunge & M. Baiz, 1991. Alimentación natural del pejerrey (*Patagonina hatcheri*) introducido en la laguna Ñe Luan, Río Negro [Natural feed of silver*side* (*Patagonina hatcheri*) introduced in lagoon Ñe Luan, Río Negro]. Biología Pesquera 20: 13–19.

Benjamin, J. R., F. Lepori, C. V. Baxter & K. D. Fausch, 2013. Can replacement of native by non-native trout alter stream-riparian food webs? Freshwater Biology 58: 1694–1709.

Bøhn, T., P.-A. Amundsen & A. Sparrow, 2008. Competitive exclusion after invasion? Biological Invasions 10: 359–368.

Browne, D. R. & J. B. Rasmussen, 2009. Shift in the trophic ecology of brook trout resulting from interactions with yellow perch: an intraguild predator-prey interaction. Transactions of the American Fisheries Society 138: 1109–1122.

Buria, L., S. J. Walde, M. Battini, P. J. Macchi, M. Alonso, D. E. Ruzzante & V. E. Cussac, 2007. Movement of a South American perch *Percichthys trucha* in a mountain Patagonian lake during spawning and prespawning periods. Journal of Fish Biology 70: 215–230.

Cervellini, P. M., M. A. Battini & V. E. Cussac, 1993. Ontogenetic shifts in the feeding of *Galaxias maculatus* (Galaxiidae) and *Odontesthes microlepidotus* (Atherinidae). Environmental Biology of Fishes 36: 283–290.

Chipps, S. R. & J. E. Garvey, 2007. Assessment of food habits and feeding patterns. In Guy, C. S. & M. L. Brown (eds), Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda: 473–514.

Clarke, K. R. & R. M. Warwick, 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd ed. Natural Environment Research Council, London.

Clarke, K. R. & R. N. Gorley, 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K. R., P. J. Somerfield & R. N. Gorley, 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366: 56–69.

Clavel, J., R. Julliard & V. Devictor, 2010. Worldwide decline of specialist species: toward a global functional homogenization? Frontiers in Ecology & Environment 9: 222–228.

Connell, J. H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131–138.

Correa, C. & A. P. Hendry, 2012. Invasive salmonids and lake order interact in the decline of puye grande *Galaxias platei* in western Patagonia lakes. Ecological Applications 22: 828–842.

Correa, C., A. P. Bravo & A. P. Hendry, 2012. Reciprocal trophic niche shifts in native and invasive fish: salmonids and galaxiids in Patagonian lakes. Freshwater Biology 57: 1769–1781.

Crawford, S. S. & A. M. Muir, 2008. Global introductions of salmon and trout in the genus *Oncorhynchus*: 1870–2007. Reviews in Fish Biology and Fisheries 18: 313–344.

Cussac, V. E., S. Ortubay, G. Iglesias, D. Milano, M. Lattuca, J. Barriga, M. Battini & M. Gross, 2004. The distribution of South American galaxiid fishes: the role of biological traits and post glacial history. Journal of Biogeography 31: 103–122.

Díaz, M., F. Pedrozo, C. Reynolds & P. Temporetti, 2007. Chemical composition and the nitrogen-regulated trophic state of Patagonian lakes. Limnologica 37: 17–27.

Eby, L. A., J. W. Roach, L. B. Crowder & J. A. Stanford, 2006. Effects of stocking-up freshwater food webs. Trends in Ecology and Evolution 21: 576–584.

Garrison, L. P., 2000. Spatial and dietary overlap in the Georges Bank ground fish community. Canadian Journal of Fisheries and Aquatic Sciences 57: 1679–1691.

Graeb, B. D. S., M. T. Mangan, J. C. Jolley, D. H. Wahl & J. M. Dettmers, 2006. Ontogenetic changes in prey preference and foraging ability of Yellow perch: insights based on relative energetic return of prey. Transactions of the American Fisheries Society 135: 1493–1498.

Grosman, F. M. & G. Rudzik, 1990. Análisis de la dieta del pejerrey patagónico (*Patagonina hatcheri*) Eigenmann, 1909, Atherinidae, de la laguna Terraplén, Chubut, Argentina [Analysis of patagonian silverside (*Patagonina hatcheri*) diet Eigenmann, 1909, Atherinidae, of lagoon Terraplén, Chubut, Argentina]. Biota 6: 71–88.

Habit, E., J. González, D. E. Ruzzante & S. J. Walde, 2012. Native and introduced fish species richness in Chilean Patagonian lakes: inferences on invasion mechanisms using salmonid-free lakes. Diversity and Distributions 18: 1153–1165.

Hayden, B., T. Holopainen, P.-A. Amundsen, A. Eloranta, R. Knudsen, K. Praebel & K. K. Kahilainen, 2013. Interactions between invading benthivorous fish and native whitefish in subarctic lakes. Freshwater Biology 58: 1234–1250.

Holt, R. D., 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12: 237–266.

Juncos, R., D. Milano, P. J. Macchi, M. Alonso & P. H. Vigliano, 2011. Response of rainbow trout (*Oncorhynchus mykiss*) to different food web structures in Northern Patagonia: implications on growth, bioenergetics and invasiveness. Transactions of the American Fisheries Society 140: 415–428.

Juncos, R., D. A. Beauchamp & P. H. Vigliano, 2013. Modeling prey consumption by native and nonnative piscivorous fishes: implications for competition and impacts on shared prey in an ultraoligotrophic lake in Patagonia. Transactions of the American Fisheries Society 142: 268–281.

Lattuca, M. E., M. A. Battini & P. J. Macchi, 2008. Trophic interactions among native and introduced fishes in a northern Patagonian oligotrophic lake. Journal of Fish Biology 72: 1306–1320.

Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explanations. Princeton University Press, Princeton.

Macchi, P. J., 2004 Respuestas poblacionales de *Galaxias maculatus* a la depredación por parte de *Percichthys trucha* y los salmónidos introducidos en la Patagonia [Population responses of *Galaxias maculatus* to predation by *Percichthys trucha* and introduced salmonids in Patagonia]. PhD Thesis. Universidad Nacional del Comahue, Río Negro, Argentina.

Macchi, P. J., V. E. Cussac, M. F. Alonso & M. A. Denegri, 1999. Predation relationships between introduced salmonids and the native fish fauna in lakes and reservoirs in Northern Patagonia. Ecology of Freshwater Fish 8: 227–236.

Macchi, P. J., M. A. Pascual & P. H. Vigliano, 2007. Differential piscivory of the native *Percichthys trucha* and exotic salmonids upon the native forage fish *Galaxias maculatus* in Patagonian Andean lakes. Limnologica 37: 76–87.

Macchi, P. J., P. H. Vigliano, M. A. Pascual, M. Alonso, M. A. Denegri, D. Milano, M. García Asorey & G. Lippolt, 2008. Historical policy goals for fish management in northern continental Patagonia Argentina: a structuring force of actual fish assemblages? American Fisheries Society Symposium 49: 331–348.

Marchetti, M. P., P. B. Moyle & R. Levine, 2004. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. Freshwater Biology 49: 646–661.

Marshall, S. & M. Elliott, 1997. A comparison of univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish. Journal of Fish Biology 51: 526–545.

McDowall, R. M., 2003. Impacts of introduced salmonids on native Galaxiids in New Zealand upland streams: a new look at an old problem. Transactions of the American Fisheries Society 132: 229–238.

Milano, D., 2003. Biología de *Galaxias platei* (Pisces, Galaxiidae): especializaciones relativas a su distribución [Biology of Galaxias platei (Pisces, Galaxiidae): specializations relating to distribution]. PhD Thesis. Universidad Nacional del Comahue, Río Negro, Argentina.

Milano, D., V. E. Cussac, P. J. Macchi, D. E. Ruzzante, M. F. Alonso, P. H. Vigliano & M. A. Denegri, 2002. Predator associated morphology in *Galaxias platei* in Patagonia lakes. Journal of Fish Biology 61: 138–156.

Milano, D., D. E. Ruzzante, V. E. Cussac, P. J. Macchi, R. A. Ferriz, J. P. Barriga, J. Aigo, M. E. Lattuca & S. Walde, 2006. Latitudinal and ecological correlates of morphological variation in *Galaxias platei* (Pisces, Galaxiidae) in Patagonia. Biological Journal of the Linnean Society 87: 69–82.

Milano, D., J. Aigo & P. J. Macchi, 2013. Diel patterns in space use, food and metabolic activity of *Galaxias maculatus* (Pisces: Galaxiidae) in the littoral zone of a shallow Patagonian lake. Aquatic Ecology 47: 277–290.

Noy-Meir, I., 1981. Theoretical dynamics of competitors under predation. Oecologia 50: 277–284.

Nunn, A. D., J. P. Harvey & I. G. Cowx, 2007. The food and feeding relationships of larval and 0 + year juvenile fishes in lowland rivers and connected waterbodies. I. Ontogenetic shifts and interspecific diet similarity. Journal of Fish Biology 70: 726–742.

Pascual, M. A., V. E. Cussac, B. Dyer, D. Soto, P. H. Vigliano, S. Ortubay & P. J. Macchi, 2007. Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change. Aquatic Ecosystem Health and Management 10: 1–16.

Penaluna, B. E., I. Arismendi & D. Soto, 2009. Evidence of interactive segregation between introduced trout and native fishes in Northern Patagonian rivers, Chile. Transactions of the American Fisheries Society 138: 839–845.

Pinkas, L., M. S. Olipham & I. L. K. Iversor, 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Fisheries Bulletin 152: 1–105.

Platell, M. E. & I. C. Potter, 2001. Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in

marine waters on the lower west coast of Australia. Journal of Experimental Marine Biology and Ecology 261: 31–54.

Rechencq, M., A. Sosnovsky, P. J. Macchi, P. A. Alvear & P. H. Vigliano, 2011. Extensive diel fish migrations in a deep ultraoligotrophic lake of Patagonia Argentina. Hydrobiologia 658: 147–161.

Ross, S. T., 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 2: 352–388.

Svanbäck, R. & P. Eklöv, 2004. Morphology in perch affects habitat specific feeding efficiency. Functional Ecology 18: 503–510.

Vander Zanden, M. J., J. M. Casselman & J. B. Rasmussen, 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464–467.

Vigliano, P. H., P. J. Macchi, M. A. Denegri, M. Alonso, D. Milano, G. Lippolt & G. Padilla, 1999. A modified sampling design for qualitative–quantitative studies of fish by depth strata in Araucanian lakes. Natura Neotropicalis 1–2: 1–11.

Vigliano, P. H., D. A. Beauchamp, D. Milano, P. J. Macchi, M. F. Alonso, M. García Asorey, M. A. Denegri, J. E. Ciancio, G. Lippolt, M. Rechencq & J. P. Barriga, 2009. Quantifying predation on galaxiids and other native organisms by introduced rainbow trout in an ultraoligotrophic lake in northern Patagonia, Argentina: a bioenergetics modeling approach. Transactions of the American Fisheries Society 138: 1405–1419.

Werner, E. E. & J. F. Gilliam, 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology, Evolution, and Systematics 15: 393–425.

Wiens, J. A., 1993. Fat times, lean times and competition among predators. Trends in Ecology & Evolution 8: 348–349.

Wissinger, S. A., A. R. McIntosh & H. S. Greig, 2006. Impats of introduced brown and rainbow trout on benthic invertebrate communities in shallow New Zeland lakes. Freshwater Biology 51: 2009–2028.