Ann. Limnol. - Int. J. Lim. 48 (2012) 21–30
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DOI: 10.1051/limn/2011055

Dietary overlap among native and non-native fish in Patagonian low-order streams

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Received 13 December 2010; Accepted 28 July 2011

Abstract – The diet composition and feeding strategy of native and exotic fish species were studied from May 2005 to February 2006 in three Patagonian low-order streams. A total of 464 fish were caught, which belonged to the exotic species *Oncorhynchus mykiss* (270), *Salmo trutta* (177) and the native species *Hatcheria macraei* (17). The analysis of 336 stomach contents indicated that at the individual level, the three species had a generalized feeding strategy based on benthic invertebrates (Plecoptera, Trichoptera, Coleoptera and Diptera). In the three streams, the widest population niches were observed in winter. There was, however, also a slight tendency toward an increased between-phenotype contribution to the niche width in same season, indicating that a small proportion of individuals within the fish populations specialized by predominantly feeding on a few specific prey species. Hence, the wide population niche widths observed throughout the year were partly a result of mixed individual feeding strategies within the populations. The higher diet overlaps were registered between exotics *O. mykiss*–*S. trutta* at Glyn and Carbón, and *O. mykiss* and the native *H. macraei* at Manguera, but it changed markedly through the year, perhaps depending on temporal changes in food availability suggesting a competitive coexistence of these species. This is mainly related to the fact that both species changed their food preferences in spring and foraged almost exclusively on *Aubertoperla illiesi*. This implies that in order to reduce the predation risk or the inter-specific competition for food, the fish species might partition the feeding habitats.

Key words: *Hatcheria macraei* / salmonids / feeding strategies / Patagonia / Argentina

Introduction

The introduction of non-indigenous fish is considered one of the most important anthropogenic impacts on freshwater ecosystems (Kolar and Lodge, 2000). Fishes of the Salmonidae family have been widely introduced in the Southern Hemisphere and their ecological impacts have been substantial (Townsend, 2003). To understand the magnitude and implications of such impacts multi-species approaches are required.

In the last century Patagonia was affected by a continuous salmonid species stocking (Pascual *et al.*, 2007). Thirteen salmonid species were introduced in the Argentinean Patagonia and among them the most widely distributed are *Oncorhynchus mykiss*, *Salmo trutta* and *Salvelinus fontinalis*. Recently, the anadromous Chinook salmon *Oncorhynchus tshawytscha* was observed spawning in headwaters of Pacific and Atlantic basins in Argentina (Pascual and Ciancio, 2007; Soto *et al.*, 2007; Di Prinzio and Pascual, 2008). There is evidence indicating that the exotic *O. mykiss* feed intensively on native fishes (McDowall, 2003; Arismendi *et al.*, 2009; among others).

The native fish species are widespread, being distributed throughout most of the region's high-order rivers (Pascual *et al.*, 2007). Their status in low-order streams is, however, poorly understood. In consequence, the understanding of the role of fish in freshwater ecosystems is important given that when species with similar feeding behaviors co-occur and the resource availability is limited in quantity or diversity some degree of food competition might be expected (Odum, 1971). In that situation, different feeding strategies may help to reduce interspecific competition. Thus, under some circumstances, competition may become an important force

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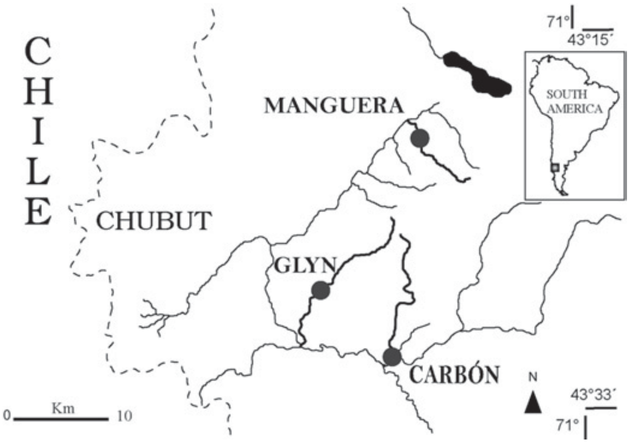


Fig. 1. Location of the three sampled streams at Northwest Chubut, Patagonia, Argentina.

determining the feeding behavior and diet composition of predators.

Vitousek (1990) mentioned that in freshwater systems, predators frequently forage selectively on certain prey types, whereas Townsend (2003) suggested that predation has important effects at individual, population, community and ecosystem levels. Thus, predation represents a strong selective force that shapes and determines the structure of populations at lower trophic levels (Peckarsky, 1982; Bechara *et al.*, 1992), and can alter the abundance and composition of the prey community (Dahl and Greenberg, 1996). Moreover, if the interactions are of great magnitude, predators can also alter the abundance of resources at lower trophic levels indirectly via "trophic cascade" by reducing consumer abundance and the consumer's consumption of resources (Brönmark *et al.*, 1997).

There have been few studies focusing on the predator–prey interactions in Patagonia (Buria *et al.*, 2007; Aigo *et al.*, 2008; Molineri, 2008) and only some of them considered the dietary overlap between native and exotic species (Ferriz, 1994; Barros *et al.*, 2001; Lattuca *et al.*, 2007). Thus, the main objective of this study is to describe the diet composition of freshwater fish at three Patagonian low-order streams. As secondary objectives we will estimate the dietary overlap and the potential resource competition among native and exotic species.

Material and methods

Study area

The study was conducted in three streams located in northwest Patagonia (Glyn 43°27'S, 71°33'W; Manguera 43°33'S, 71°26'W and Carbón 43°32'S, 71°28'W) in the Andean-Humid and the Sub-Andean Sub-humid biozones (Fig. 1). The landscape is strongly influence by glacial action and strong fluvial erosion. River discharge is bimodal and determined by rainfall, which occurs mainly in winter and by the snowmelt in spring (Coronato and del Valle, 1988). The streams under study are second (Glyn) or third (Manguera and Carbón) order and belong to the Carrenleufú basin. The streams are 15 km (Manguera), 25 km (Glyn) and 30 km (Carbón) long. Catchments are surrounded by sub-Antartic forest characterized by perennial (*Austrocedrus chilensis*, *Nothofagus dombeyi* and *Maytenus boaria*) and deciduous (*Nothofagus pumilio* and *Nothofagus antarctica*) species.

Measurement of physical and chemical variables

Samples were obtained in May (autumn), September (winter) and December (spring) 2005 and in February 2006 (summer). In each sampled site, flow velocity, water depth, dry widths of channel, water discharge, water temperature, conductivity, pH, dissolved oxygen, turbidity, total suspended solids, soluble reactive phosphate, nitrate plus nitrite nitrogen and ammonia were calculated to determine whether environmental conditions were similar between rivers and stable. Statistical comparisons of values obtained for physical and chemical variables at each site were conducted by applying the Kruskal–Wallis test (Sokal and Rohlf, 1995).

Fish sampling

Fish were sampled seasonally, in May (autumn), September (winter) and December (spring) 2005 and in February 2006 (summer) using a portable backpack electrofishing gear (Coffelt Mark-10 CPS, output 350 V) along reaches of 100 m long. The width of the sampling area was coincident with the stream width, except for those sections presenting non-wadeable sites with swift currents (Carbón stream). The sampled area was estimated considering the reach length and width. The fish sampled were identified to species, counted, measured in total length (cm) and weighted (g). The sampling area was estimated considering the length and width of the reach. Thus, for each stream the density and biomass were estimated and expressed as the number of individuals (individuals.m^{-2}) and biomass (g.m^{-2}) per area sampled, respectively. The development of a sampling program may affect the fish populations under study (Casaux and Barrera-Oro, 2002), thus only up to 30 individuals (selected randomly) per species were freezed in the field at −10 °C and at the laboratory were dissected for diet analysis.

Dietary analyses

Fish were dissected and the stomachs were separated for diet analysis. The stomach fullness was assessed using a five-point scale method employing a percentage scale ranging from empty (0%) to full (100%) (Amundsen *et al.*, 1996). Food items were removed and identified to the lowest taxonomic level possible. The composition of the diet was calculated in terms of percent abundance (A_i), frequency of occurrence (F_i) and prey-specific abundance (P_i) following Amundsen *et al.* (1996):

$$A_i = \left(\sum S_i \Big/ \sum S_t\right) \times 100$$

$$F_i = N_i/N$$

$$P_i = \left(\sum S_i \Big/ \sum St_i\right) \times 100$$

where S_i is the contribution of prey i to stomach fullness, St_i is the total stomach fullness of fish with prey i in their stomach and S_t is the total stomach fullness of the fish, N_i is the number of fish with prey i in their stomach and N is the total number of fish with stomach contents.

The diet width (B) was calculated using Levins (1968) index:

$$B = 1\Big/\sum p_i^2$$

where p_i is the proportion of each prey type i in the diet and equals A_i expressed as fraction rather than percentage.

Diet overlap

Dietary overlap between the fish species was calculated as an index expressed as a percentage overlap (Krebs, 1989):

$$P_{jk} = \left[\sum_{1}^{n} \text{minimum } P_{ij},\ P_{ik}\right] \times 100$$

where P_{ik} is the percentage overlap between species j and species k, P_{ik} are the proportions of resource i in relation to the total resources used by species j and k, respectively, and n is the total number of prey categories. The overlap is considered to be significant when the index value exceeds 60% (Wallace, 1981).

Feeding strategy and phenotype contributions to the niche width

Food-niche characteristics were analyzed by the graphical method of Amundsen *et al.* (1996). For each prey type, the prey-specific abundance (P_i) is plotted against the frequency of occurrence (F_i) on a two-dimensional graph. Prey importance, feeding strategy and phenotype contribution to the niche width can be interpreted along the diagonals and axes of the diagram (see Amundsen *et al.*, 1996). The diagonal from the lower left to the upper right corner provides a measure of prey importance for the whole population with dominant prey at the upper, right corner and rate and unimportant prey at the lower end. The vertical axis represents the feeding strategy in terms of specialization or generalization: specialists have prey points positioned in the upper part of the graph, whereas generalists have all prey points in the lower part. Points located in the upper left indicate specialization by subgroups of the predator population, whereas points in the upper right indicate specialization by the whole predator population on given prey. Hence, if one or a few points are located in the upper right, this reflects a predator population with a narrow niche width. When there are no prey points in this part of the diagram this reflects a predator population with a broader niche width. Prey points in the upper left and lower right corner represent the same percent abundance in the diet of the population as a whole, but illustrate totally different feeding strategies among the individual predators. Prey with high specific abundance and low occurrence (upper left) have been consumed by a few individuals displaying specialization, whereas prey with a low specific abundance and a high occurrence (lower right) have been eaten occasionally by most individuals. These differences are related to the between- and within-phenotype contributions to niche width, respectively. Points in the upper right part of the graph (*i.e.*, above the diagonal from lower left to upper right) reflect a population with a high between-phenotype component (high BPC) with individuals specializing on different prey categories. Points in the opposite part (below the diagonal from lower left to upper right) represent a high within-phenotype component (high WPC) and the individuals utilize many common preys none of which dominate the diet (Roughgarden, 1972; Amundsen, 1995). In practical terms, a high WPC occurs when all prey categories have been eaten by most predators, but in small proportions, whereas a high BPC occurs when each prey category has been subjected to specialization, but only by a small fraction of the predator population.

Results

Environmental features

Sites were located between 403 m. a.s.l. (Carbón) and 699 m.a.s.l. (Manguera) (Table 1). Flow velocity was comprised between 0.8 m.s^{-1} (Carbón) and 1.1 m.s^{-1} (Glyn). The streambed wet width ranged from 4.2 to 18.8 m in Glyn and Carbón, respectively. The lowest dissolved oxygen content was observed at Carbón (11.9 mg.L^{-1}) and the highest one at Glyn (12.4 mg.L^{-1}). Carbón stream presented the highest conductivity (70.3 $\mu\text{S}_{20}.\text{cm}^{-1}$), whereas the highest concentrations of soluble reactive phosphate (0.8 $\mu\text{g.L}^{-1}$) and total suspended solid (5.1 mg.L^{-1}) were registered at Manguera stream. Wet width and mean discharge was significantly higher (Kruskal–Wallis, $P < 0.05$) in Carbón stream than in the remaining sites.

Fish analysis

A total of 464 fish was caught and the individuals belonging to exotic species (*O. mykiss* and *S. trutta*) largely

Table 1. Locations of the three sampled streams and environmental features during the study period ($n = 4$). Values are presented as mean values (± SD).

	Glyn	Manguera	Carbón
Latitude (S)	43°27'33.7"	43°33'25"	43°32'12.5"
Longitude (W)	71°33'25"	71°26'35.1"	71°28'20.3"
Altitude (m a.s.l)	615	699	403
Stream order	2	3	3
Wet width (m)	4.2 ± 0.8	5.8 ± 0.7	18.8 ± 3.7*
Depth (m)	0.2 ± 0.1	0.2 ± 0.0	0.3 ± 0.1
Water temperature (°C)	7.4 ± 2.2	7.1 ± 1.4	8.1 ± 2.1
Flow velocity (m.s^{-1})	1.1 ± 0.5	0.9 ± 0.4	0.8 ± 0.2
Discharge (m.seg^{-3})	1.1 ± 1.1	1.0 ± 0.8	4.8 ± 2.9*
pH	7.2 ± 0.1	7.4 ± 0.4	7.2 ± 0.2
Dissolved oxygen (mg.L^{-1})	12.4 ± 3.7	12.3 ± 2.0	11.9 ± 3.6
Conductivity (µS$_{20}$.cm^{-1})	56.8 ± 15.8	65.0 ± 21.6	70.3 ± 18.4
Turbidity (NTU)	10.3 ± 17.9	8.5 ± 12.4	7.0 ± 6.8
Ammonia (µg.L^{-1})	0.9 ± 0.8	1.0 ± 0.8	1.0 ± 0.7
Nitrate + nitrate nitrogen (µg.L^{-1})	0.3 ± 0.2	0.2 ± 0.3	0.3 ± 0.2
Soluble reactive phosphate (µg.L^{-1})	0.4 ± 0.2	0.8 ± 0.6	0.5 ± 0.1
Total suspended solids (mg.L^{-1})	1.1 ± 0.6	5.1 ± 7.3	2.6 ± 1.31

*Indicates significant differences between values (Kruskal–Wallis test, $P < 0.05$).

Table 2. Fish abundance, in terms of density (ind.m^{-2}) and biomass (g.m^{-2}), at the three sampled sites at Northwest Patagonia, Argentina. – indicates no captures.

		Glyn		Manguera		Carbón	
	Specie	(ind.m^{-2})	(g.m^{-2})	(ind.m^{-2})	(g.m^{-2})	(ind.m^{-2})	(g.m^{-2})
Autumn	*O. mykiss*	0.19	4.40	0.17	1.95	0.16	2.33
	S. trutta	0.18	1.84	–	–	0.10	2.28
	H. macraei	0.00		0.02	0.05	–	–
	Total	**0.37**	**6.24**	**0.19**	**2.01**	**0.26**	**4.61**
Winter	*O. mykiss*	0.13	0.20	0.03	0.42	0.23	3.35
	S. trutta	0.17	0.64			0.11	0.99
	H. macraei	0.00		0.01	0.04		
	Total	**0.30**	**0.84**	**0.04**	**0.45**	**0.34**	**4.34**
Spring	*O. mykiss*	0.04	0.87	0.01	0.09	0.07	0.63
	S. trutta	0.09	3.15	–	–	0.09	2.03
	H. macraei	0.01	0.12	0.006	0.03	–	–
	Total	**0.15**	**4.15**	**0.02**	**0.12**	**0.16**	**2.66**
Summer	*O. mykiss*	0.38	4.26	0.06	1.29	0.28	3.62
	S. trutta	0.30	3.03	–	–	0.30	2.57
	H. macraei	0.01	0.02	0.01	0.06	–	–
	Total	**0.69**	**7.31**	**0.07**	**1.36**	**0.58**	**6.19**
Annually (mean)	*O. mykiss*	0.19 ± 0.14	2.43 ± 2.21	0.07 ± 0.07	0.94 ± 0.85	0.18 ± 0.09	2.48 ± 1.35
	S. trutta	0.19 ± 0.09	2.17 ± 1.18	–	–	0.15 ± 0.10	1.96 ± 0.69
	H. macraei	0.01 ± 0.01	0.07 ± 0.07	0.01 ± 0.00	0.05 ± 0.02	–	–

predominate samples (96.34%). *O. mykiss* was the most abundant fish (270 individuals, 0.44 ind.m^{-2}), followed by *S. trutta* (177 individuals, 0.34 ind.m^{-2}) and *Hatcheria macraei* (17 individuals, 0.02 ind.m^{-2}) (Table 2). A similar pattern was observed in the contribution of the different species to the samples by biomass: *O. mykiss* 5.85 g.m^{-2}, *S. trutta* 4.13 g.m^{-2} and *H. macraei* 0.12 g.m^{-2}. The size of the fish caught ranged between 3.0 (*H. macraei* at Manguera) and 27.0 cm (*S. trutta* at Carbón), whereas their weight ranged between 0.1 (*H. macraei* at Manguera) and 378.8 (*O. mykiss* at Glyn) g (see details in Table 3).

Dietary analyses

The diet composition of the three fish species (336 stomachs) was diverse and benthic organisms largely dominated in the samples. A total of 88 prey taxa were identified from the stomach contents (Fig. 2). Depending on the season and site, the most important prey species of *O. mykiss* were *Aubertoperla illiesi*, *Antactoperla michaelseni*, *Nousia delicata*, *Smicridea annulicornis*, *Parasericostoma ovale*, Simuliidae larvaes and vegetable fragments. Similarly, *A. michaelseni*, *Limnoperla jaffueli*, *N. delicata*, *A. illiesi*, *S. annulicornis* and Athericidae

Table 3. Seasonal changes in the total length (TL in cm) and weight (in g), represented as mean ± standard deviation and range, observed in the fish sampled at three steams in Northwest Patagonia, Argentina. – indicates no captures.

		Glyn				Manguera				Carbón			
		Total length		Weight		Total length		Weight		Total length		Weight	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
Autumn	*O. mykiss*	6.5–23.0	10.0 ± 4.4	2.5–378.8	30.4 ± 75.5	5.4–18.3	9.3 ± 3.5	1.6–59.3	12.5 ± 14.1	6.7–26.7	10.9 ± 4.7	2.8–202.0	22.6 ± 46.6
	S. trutta	6.6–8.3	7.7 ± 0.4	3.0–6.8	5.2 ± 0.8	–	–	–	–	8.0–27.0	11.2 ± 4.0	4.8–214.0	22.1 ± 47.9
	H. macraei	–	–	–	–	3.0–9.8	6.8 ± 2.8	0.1–6.8	2.9 ± 2.8	–	–	–	–
Winter	*O. mykiss*	5.6–12.5	8.7 ± 2.5	1.6–19.1	7.5 ± 6.0					7.8–21.4	11.0 ± 3.9	4.7–118.0	21.3 ± 32.8
	S. trutta	8.4–8.4	8.4 ± 0.0	5.9–6.0	6.0 ± 0.1	–	–	–	–	9.5–11.4	10.3 ± 0.6	8.8–15.9	11.5 ± 2.3
	H. macraei	–	–	–	–	9.2–9.4	9.3 ± 40.1	4.9–5.3	5.1 ± 0.3	–	–	–	–
Spring	*O. mykiss*	8.8–19.1	11.7 ± 3.2	7.7–80.3	22.9 ± 23.8	6.9–10.0	8.6 ± 1.3	3.6–10.3	7.4 ± 2.9	9.5–11.2	10.5 ± 0.6	9.2–15.2	12.2 ± 1.9
	S. trutta	8.4–8.8	8.6 ± 0.1	6.1–7.4	6.8 ± 0.3	–	–	–	–	12.8–16.1	14.2 ± 1.2	19.6–40.1	30.3 ± 7.7
	H. macraei	8.8–12.6	10.4 ± 1.9	5.1–14.0	8.5 ± 4.7	9.80	–	7.25	–	–	–	–	–
Summer	*O. mykiss*	5.6–24.5	8.7 ± 3.9	2.1–182.4	14.3 ± 27.5	4.0–18.0	11.5 ± 2.8	0.5–65.0	19.9 ± 13.8	5.1–20.2	9.2 ± 3.8	1.4–88.1	14.1 ± 22.6
	S. trutta	8.8–25.2	12.8 ± 3.6	7.2–209.8	29.5 ± 34.3	–	–	–	–	6.4–18.2	9.2 ± 1.7	3.1–68.1	10.0 ± 9.7
	H. macraei	7.5	–	3.05	–	8.5–10.6	9.6 ± 0.8	4.1–8.7	6.2 ± 4.7	–	–	–	–

larvaes were the most important preys in the diet of *S. trutta*. *Hatcheria macraei* foraged predominantly on *A. illiesi*, *A. michaelseni*, Simuliidae larvaes, *Paratrichocladius* sp. and stones. The differences in the yearly composition of the diet between *O. mykiss* and *S. trutta* at Glyn ($\chi^2_{47} = 206.61$; $P < 0.05$) and Carbón ($\chi^2_{47} = 288.17$; $P < 0.05$) were statistically significant. Likewise, the composition of the diet of *O. mykiss* and *H. macraei* at Manguera differed statistically ($\chi^2_{42} = 400.00$; $P < 0.05$).

The total number and weight of prey and the species richness observed in the stomach contents did not vary significantly according to site and season (Kruskal–Wallis, $P =$ n.s.), but differed among fish species (Kruskal–Wallis, $P < 0.05$). Thus, the total number and weight of prey and the species richness observed in the stomach contents of *H. macraei* were significantly lower than in the salmonid species.

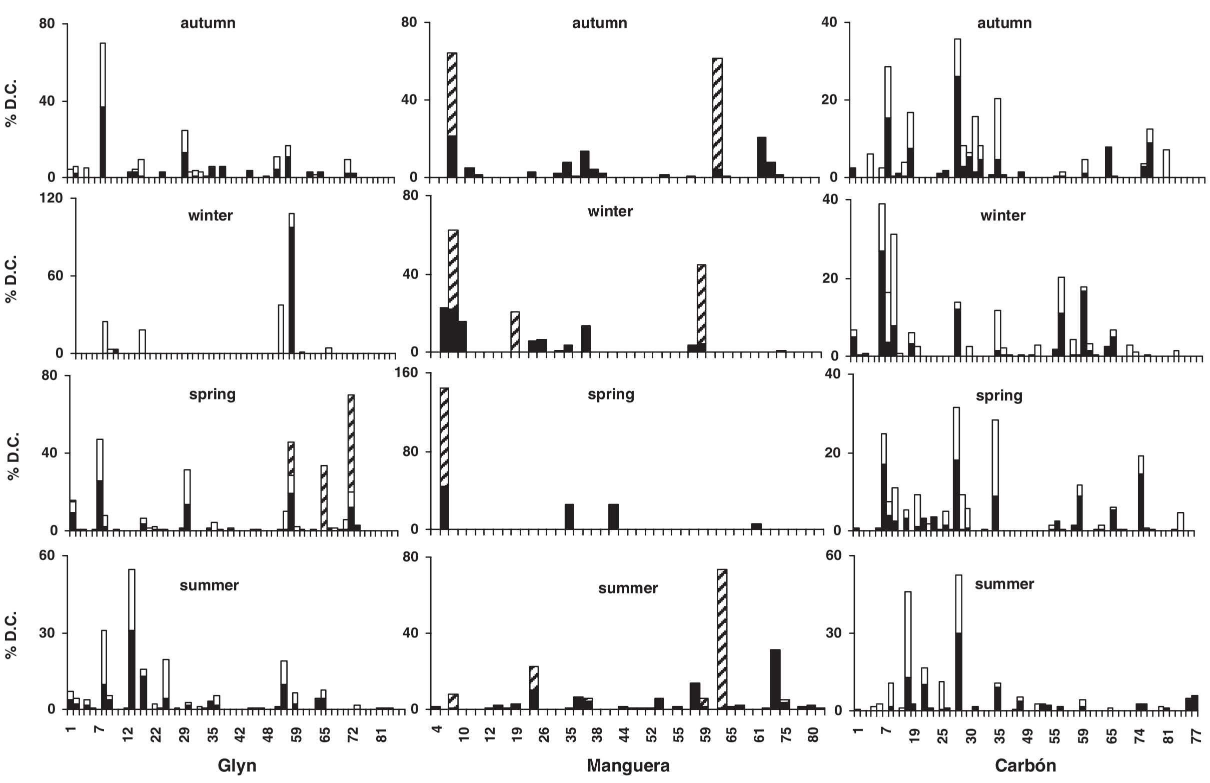
Diet overlap

Overall, only minor dietary overlap was observed in winter between all three species (Table 4). The dietary overlap observed between the introduced *O. mykiss* and *S. trutta* at Glyn exceeded 60% in autumn, spring and summer (Table 4). The dietary overlap between *O. mykiss* and *H. macraei* at Manguera exceeded 60% only in spring (Table 4). The dietary overlap between *O. mykiss* and *S. trutta* exceeded 60% only in autumn, but in spring such value approached significance (Table 4).

Feeding strategy and phenotype contributions to the niche width

The maximum value of diet-width index varied with the season and site. Thus, at Glyn *O. mykiss* showed the maximum value of this index in autumn, while in *S. trutta* this occurred in winter. At Manguera, the maximum value of diet-width index of *O. mykiss* and *H. macraei* occurred in spring and autumn respectively. At Carbón the maximum value of diet-width index of *O. mykiss* was in spring, whereas in *S. trutta* was in autumn (Table 5).

Most of the prey types had very similar contributions to the diet of the three fish species both in terms of frequency of occurrence and prey-specific abundance (Fig. 3), and the three fish species exhibited a remarkable similarity in their feeding strategies and prey utilization patterns. At the individual level, there was a clear generalized feeding strategy within the three species as the prey points were mainly located in the lower half of the diagram and the prey-specific abundance only occasionally exceeded 50% (Fig. 3(A, E, G, H, I, L)). The prey species that showed high specific abundance and low occurrence (upper left) have been consumed by a few individuals displaying specialization were *Lymnaea* sp. for *S. trutta* and Limnephilidae for *O. mykiss* in Glyn (autumn) (Fig. 3(A)). In the same way, in Manguera the



1	*Limnodrilus variegatus*
2	*Diplodon chilensis*
3	*Chilina patagonia*
4	Arachnida
5	*Lymnaea* sp.
6	Plecoptero (A)
7	*Aubertoperla illiesi*
8	*Antarctoperla michaelseni*
9	*Perlugoperla personata*
10	*Lymnoperla jaffueli*
11	*Udamocercia arumífera*
12	*Ceratoperla schwabei*
13	*Notoperlopsis femina*
14	*Notoperla magnaspina*
15	*Potamoperla myrmidon*
16	*Nousia delicata*
17	*Nousia crena*
18	*Meridialaris chiloeensis*
19	*Meridialaris laminata*
20	*Meridialaris diguillina*
21	*Penaphlebia chilensis*
22	*Penaphlebia flavidula*
23	*Americabaetis*
24	*Andesiops*
25	Ephemeroptera sp.1
26	*Myotrichia murina*
27	*Parasericostoma ovale*
28	*Hudsonema flamini*
29	*Brachysetodes* sp.
30	*Oxyethira bidentata*
31	*Neoatopsycha unispina*
32	*Neoatopsycha brevispina*
33	*Metrichia patagonica*
34	*Smicridea annulicornis*
35	*Cailloma* sp.
36	Trichoptera sp.1
37	*Philorhethridae*
38	*Eosericostoma* sp.
39	Limnephilidae
40	*Mastigoptila longicornuta*
41	Trichopetro (A)
42	Elmidae (L)
43	Luchoelmis (L)
44	Staphynilidae
45	*Stethelmis kaszabi*
46	Curculionidae
47	Melynidae
48	Elateroidea (L)
49	Nitidulidae (A)
50	Coleoptera sp.1
51	*Desmopachria punctatissima*
52	Melandrydae (A)
53	Diptera (A)
54	Diptera (P)
55	Athericidae (L)
56	Musciadae (L)
57	Simuliidae(L)
58	Simuliidae (P)
59	*Edwarsina edwarsina*
60	Ceratopogonidae
61	Empididae (L)
62	*Paratrichocladius* sp.
63	*Thienemanniella*
64	Psychadidae
65	Ceratopogonidae
66	Diamesinae
67	*Orthocladius* sp.
68	sp.2
69	sp.1
70	Lepidoptera (L)
71	chironomid fragment
72	vegetal fragment
73	stone
74	Acari
75	Aegla aff neuquensis
76	Sicadelidae
77	Tabanidae (L)
78	Orthoptera
79	Formicidae
80	Fish Fragment
81	Dermaptera
82	Aphididae
83	Hymenoptera
84	Hemiptera
85	Diplodos
86	Isopodo

Fig. 2. Diet overlap pattern between *O. mykiss* (black bars), *S. trutta* (white bars) and *H. macraei* (hatched bars) through the year sampled in three Northwest Patagonian streams (Argentina). %D.C.: Diet contribution percentage. Values scales of *Y*-axes are represented to easy the interpretation graphs.

prey species that showed high specific abundance and low occurrence for *O. mykiss* were *Mastigoptila longicornuta* (autumn), *Metrichia patagonica* and *S. annulicornis* (spring) and Coleoptera sp.1 (summer), while for *H. macraei* was *Paratrichocladius* sp. (autumn and summer) and *A. illiesi* in spring (Fig. 3(E, G, H)). In Carbón, Dermaptera and *Oxyethira bidentata* were the most consumed prey in autumn by *S. trutta* (Fig. 3(I)) and *Aegla aff neuquensis* for *O. mykiss* (summer) (Fig. 3(L)).

Table 4. Prey overlap (%) among fish represented in three streams located in Northwest Patagonia Argentina. – indicates no captures.

		Glyn	Manguera	Carbon
Autumn	*O. mykiss–S. trutta*	61.16	–	60.96
	O. mykiss–H. macraei	–	15.73	–
Winter	*O. mykiss–S. trutta*	30.55	–	43.74
	O. mykiss–H. macraei	–	29.03	–
Spring	*O. mykiss–S. trutta*	73.39	–	57.23
	O. mykiss–H. macraei	1.24	62.50	–
	S. trutta–H. macraei	2.85	–	–
Summer	*O. mykiss–S. trutta*	62.89	–	46.81
	O. mykiss–H. macraei	–	14.74	–

Table 5. Population niche width (Levins index, B) of the three species presented in the three streams studied in the Northwest Patagonia, Argentina. – indicates no captures.

		Autumn	Winter	Spring	Summer
Glyn	*O. mykiss*	0.27	0.06	0.22	0.24
	S. trutta	0.29	0.50	0.22	0.26
	H. macraei	–	–	–	–
Manguera	*O. mykiss*	0.30	0.45	0.71	0.22
	H. macraei	0.96	–	–	0.16
Carbon	*O. mykiss*	0.31	0.23	0.32	0.31
	S. trutta	0.61	0.34	0.43	0.27

At the population level, both *H. macraei* (Manguera) and *O. mykiss* (Glyn) showed two different feeding strategies by specialization in spring, summer (Fig. 3(G, H)) and winter (Fig. 3(B)), respectively and a generalization at the rest of the year. The population specialization of the two species was exposed by one prey point being located toward upper right of the diagram. In contrast, no prey types emerged as particularly important in the diet of these species and all prey points were located along or below the diagonal from the upper left to the lower right corner (Fig. 3(E, F, A, C, D)). In spring, the population specialization of *H. macraei* was directed toward the Plecoptera *A. illiesi*, whereas in summer with the Diptera *Paratrichocladius*. The population specialization in *O. mykiss* was related to the Diptera Simuliidae larvae. Thus, a large number of prey types were utilized, but all had a low contribution to the diet, resulting in pronounced population generalizations and large niche widths of both species during the rest of the year (Table 5).

Overall, in the three streams, the wider population niches observed was in winter (Fig. 3(B, F, J)), spring (Glyn and Carbón) (Fig. 3(C, J)) and summer (Glyn) (Fig. 3(D)). This is illustrated in the diagram by most of the prey points being located to the lower right of the

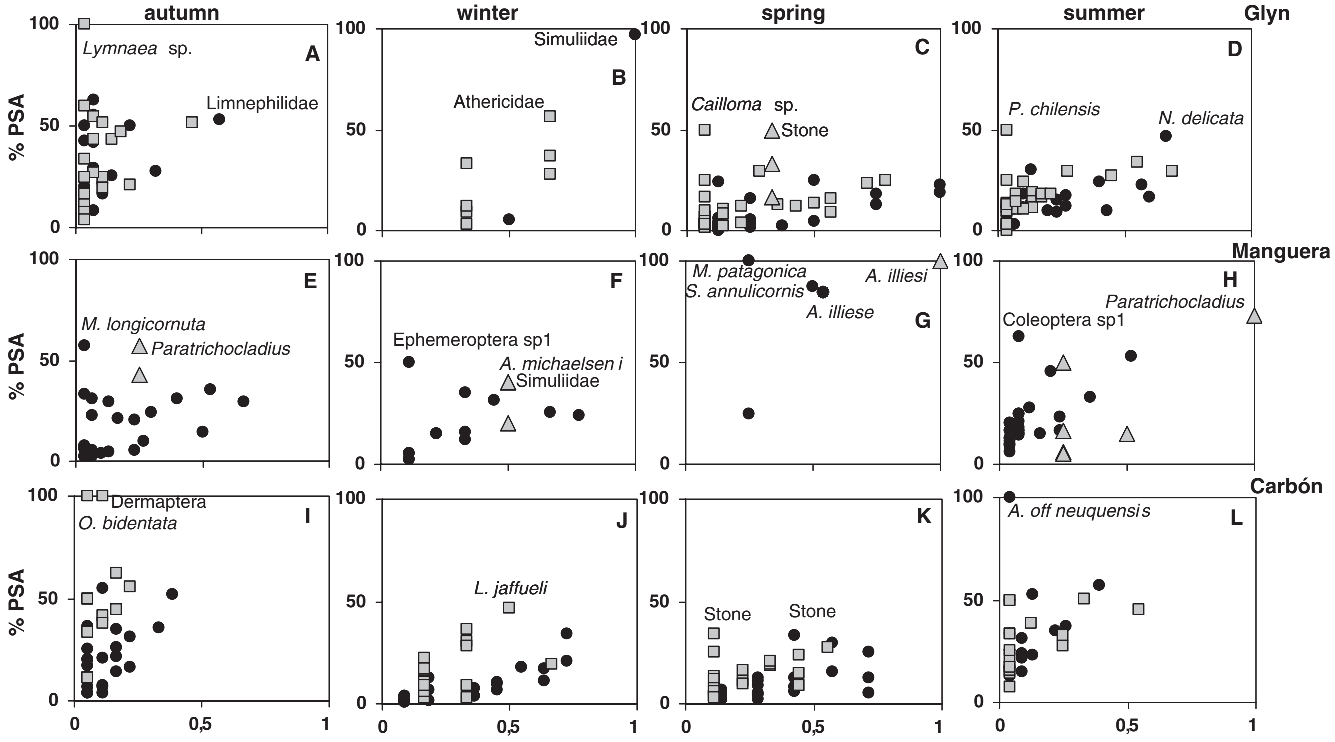


Fig. 3. Feeding strategy of *O. mykiss*, *S. trutta* and *H. macraei* through the year sampled in three Northwest Patagonian streams (Argentina). The most important prey categories are identified by shortened names. % PSA: prey-specific abundance percentage. *S. trutta* ▨; *O. mykiss* ●; *H. macraei* △.

diagonal from the origin to the upper right corner. There was, however, also a slight tendency toward an increased between-phenotype contribution to the niche width particularly in autumn (Glyn and Carbón) (Fig. 3(A, I)), in spring (Manguera for *O. mykiss*) (Fig. 3(G)) and in summer (Carbón) (Fig. 3(D)), as a few prey types were skewed toward the upper left of the diagram. This indicates that small fractions of individuals within the fish populations tended to specialize by predominantly feeding on a few specific prey.

Discussion

The streams considered in this study were dominated by the exotic *O. mykiss* in terms of both density and biomass, whereas the native *H. macraei* was scarcely represented in the samples, similar to findings by Di Prinzio *et al.* (2009). *Hatcheria macraei* is a rheophilic and negatively phototactic catfish (Menni, 2004) which inhabits fast flowing, clear, cold and well-oxygenated waters (Ringuelet 1975). This fish was widely distributed in Patagonia in the past, but is currently considered as rare (López *et al.*, 2003). Their current restricted distribution could be related to a variety of causes like habitat loss, predation and competition from salmonids (Pascual *et al.*, 2007).

According to the graphical method of Amundsen *et al.* (1996), the three fish species showed to be considered as generalist feeders. Overall, benthic invertebrates (Plecoptera, Trichoptera, Coleoptera and Diptera) were the main prey. These results are in line with those reported for these fish species at other localities of Patagonia (Ferriz, 1994; Arismendi *et al.*, 2009; Barriga and Battini, 2009; Buria *et al.*, 2009). The difference in the resource niche between exotic and native species is agreed with the competitive exclusion principle, which states that coexisting species should segregate in resource use. Under such circumstances, different feeding strategies may help to reduce interspecific competition. The higher diet overlaps were registered between *O. mykiss* and *S. trutta* at Glyn and Carbón, which suggests that there is a competitive coexistence of these species in spite of their extensive niche overlap. Extensive niche overlap has been suggested to occur between competitors that are similar in their skills to compete for resources (Ågren and Fagerstrøn, 1984; Keddy, 1989), such as when consumers differ in their foraging behavior toward the same renewable resource (Wilson *et al.*, 1999). According to Ågren and Fagerstrøn (1984), competitors can survive by segregating along a resource gradient if they have ample differences in their ecological niches, but they can also coexist under conditions of extensive overlap if they are highly similar in their niche utilization, and thereby equal competitors (see also Keddy, 1989). It was observed that *O. mykiss* and *H. macraei* reflected significant diet overlap at Manguera in spring. It may be surprising that dissimilar species such as salmonids and a freshwater catfish have diets that are highly similar, as one should expect their distinct morphological differences to be reflected in segregated food niches. *Hatcheria macraei* is morphologically adapted for living at the bottom of the river and are regarded as strictly benthic fishes. The salmonids are, in contrast, morphologically adapted to adopt different positions in the water column and may feed on either benthic or drifting preys (Kalleberg, 1958). However, these two species, showed different niche width in spring, while *O. mykiss* reflected a broad niche width, *H. macraei* presented a narrow width wide with a specialization at population level. This is mainly related to the fact that both species changed their food preferences in spring and foraged almost exclusively on the Plecopteran *A. illiesi* (Fig. 3(G)). This pattern is similar to the one reported by Gabler and Amundsen (2010) for the Altantic salmon parr and the alpine bullhead in a sub-Arctic river and by Barriga and Battini (2009) who suggested that in order to reduce the predation risk or the inter-specific competition for food, *H. macraei* might partition the use of the feeding habitat in a Patagonian river. Accordingly, Penaluna *et al.* (2009) observed that three native fish species had niche overlap with the introduced *O. mykiss* and *S. trutta*, and that they changed their mesohabitat use after the reduction of salmonids abundance in two Patagonian rivers (Chile).

The levels of prey overlap observed between *O. mykiss* and *S. trutta* in Glyn and Carbón also changed markedly through the year and may be a reflection of temporal changes in food availability. However, some studies have indicated that when prey overlap between species is high, the resource competition is often low as a result of high abundance of their principal prey (Klemetsen, 1993; Høines and Bergstad, 2002; Barrera Oro, 2003). McIntosh *et al.* (1992) observed in New Zealand streams that native and exotic species temporally and spatially segregated the use of food resources and observed a small proportion of the fish populations specialising by predominantly feeding on a few specific prey. Hence, the wide population niche widths observed along the year were partly a result of mixed individual feeding strategies within the populations.

The magnitude of the impact of introduced salmonids on Patagonian native fish is difficult to determine due to the absence of pre-introduction information (Pascual *et al.*, 2007). Similarly, Baigún and Ferriz (2003) indicated that it is not well understood how exotic fish have modified the structure of the communities in different Patagonian basins. Thus, the studies on food competition between native and exotic species might help to understand the co-adaptive process related to the salmonids' introduction.

Acknowledgements. This study was partially supported by CONICET (PIP5733), PADI FOUNDATION (Grant 19/2006). Special thanks to Drs M.L. Miserendino and M. Archangelsky, and Lic C. Brand for fieldtrip assistance. Thanks to anonymous reviewers for valuable comments that greatly improved the manuscript. This is the contribution to the Laboratorio de Investigaciones en Ecología y Sistemática Animal (LIESA) No. 76.

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