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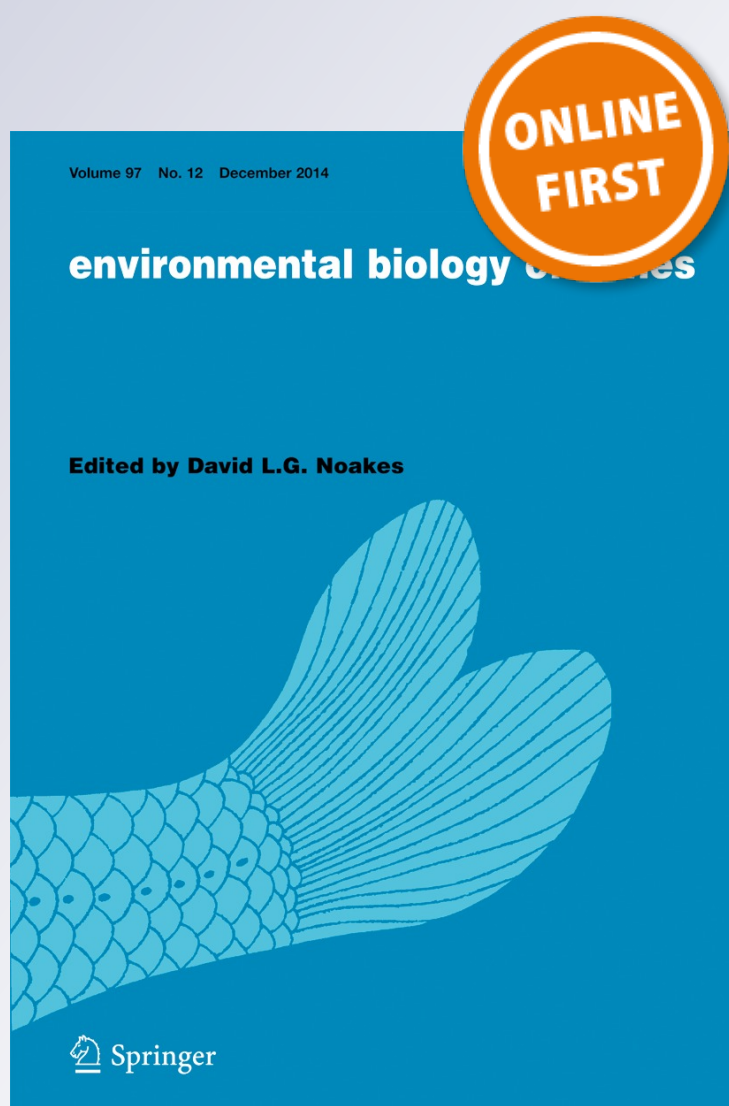
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A natural experiment of dietary overlap between introduced Rainbow Trout (*Oncorhynchus mykiss)* and native Puyen (*Galaxias maculatus*) in the Santa Cruz River, Patagonia

**Marina Tagliaferro · Ivan Arismendi ·
Julio Lancelotti · Miguel Pascual**

Abstract Diet overlap between the native Puyen (*Galaxias maculatus*) and juvenile exotic Rainbow Trout (*Oncorhynchus mykiss*) was studied in 52 sites located along 306 km of the mainstem of the Santa Cruz River, one of the largest rivers in Patagonia. The relative abundance of both species varied along the river, with three clearly defined areas including an upstream "high Rainbow Trout to Puyen ratio" area (with abundances of 75 and 25 %, respectively), a midstream "intermediate Rainbow Trout to Puyen ratio" area (relative abundances between 75 and 25 %), and a downstream "low Rainbow Trout to Puyen ratio" area. The diet of the 2 species was analyzed across these 3 areas examining stomach content. Diet similarity between species was analyzed using a nonmetric multidimensional scaling ordination technique; prey electivity was evaluated with the Ivlev's Index; feeding tactics were studied by estimating prey-specific abundance. Both species showed a generalist feeding tactic, with Puyen exhibiting a more varied diet. Prey electivity was similar in both species, with the mayfly (*Meridialaris chiloeensis*), stoneflies (*Klapopteryx kuscheli* and *Antarctoperla michaelseni*), and the amphipod (*Hyalella* sp.) being the most frequently consumed prey. A significant diet overlap was found only in the downstream areas where a higher proportion of native fish occurs. The low diet overlap in upstream locations might be because of the high density of Rainbow Trout; while mid-stream could be due to the high secondary productivity spots. Our results suggest that the diet of native Puyen changed in relation to the abundances of Rainbow Trout in the stream.

Introduction

Major decreases in the biodiversity of aquatic systems during the last century have been attributed to habitat loss and species introduction (Mack et al. 2000; Muotka and Syrjänen 2007). Salmonids (genus *Oncorhynchus*, *Salmo* and *Salvelinus*) are among the most widely introduced fish taxa around the globe (Welcomme 1988), mostly for recreational and aquaculture purposes (McDowall 1994; Pascual and Ciancio 2007). Salmonid introductions have been broadly implicated in the decline of native biota (Crowl et al. 1992; Greig and McIntosh 2006; Soto et al. 2007; Arismendi et al. 2009), with consequences at all levels of ecological organization including behavior alterations at individual level (Simon and Townsend 2003), reduction in population abundance (Moyle and Light

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1996; Townsend 2002), and trophic cascades (Simon and Townsend 2003).

Starting in the early 20th century, and pushed by the high value of salmonids for fisheries and aquaculture, governments in Chile (Basulto 2003), New Zealand (McDowall 1990; Flecker and Townsend 1994), and Argentina (Tulian 1908; MacCrimmon 1971; Lever 1996) promoted the introduction and establishment of salmonids in the Southern Hemisphere. More than ten salmonids species were introduced in southern rivers in Chile (Arismendi et al. 2014) and Argentina (Pascual et al. 2002). However, it has only been during the last 30 years that the ecological consequences of salmonid establishment in these areas started to be observed and investigated with a special focus on their effect on native communities (e.g., Crowl et al. 1992; Arismendi et al. 2009; Young et al. 2010), the resources used (Kusabs and Swales 1991; Buria et al. 2007; Penaluna et al. 2009), competition and predation (McIntosh et al. 1992; Macchi et al. 1999; McDowall 2003), and niche overlap (Vargas et al. 2010; Arismendi et al. 2012; Correa et al. 2012; McHugh et al. 2012).

The study of diet breadth between the exotic and selected native species provides a practical entry point to the understanding of the impacts of salmonids in Patagonia (Soto et al. 2007; Habit et al. 2010). Whereas niches may be characterized as measures of resource utilization (Giller 1984), diet breadth refers to the utilization of some of the same type of resources by two or more species of resource consumers (Colwell and Futuyma 1971; Abrams 1980). In particular, exotic species provide natural experiments where the ecological theory (e.g. optimal foraging after an invasion) may be tested empirically through evaluating habitat segregation, density reduction, niche shifts, food intake reduction, prey composition alteration, or size structure changes (Bøhn et al. 2008), with possible temporal shifts in feeding habits (Coghlan et al. 2007).

Experimental manipulations of the density of exotic species arguably provide the most powerful approach to study system-level effects of single species on native communities (Tilman 1987; Hansson et al. 1998). However, rivers are large and open systems where fish are highly mobile and thus, manipulation is often very difficult. Researchers are then limited to looking for natural experiments, where naturally contrasting densities occur. This approach has been applied, for instance, to study the effects of Rainbow Trout (*Oncorhynchus mykiss*) on galaxiids (*Galaxias* spp.) niche width (Townsend 2002; McHugh et al. 2012) and the interaction for food and space between

populations of galaxiids and juvenile trout in New Zealand (Glova et al. 1992; McIntosh 2000; McDowall 2003; McIntosh et al. 2010). It has also been used in South America to study habitat use and segregation of native fishes and trout in Chilean streams (Penaluna et al. 2009) and differential piscivory effects on galaxiids by native predators and trout in Northern Patagonia (Arismendi et al. 2012; Juncos et al. 2013).

One of the main deficiencies in our current knowledge concerning exotic trout in southern Patagonia is about trophic relationships and interactions with conspicuous native fishes such as Galaxiids and Siluriforms (Pascual et al. 2002). The aim of the present study is to evaluate diet overlap of underyearling Rainbow Trout (*Oncorhynchus mykiss* Walbaum 1792) in sympatry with the most abundant native species Puyen (*Galaxias maculatus* Jenyns, 1842), in the Santa Cruz River, one of the largest rivers in the region. We concentrated our effort during the low flow season (springtime) along 306 km of the mainstem of the Santa Cruz River, between the head lake, Lago Argentino, and the outflow into the Atlantic Ocean (Fig. 1). We evaluated if Rainbow Trout and Puyen are using similar food resources along a gradient of contrasting relative abundance of both species as a preliminary exploration of mechanisms of competition avoidance.

Since no information regarding native galaxiids distribution and feeding habits before trout invasion is available for large rivers, this study represents an important first approximation to examine interspecific interactions between salmonids and native fishes in this understudied region. Because the Santa Cruz River can be considered a minimally human-influenced river (Brunet et al. 2005; Tagliaferro et al. 2013), our study will also provide a baseline for future comparison with other large rivers.

Materials and methods

Study area

The Santa Cruz River (50° S; 70° W) originates in two oligotrophic to ultra-oligotrophic large glacial lakes, Viedma and Argentino, and flows uninterrupted for 382 km across the Patagonian plateau to drain into the Atlantic Ocean (Fig. 1; Brunet et al. 2005). The river has an average discharge of 691 m^3 s^{-1} (min. 278.1 m^3 s^{-1} in September and max. 1,278 m^3 s^{-1} in March), which is highly predictable due to a glacial dominated regime
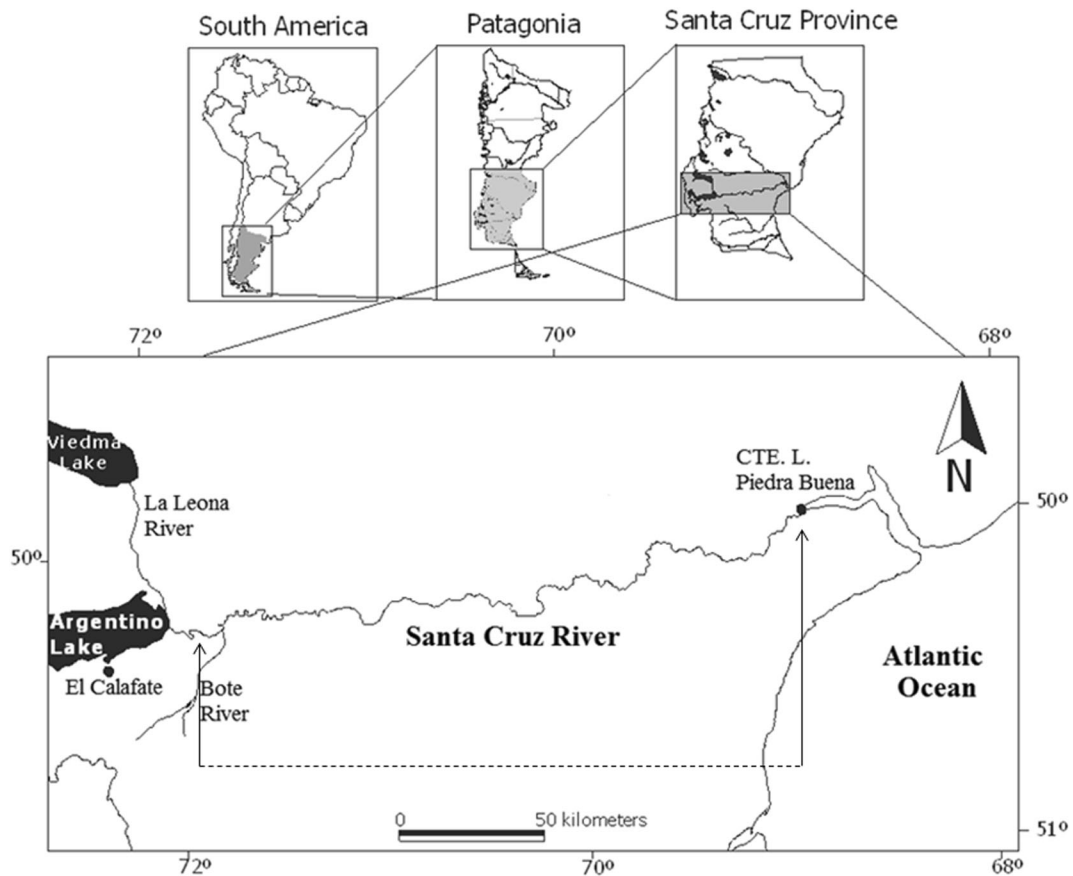
Fig. 1 Map of the Santa Cruz River, Argentina. Sampling sites are located between Charles Fuhr Bridge and Comandante. Luis Piedra Buena Town (between arrows)

(Tagliaferro et al. 2013). This river has low variability of the environmental structure (Tagliaferro et al. 2013); it is an un-braided river (100–200 m wide×382 km length) and temperature between upstream/ downstream areas differs only by 3–5 °C at a given time of the year. Along the river, temperature varies only in 2 to 5 °C during a period of few weeks, e.g. temperature variation during sampling was 5.7±0.5 °C, 7.0±0.9 °C, and 8.6±0.9 °C for upstream, midstream and downstream areas respectively). The Santa Cruz River has been characterized as the one of the poorest in terms of macroinvertebrate abundance among 40 Patagonian rivers (Miserendino 2001).

Sampling

We sampled fish and macroinvertebrates during September 2010 (low flow period) in 52 sites at intervals of 6 km along the Santa Cruz River (50° S; 70° W,

Fig. 1). The uppermost site was located in Charles Fuhr (9.8 km downstream from the Lake Argentino, 50°16′ S; 71°53′ W) and the lowermost site was located in Comandante Luis Piedra Buena (50° S; 70°60′W), close to the river's estuary and 315.8 km from Lake Argentino. We captured fish (length range: 50– 140 mm) using standard single-pass electrofishing procedures from littoral zone to depths of 0.6 m (Jones and Stockwell 1995; Meador et al. 2003). The equipment used was a Smith-Root LR-24 electrofisher set to a frequency of 90 Hz and a pulse width of 3 ms. At each site, a coastal wadable stretch of 100 m was sampled following a zig-zag track. Catchability may have differed between fish species, but we assumed it to be similar throughout sample sites. All fish were counted, fork length-measured with a digital caliper (0.01 mm nearest unit), and weighed on a Mettler PC 440 Delta Range balance (0.003 g nearest unit). We used the number of individuals captured in the 100 of river as

an indirect measurement of abundance (CPUE). Stomachs from 5 to 10 randomly selected fish from each species and site were removed and stored. Macroinvertebrate samples were obtained with a kick-net of 450 μm mesh size covering 0.25 m², integrating one area for each sample (Tagliaferro et al. 2013). Drift samples were not included in the analyses because the biomass contribution to the total macroinvertebrate was less than 2 % along the river (Tagliaferro 2014). Macroinvertebrate samples were stored in a portable freezer at −18 °C. At the laboratory, both stomach contents and macroinvertebrate samples were transferred into 70 % ethanol for further separation and identification of organisms to the lowest possible taxonomic level, employing a Zeiss stereomicroscope (6.5 X). We identified taxa following Lopretto and Tell (1995), and Domínguez and Fernández (2009).

We measured free-living macroinvertebrates richness and abundance, and dry weight of consumed prey for the data analysis. To calculate dried weight, we assigned individuals to a given taxon, dried to a constant weight at 65 °C (24 h), and weighed on an analytical Shimadzu AUW-220 scale (range: 220 g – 10 mg, error: 1 mg). When prey was partially digested, weight was estimated from complete items of the same length. Chironomidae species, which were similar in size and ecological role, were pooled as one group. Other small taxa (e.g. Oligochaeta, Glossosomatidae, and Trichoptera) were also pooled as one group.

Fish relative abundances were estimated for each sampling site to assess patterns of distribution of Rainbow Trout and Puyen. Three different sections of the river were defined based on the Rainbow Trout to Puyen ratio: an "upstream" area, with high proportion of Rainbow Trout (over 0.75), a "downstream" with low proportion (less that 0.25), and a "mid-stream" with intermediate proportion (0.25 and 0.75). Stomach contents of 17 Puyen and 32 Rainbow Trout were analyzed in the upstream area; while in mid-stream, 82 Puyen and 116 Rainbow Trout, and in downstream area 101 stomachs of Puyen and 44 of Rainbow Trout were examined.

Fish diets

We used three methods to characterize the fish diets (Hyslop 1980; Chipps and Garvey 2007): including (a) the frequency of occurrence (%Fi) of a given prey type, defined as the mean number of stomachs in which that prey occurs in relation to all the stomach studied for each area; (b) the biomass contribution (%Bi) of a prey to the dry weight of each stomach contents, and (c) prey specific abundance (Pi; Amundsen et al. 1996). These indices were calculated as follow:

$$\%F_i = \frac{N_i}{N}$$

$$\%B_i = \left(\sum_i^t \frac{S_i}{S_t} \right) *100$$

$$P_i = \left(\sum_i^t \frac{S_i}{S_{ti}} \right) *100$$

where N_i is the number of fish with prey i in their stomach, N is the total number of fish with stomach contents, S_i is the contribution of prey i to stomach fullness in dried mass, S_t is the total stomach biomass of all fish, and S_{ti} is the total stomach fullness of fish with prey i in their stomach. At each area (upstream, mid-stream, and downstream), Fi and Pi were used to create a diagram of "feeding tactics" (Amundsen et al. 1996).

Multivariate analysis of diets

We used a non-metric multidimensional scaling (N-MDS) ordination technique to compare the similarity of diets between species and across areas using the Bray–Curtis distance metric (Clarke 1993; Marshall and Elliott 1997). Based on an iterative optimization procedure, diet compositions were rearranged to minimize a measure of disagreement or stress between their distances in 2-D (Kruskal 1964). The resulting coordinates of each point from the 2-D plot provided a collective index of how unique the diet of a given fish was. The proximity of points in a 2-D plot indicates a higher degree of similarity, whereas more dissimilar points are positioned further apart. We used the standard squared root transformation to down-weight the importance of the highly abundant preys (see Clarke and Warwick 2001 for more details). We used the software PRIMER v6.1.5 (Clarke and Gorley 2006) to produce the ordination plot of the Bray–Curtis similarity coefficient of square root transformed % frequency of prey for each individual (Rainbow Trout or Puyen) and % biomass of each prey at each fish species (Clarke and Warwick 2001).

We tested the hypothesis of no difference among groups (fish species and areas) of diets using an analysis of similarity (ANOSIM). The ANOSIM is a

Table 1 Macroinvertebrate natural abundance (%D), frequency of occurrence (%Fi) and prey-specific abundance in biomass (Pi-B) of preys in stomach contents of *O. mykiss* and *G. maculatus*; values are calculated at each area

Taxa	Upstream							Mid-stream							Downstream						
	%D	Trout			Puyen			%D	Trout			Puyen			%D	Trout			Puyen		
		%Fi	%Bi	Pi	%Fi	%Bi	Pi		%Fi	%Bi	Pi	%Fi	%Bi	Pi		%Fi	%Bi	Pi	%Fi	%Bi	Pi
Mollusca																					
Chilina sp. (Ch)	22.5	—	—	—	—	—	—	—	6.5	0.3	19.9	3.7	0.2	13.6	0.7	—	—	—	—	—	—
Heleobia sp. (He)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.1	2.4	0.9	37.8	—	—	—
Lymnaea sp. (Ly)	—	2	0.6	21	3	3.6	23.9	38	9.7	4.8	35.7	14.8	0.8	41.8	52.9	2.3	2.6	79.5	4.0	4.9	30.4
Annelida																					
Hirudinea (Hir)	0.1	—	—	—	—	—	—	0.3	—	—	—	3.7	0.3	18.7	1.8	—	—	—	—	—	—
Naididae (N)	0.2	—	—	—	2	0.1	2.06	0.1	3.2	0.9	100	7.4	0.8	3.6	—	—	—	—	4.0	0.3	2.0
Acari																					
Acari spp. (Ac)	0.1	—	—	—	<0.1	0.1	1.54	—	—	—	—	—	—	—	—	—	—	—	4.0	0.2	1.0
Crustacea																					
Hyalella spp. (H)	22.6	42	13.4	21.0	45.0	31.4	20.5	18	71.0	21.2	37.4	55.6	24.1	33.5	17.4	35.0	9.5	21.5	20.0	5.7	17.0
Ephemeroptera																					
Andesiops sp. (Ad)	0.2	19	5.1	18.0	16.0	5.5	17	—	9.7	2.8	4.0	7.4	1.5	3.7	0.3	10.0	1.5	11.0	4.0	1.3	16.5
Meridialaris chiloeensis (Mc)	19.9	63	29	38.5	17.0	10.4	98	11	9.7	13.1	25.6	7.4	15.0	19.2	4.4	57.0	21.6	38.5	24.0	9.1	41.0
Plecoptera																					
Aubertoperla illiesi (Ai)	5.1	5	0.6	22.0	—	—	—	0.6	54.8	1.9	74.4	—	—	—	1.7	—	—	—	16.0	<0.1	13.5
Antarctoperla michaelseni (Am)	0.0	24	12	42.0	23.2	10.0	22.1	—	25.8	8.5	32.2	33.3	5.9	35.2	0.1	46.1	21.4	42.0	24.0	14.5	86.3
Klapopteryx kuscheli (Kk)	0.2	22	13	84.0	16.0	8.8	79.4	4.9	6.5	16.4	65.3	11.1	10.6	76.9	0.2	16.2	8.9	67.3	8.0	8.1	92.0
Limnoperla jaffueli (Lj)	—	38	9.1	7.3	15.0	8.8	33	2.5	61.3	14.1	12.3	37.0	10.7	14.3	6.1	84.3	21.5	16.3	63.0	29.1	38.9
Coleoptera																					
Luchoelmis cekalovici (Lc)	14.2	12	2	4.5	11.0	2.5	28	19	48.4	6.7	7.9	25.9	7.3	4.3	8.3	18.0	3.0	1.3	8.0	0.9	11.3
Luchoelmis cekalovici adult (elA)	—	—	—	—	3	<0.1	8.84	—	3.2	—	2.7	—	—	—	—	—	—	—	—	—	—
Veliidae	—	—	—	—	—	—	—	—	—	—	—	14.8	0.3	72.7	—	—	—	—	—	—	—
Trichoptera																					
Mastigoptila sp. (M)	0.3	12	—	7.2	2.5	0.2	2.06	—	19.4	0.3	2.0	3.7	0.2	0.9	—	—	—	—	—	—	—
Rheochorema/Atopsyche sp. (Hy)	0.2	20	3.5	16.7	18.0	2.1	17	—	22.6	1.9	8.4	11.1	1.8	12.6	0.3	26.0	6.7	17.0	8.0	1.7	2.8
Cailloma sp. (C)	0.0	4	2	0.4	7.0	3.7	6	—	—	0.4	—	—	—	—	—	3	0.2	8	—	—	—
Smicridea dithyra (Sd)	2.2	8	0.1	2.1	8.0	0.8	7.66	1.2	6.5	0.1	4.5	—	—	—	—	—	0.1	—	—	—	—

Table 1 (continued)

Taxa	Upstream %D	Upstream Trout %Fi	%Bi	Pi	Upstream Puyen %Fi	%Bi	Pi	Mid-stream %D	Mid Trout %Fi	%Bi	Pi	Mid Puyen %Fi	%Bi	Pi	Downstream %D	Down Trout %Fi	%Bi	Pi	Down Puyen %Fi	%Bi	Pi
Oxyethira sp. (O)	0.0	–	–	–	<0.1	<0.1	3.15	–	–	–	–	3.7	0.1	9.4	–	–	–	–	–	–	–
Dyctisidae	–	–	–	–	–	–	–	–	–	–	–	3.7	0.6	18.3	–	–	–	–	–	–	–
Diptera																					
Chironomidae	11.6	0	0.1	2.6	9.4	5.8	21	4	–	0.1	–	25.9	1.4	8.7	0.2	0.3	<0.1	1.4	23.1	8.9	17.9
Eukiefferiella sp. (Eu)																					
Paratrichocladius sp. (Pcl)																					
Endotribelos sp. (En)																					
Parachironomus sp. (Pch)																					
Alotanipus sp. (Al)																					
Other larvae	0.1	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	4.0	0.3	2.3
Pelecorhynchidae (Pe)																					
Empididae sp. (Em)																					
Muscidae sp. (Mu)																					
Simuliidae	0.6	31	2.4	1.9	22.5	6.2	11	0	25.8	1.1	1.8	11.1	1.1	6.0	0.4	36.0	2.1	4.3	28.0	7.0	9.7
Terrestrial Preys																					
Trichoptera	0.0	16	7	46.2	–	–	–	–	–	3.2	–	33.3	13.0	32.2	–	4	<0.1	59	4.0	7.4	79.0
Ephemeroptera	–	–	–	–	–	–	–	–	–	–	–	7.4	3.9	40.9	–	–	–	–	<0.1	0.8	2.5
Formicidae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.0	0.2	3.8

nonparametric procedure analogous to analysis of variance (ANOVA) that tests differences in distance in the ordination matrix of fish diets against random groups (a detailed procedure is provided by Clarke 1993). We conducted 99,999 random permutations to estimate the significance of the R test statistic associated with ANOSIM and the posteriori pairwise tests. The R statistic ranges between −1 and +1, where −1 indicates more similarity between groups than within groups, 0 indicates no effect of groups and +1 indicates less similarity between groups than within groups. Though an R value of 0.45 is expected when groups exhibit significant differences; when analyzing a large number of replicates, R value could be smaller and statistically significant (Clarke 1993). In addition, we performed a similar procedure to evaluate possible differences in macroinvertebrates abundances and biomass among upstream, mid and downstream areas.

A SIMPER, or 'similarity percentage', analysis was performed on squared-root transformed data providing a ranking that shows which prey items contributed most by percentage to the similarity in a within group test, or the percentage of dissimilarity contributed to a between group test. SIMPER decomposes average Bray– Curtis similarities between all pairs of samples in groups (or between groups of samples) into percentage contributions from each dietary item (Clarke 1993). Finally, the similarity within groups was ranked by estimating the index of multivariate dispersion, which provides information on diet width (MVDISP; Warwick and Clarke 1993).

Degree of dietary overlap and prey electivity

As a complement of the N-MDS and ANOSIM analysis, we calculated the degree of the dietary overlap between Puyen and Rainbow Trout at each area using the Schöener index (1970):

$$C_{Puyen/trout} = 1 - 0.5 * \left(\sum \left| p_{Puyen,i} - p_{trout,i} \right| \right),$$

where $p_{,puyen,i}$ is the proportion of prey i in Puyen, and $p_{trout,i}$ is the proportion of prey i in Rainbow Trout. Following Wallace (1981), we considered a $C_{Puyen/trout} =$ 0.6 or above as a significant diet overlap. A value of 0.6 indicates a 60 % of overlap in the diet.

In addition, we calculated the Ivlev electivity index (Ivlev 1961) as a measurement of fish electivity of prey as follows:

$$I_i = \frac{r_i - p_i}{r_i + p_i}$$

where r_i and p_i are the proportion of item or prey i in the stomach content and environment, respectively. The range of I_i varies from −1 (complete rejection) to +1 (positive chosen), with values around zero indicating that feeding is proportional to item abundance in the
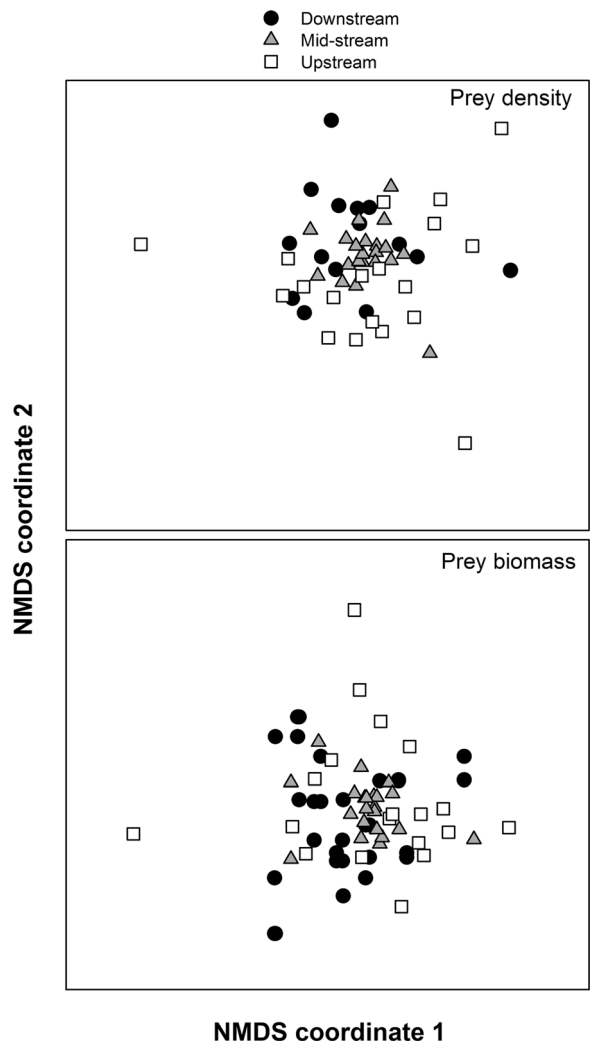

Fig. 2 Non-metric MDS ordination plot (2D) showing the degree of similarity of prey density (upper panel; stress 0.17) and prey biomass (lower panel; stress 0.17) among the 52 sites grouped by up- mid and downstream areas using Bray-Curtis similarity index. Proximity of symbols indicates a higher degree of similarity

environment. We considered positive or negative electivity when I_i was above 0.5 and below −0.5 respectively.

Results

A total of 587 Rainbow Trout and 1,183 Puyen were captured with fork length 40–90 mm and weight 0.5–9.0 g, similar for both species along the 306 km of river. A total of 192 and 200 stomach contents of Rainbow Trout and Puyen, were analyzed respectively. Twenty-eight prey types for Rainbow Trout and 38 for Puyen were found, from autochthonous and allochthonous (terrestrial) origin. A total of 38 exclusive benthic macroinvertebrates were found within all the sampling sites (Table 1).

ANOSIM showed a significant dissimilarity among areas (for prey density R statistic=0.059, P=0.001; for prey biomass R statistic=0.071, P=0.009). Pairwise ANOSIM results for prey density showed significant statistical differences between upstream and mid-stream areas (R statistic=0.11, P=0.001), and between mid-stream and downstream areas (R statistic=0.09, P=0.006), but not for upstream versus downstream areas (R statistic=0.001, P=0.34). Moreover, pairwise ANOSIM results for prey biomass showed significant statistical differences between upstream and mid-stream areas (R statistic=0.12, P=0.006), and between mid-stream and downstream areas (R statistic=0.08, P=0.008), but not for

upstream versus downstream areas (R statistic=0.05, P=0.12). Mid-stream areas exhibited a greater variability with many sites with high macroinvertebrates biomass, a possible reason why the non-metric MDS ordination plot showed the distribution overlap of prey density and prey biomass among the 52 sites grouped by up- mid and downstream areas using Bray-Curtis similarity index (Fig. 2).

Because the distribution of fish showed high predominance of Rainbow Trout from upstream towards mid-stream sites, and decreased in downstream sites, where Puyen were more predominant, (Fig. 3) diet overlap was compared among areas. In upstream areas, Rainbow Trout-Puyen ratio ranged from 0.75 to 1, where Puyen exhibited the lowest CPUE values from 0 to 13 ind. per 100 linear meters. In downstream areas, Rainbow Trout-Puyen ratio ranged from 0.1 to 0.25. The mid-stream area showed a Rainbow Trout-Puyen ratio ranging between 0.25 to 0.75 with CPUE values of 22 ± 17 ind. per 100 linear meters and 25 ± 17 ind. per 100 linear meters for Rainbow Trout and Puyen respectively. We assumed that the species-specific catchability remained unchanged along the river.

Diet overlap

A higher degree of dietary similarity between Rainbow Trout and Puyen was found in both biomass and number of prey only for the area downstream, (diet overlap for

Fig. 3 Capture per unit of effort (CPUE; fish per 100 m of river) of Puyen (G. maculatus) and Rainbow Trout (O. mykiss) at the 52 sampling sites located 6 km from each other and grouped by the three up- mid and downstream areas. Box-plots represent 5th, 25th, median, 75th and 95th percentiles. Numbers above each box-plot indicates the range of fish ratios at each area
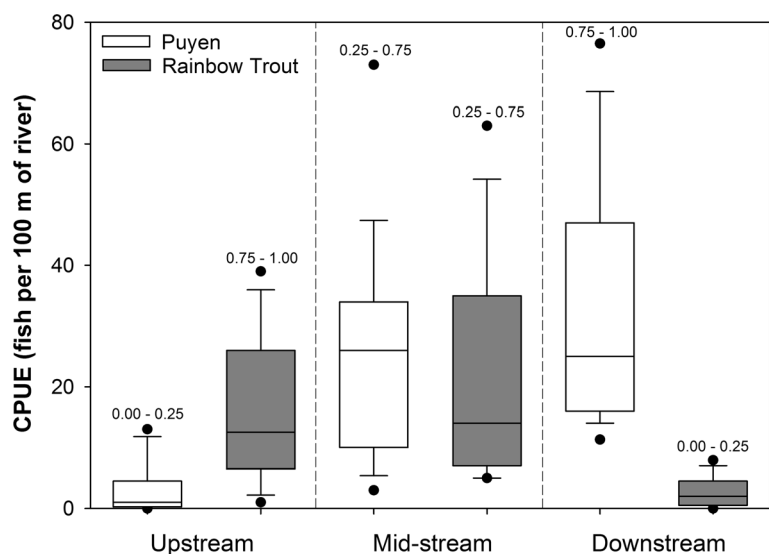
%Fi and %Bi; P=0.19; Fig. 4; Table 2). The other two areas, upstream and mid-stream, showed statistically significant differences in the similarity of diets between Rainbow Trout and Puyen. Also, each species' diet varied across river areas, both in biomass and number of prey (Table 2, bottom part). Of all species-specific pairwise comparisons between areas, only those for Rainbow Trout between upstream and downstream

Fig. 4 Non-metric MDS ordination plot (2D) showing the degree of similarity among individual fish diets of Puyen (*G. maculatus*) and Rainbow Trout (*O. mykiss*) from the up- mid and downstream areas using Bray-Curtis similarity index. In the upper panel, individual fish diets are grouped by %Fi (stress=0.20) and in the lower panel by %Bi (stress=0.19). Proximity of symbols indicates a higher degree of similarity

areas were non-significant. Even small visual differences appeared in the N-MDS plot (Fig. 4), there was a statistically significant difference in the diet between species in sites both upstream and midstream (for *%Fi* and *%Bi* R statistic ranged between 0.09 and 0.18, P<0.001; Table 2).

The degree of overlap in diets between Puyen and Rainbow Trout, estimated as the Schöener index, showed a differential response among areas, which was concordant with the N-MDS and ANOSIM analyses. Lowest values were found upstream at 20 to 30 % overlap detected, while the range of values in the midstream area was intermediate (25 to 45 %), indicating a low diet overlap between species at that area. The highest Schöener index was found downstream where the Rainbow Trout presented the lowest abundance, including sites with 20 to 80 % diet overlap. Despite the large amplitude range, only this area exhibited sites with diet overlap of up to 80 % between the two species. Therefore, high diet overlap occurred between Puyen and Rainbow Trout only in the downstream area with overlap degrees of up to 80 %.

The SIMPER analysis showed that the amphipod *Hyalella* sp., the stonefly *Limnoperla jaffuelli*, the mayfly *Meridialaris chiloeensis,* and Simuliidae larvae accounted for most of the dissimilarity in diet between species for both upstream and mid-stream areas (Table 3). While in mid-stream areas the elmid *Luchoelmis cekalovici* was also a prey that significantly contributed to diet differences between Rainbow Trout and Puyen (13.5 %), in upstream areas, the stonefly *Antarctoperla michaelseni* accounted for 8.2 % of the differences. Generally, a higher number of prey contributed to the Puyen diet, which is consistent with a higher multivariate dispersion index (MVDISP). This index indicates that the Puyen's diet was more dispersed than Rainbow Trout in all three areas (for *%Fi* and *%Bi*).

Feeding tactics and prey electivity

Both Rainbow Trout and Puyen showed a generalist feeding tactic in all three areas (Fig. 5). The frequency of occurrence and prey-specific abundance of stomach contents in Rainbow Trout and Puyen generally displayed a comparable pattern with both species consuming similar proportions on different prey items. Diets of both Rainbow Trout and Puyen was characterized by the occurrence of many rare prey and few
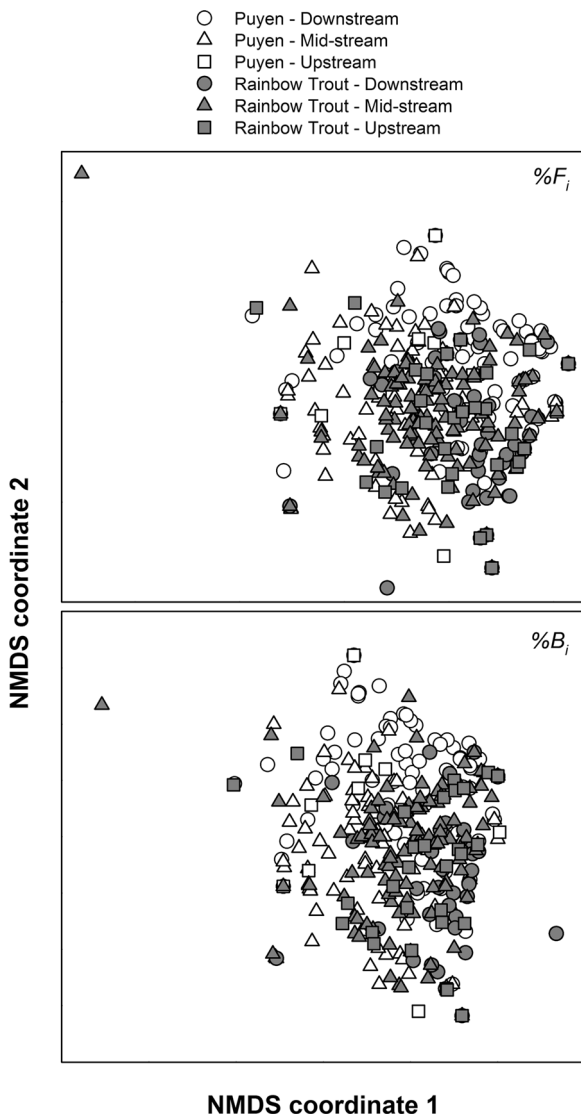
Table 2 Pairwise ANOSIM results by species and areas

	Pairwise Tests	Biomass			Number		
	Groups	R- Statistic	p level		R- Statistic	p level	Significance
Between species							
	Upstream	0.17	0.003	**	0.18	0.001	**
	Mid-stream	0.12	< 0.001	***	0.09	<0.001	***
	Downstream	0.03	0.190		0.02	0.265	
Between areas							
Trout	Up vs mid-stream	0.13	0.007	**	0.14	0.003	**
	Up vs downstream	0.04	0.077		0.03	0.155	
	Mid vs downstream	0.08	0.024	*	0.14	< 0.001	***
Puyen	Up vs mid-stream	0.18	0.002	**	0.18	0.002	**
	Up vs downstream	0.20	0.003	**	0.20	0.002	**
	Mid vs downstream	0.16	< 0.001	***	0.16	< 0.001	***

consumed species frequently found such as the amphipod *Hyalella sp.*, the mayfly *Meriadialaris chiloeensis*, the stoneflies *Limnoperla jaffueli, Antarctoperla michaelseni,* the elmid *Luchoelmis cekalovici*, and adult midges. These five taxa, with the exception of the midges, were the most widely distributed taxa in the benthos along the river (Table 1) underlying the generalist feeding tactic by both species. Diptera, Simuliidae, and Chironomidae were the families most frequently consumed by both fish species. *M. chiloeensis,* being one of the most recurrent preys in Rainbow Trout across the three areas (Fig. 5) and resulted in a departure from the homogeneity in the diet of both species.

Electivity of prey exhibited a similar general pattern in both Rainbow Trout and Puyen (Fig. 6). Both species positively selected Simuliidae larvae, the stoneflies *Limnoperla jaffuelli* and *Antarctoperla michaelseni*, larvae of the caddisfly Hydrobiosidae and adult caddisfly. On the other hand, the elmid *Luchoelmis cekalovici*, the gastropod *Lymnaea* sp. and the caddisfly *Smicridea dythira* were avoided by both Rainbow Trout and Puyen. One of the most abundant macroinvertebrates, the amphipods, *Hyalella araucana* and *H. curvispina*, and the mayfly *Meridialaris chiloeensis* were consumed in comparable proportion to environmental availability along the river. In addition, Rainbow Trout positively elected the stonefly *Klapopteryx kuscheli* and the mayfly *Andesiops* sp., and avoided chironomids larvae; while the Puyen consumed these prey in similar proportions to those available in the stream.

Discussion

In agreement with previous studies conducted in Patagonia (Lattuca et al. 2008; Di Prinzio and Casaux 2012), we show that Rainbow Trout and Puyen are generalist predators, with a relatively low electivity of prey. The Puyen, however, appear to have a wider diet breath than Rainbow Trout in the Santa Cruz River. The use of wider feeding sources in Puyen could explain the low diet overlap with Rainbow Trout. This wider diet breath may be a response of native Puyen to feed on less desirable resources and thus, a response to a higher dominance of Rainbow Trout. Differences in the diet of galaxiids with and without Rainbow Trout were attributed to the interaction with the latter (Glova et al. 1992; Glova and Sagar 1993; Elgueta et al. 2013). Rainbow Trout are known to exhibit a more voracious feeding behavior than galaxiids, which is consistent with the diet differences found in the areas where Rainbow Trout were more abundant. Alternatively to the competitive interactions based on diet overlap includes predation on both species, the availability of suitable environment, and the river productivity to support the two species (Arismendi et al. 2012, 2014). However, there is no predation between the two species at this life stage. Indirect interactions might occur such as habitat segregation (e.g. Penaluna et al. 2009) and it should be tested in future comparisons. However, in the Santa Cruz River there is not much cover (Tagliaferro et al. 2013;

Table 3 SIMPER results between trout and puyen diets in upstream and mid-stream areas. Average abundance of prey in diet of trout and puyen, percentage of contribution to diet (Cont. %), and cumulative percentage (Cum. %). Preys that contributed less than 2.5 % were excluded from the table

Upstream	Average Abundance		Cont. %	Cum. %
	Trout	Puyen		
M. chiloeensis	2.32	0.16	18.0	18.0
Hyalella sp.	1.35	1.68	16.7	34.7
Simuliidae	0.84	0.74	11.5	46.3
L. jaffuelli	0.97	0.37	10.6	56.8
A. michaelseni	0.57	0.26	8.2	65.0
Andesiops sp.	0.22	0.16	5.4	70.4
K. kuscheli	0.43	0.11	5.3	75.7
Chironomidae	0.14	0.79	4.9	80.6
Hydrobiosidae	0.38	0.05	4.5	85.1
L. cekalovici	0.11	0.68	4.4	89.5
Adult Trichoptera	0.3	0,00	3.5	93.0
Mid-stream				
Hyalella sp.	2.97	2.18	15.6	15.6
L. cekalovici	1.75	2.03	13.5	29.1
L. jaffuelli	1.92	0.7	13.0	42.1
M. chiloeensis	1.17	0.77	10.4	52.5
Simuliidae	0.99	0.57	7.1	59.6
Adult Trichoptera	0.18	0.57	5.7	65.3
A. michaelseni	0.41	0.21	5.1	70.4
K. kuscheli	0.31	0.21	4.9	75.3
Hydrobiosidae	0.24	0.12	3.5	78.8
Chironomidae	0.03	0.55	3.3	82.1
Andesiops sp.	1.01	0.06	3.0	85.1
Lymnaea sp.	0.46	0.08	3.0	88.1
Adult Ephemeroptera	0.06	0.48	2.3	90.4

Quiroga pers. comm.) and therefore, we consider that other possible interactions besides competition for food might be less important.

Moreover, throughout the study area, the electivity of prey is similar for both species, except in few prey such as *K. kuscheli*, (one of the largest food items), or small chironomids larvae (found in shallow water). Possible explanations include the ideas that fish species may be choosing the same prey of different size (Di Prinzio et al. 2013), feeding in different places or at different times (Holt 1987), or exhibit food partitioning or feeding modes (Kusabs and Swales 1991). Despite the short time of co-existence between trout and galaxiids, some

galaxiids already have shown differences in timing of their feeding (Glova et al. 1992), changes in diet composition and specialization (Elgueta et al. 2013), and restriction to shallow covered areas (Habit et al. 2010; Correa et al. 2012) concordant with the possible avoidance of interaction with salmonids.

Similarities in diet between trout and galaxiids evidenced that both species might feed at the same trophic level (McHugh et al. 2012), but the segregation of habitat or prey resources contributes to long-term coexistence. In addition, because Puyen is a small fish, the prey it consumes are restricted to the mouth and stomach size, which might generate a reciprocal trophic niche displacement, similar to that found between *G. platei* and trout (Correa et al. 2012). Thus, despite the negative effect that trout can generate on these native fishes, the small size of Puyen may be advantageous for differential use of resources and therefore facilitate the coexistence with trout.

Because the Santa Cruz River is a homogeneous river, with low primary and secondary production (Miserendino 2001) and hydrologically very stable (Tagliaferro et al. 2013), juvenile trout and Puyen may select different habitat at the mesohabitat level to avoid food competition (see Penaluna et al. 2009). Although the specific mechanisms are to be explored, our study shows the potential for a diet overlap between these two species, and possible changes along this large river. Whereas there is evidence that adult Rainbow Trout may feed on galaxiids, especially in lakes (Macchi et al. 1999; McDowall 2003; Arismendi et al. 2009), we found no evidence of juvenile rainbow Rainbow Trout predation on Puyen (see also Arismendi et al. 2012). This suggests that the trophic interaction between underyearling Rainbow Trout and native galaxiids should be contemplated from a competition point of view.

The contrasting distribution pattern of Puyen and Rainbow Trout along the mainstem of the Santa Cruz River may be related to the differential habitat requirement of both species or displacement of galaxiids by Rainbow Trout. Similar to New Zealand counterpart, Puyen in Patagonia evolved in isolation from salmonids, and even if it coexisted with other fish predators, (e.g. perch), its predator-avoidance behavior might not be efficient enough to withstand the predation by adult salmonids. Recent studies explained that most of the
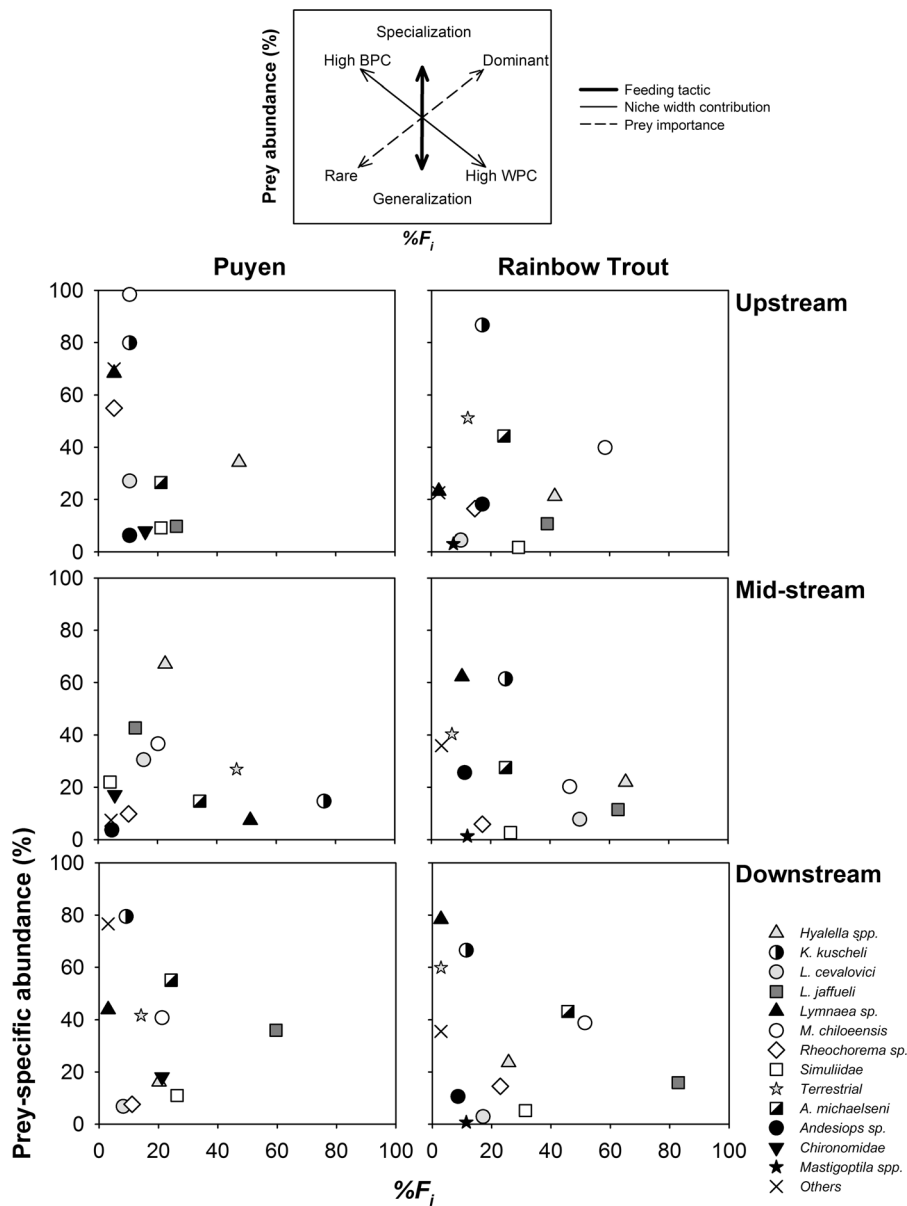
Fig. 5 Amundsen diagrams (see Amundsen et al. 1996) of feeding tactics for Puyen (*G. maculatus*) and Rainbow Trout (*O. mykiss*) at the three river areas. The upper panel represents the explanatory diagram for interpretation of feeding tactics, niche width contribution and prey importance. For the niche width contribution, HPC=high between-phenotype component to niche width, and WPC=high within-phenotype component to niche width

naturalized juvenile Rainbow Trout are descendent from anadromous Rainbow Trout, which spawn at the mid-upstream area of the Santa Cruz River (Liberoff 2013), this might generate higher abundances of Rainbow Trout and consequently a higher competition pressure. On the other hand, Puyen has both landlocked and diadromous behavior (Carrea et al. 2013; Tagliaferro et al. 2014) that spawn downstream in estuarine zones

explaining the greater abundance of this species close to the river mouth.

This study represents the first extensive research concerning diet composition of native galaxiids and Rainbow Trout along the second largest river in Patagonia. Given the un-disturbed hydrological and production characteristics of this river, this research provides valuable baseline data on the feeding tactics
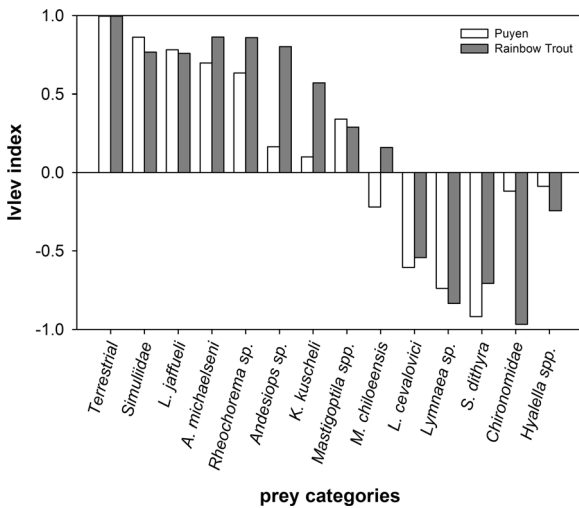
Fig. 6 Ivlev Index of prey selectivity for Rainbow Trout and Puyen. Index value above 0.5 indicates possitive electivity, and below -0.5 indicates avoidance of prey

of native and exotic fish to be used to contrast with other large rivers affected by human activities like agriculture, urbanization or stream regulation.

Future considerations on habitat preference should also be taken into account. Changes in microhabitat could produce a higher interaction between trout and native galaxiids (McIntosh et al. 1992); species habitat width might change in presence of the invader (Penaluna et al. 2009) and the wider the environmental range, the more likely the coexistence between species will be (Meszéna et al. 2006). Due to the low habitat variability characteristic of the Santa Cruz River, which is reflected in the structure of macroinvertebrate communities (Tagliaferro et al. 2013), we expect Rainbow Trout and galaxiids to have reduced opportunities for habitat segregation, and a larger potential for competition and displacement in feeding habits.

One obstacle when studying remote places, like Southern Patagonia, is that previous research is scant and baseline data inexistent. Moreover, non-invaded, control areas are scarce. The existence of areas with differential relative abundances of Rainbow Trout provided us with a means to evaluate the potential trophic interaction and segregation between native and exotic fish in this large river and contributed to the understanding of the invasive fish role during the first year of life.

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