

Impact of exotic rainbow trout on the benthic macroinvertebrate community from Andean-Patagonian headwater streams

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With 6 figures and 2 tables

Abstract: Introduction of salmonids is a common and widespread practice in rivers and lakes of Patagonia, but their impacts remain poorly understood. We analyse the effect of exotic introduced salmonids (rainbow trout *Oncorhynchus mykiss*) on the benthic macroinvertebrate community of low order streams. We conducted a field survey in three headwater streams (Challhuaco, Cascada and Pescadero streams) in the northern Andean-Patagonian region (around 41° S and 1500 m above sea level). The streams are canopied by deciduous *Nothofagus pumilio* forest. On each system, we established fishless and contiguous fish sites separated by waterfalls that limit fish access to upper sections. At each site we determined benthic macroinvertebrate size, taxonomic and functional structure in addition to trout gut contents. In the presence of trout, we observed significant shifts in invertebrate body size towards smaller individuals, thus a decrease in total macroinvertebrate biomass was observed. We found that large taxa (*Klapopteryx kuscheli*, *Tipula* sp.) and active swimming species (*Metamonius anceps* and *Hyalella curvispina*) were reduced in abundance or were absent in reaches with trout. At the same time, we found that trout positively selected large size classes of invertebrates. As a consequence of species losses, benthic community structure changed drastically in the presence of trout: shredders were the feeding group most affected negatively (–68%) followed by scrapers. The reduction of shredders may suggest a potential effect on *Nothofagus* leaf litter breakdown and hence, supply of FPOM to downstream reaches.

Key words: biological invasion, benthic macroinvertebrates, functional feeding groups, salmonids, Andean Patagonian headwaters.

Introduction

Top fish predators can alter fundamental ecological properties such as the dominance of a certain species and the ecosystem's physical features, primary productivity and nutrient recycling (Vitousek 1990). In freshwater systems, fish have important effects at individual, population, community and ecosystem levels (Power 1992, Nyström et al. 2001, Townsend 2003). Evidence of direct impacts causing the elimi-

nation of native species is common (Flecker & Townsend 1994, McIntosh 2000, Mack et al. 2000). In addition, fish can affect several trophic levels via cascade effects (Power 1992, Brönmark et al. 1997, Huryn 1998). In particular, fish have played an important role in the differential elimination of species of diverse sizes and food niches (Townsend 1996). Usually, visual predators exert a strong size-selective force (Gilliam et al. 1989, McIntosh 2000), and may determine the size structure of the community

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through selective removal of certain sizes (Peckarsky 1982, Bechara et al. 1992, 1993). Salmonids were widely introduced in different parts of the world, and available information suggests that their impacts may be severe and rapid (Townsend 2003). Salmonids are visual size-selective predators, which feed mainly on drifting invertebrates (Newman & Waters 1984). Previous studies showed that following salmonid introduction reductions of large or active swimmer species can occur (e. g. Townsend & Hildrew 1984). As a consequence changes in size structure of the invertebrate community towards smaller sizes have been reported (Wilzbach et al. 1986, Bechara et al. 1993, Usio & Townsend 2000). These changes would have important implications for ecosystem functioning because they might influence food-chain efficiency and energy transfer in aquatic food webs.

Patagonia has a complex landscape with many lakes, rivers and small streams. In this region, the introduction of salmonids has been a common practice that began early in the twentieth century to enhance wild fish populations with valuable sport fishes (Pascual et al. 2002). Nowadays, the Patagonian fish fauna is dominated by exotic salmonids (mainly rainbow trout), however, their impact on native fish and other aquatic biota remains poorly understood (Modenutti & Balseiro 1994, Pascual et al. 2002).

Headwaters in Patagonia are located in the Andes at 1100 m a. s. l. where streams are canopied by deciduous endemic beeches of the genus *Nothofagus*, which are responsible for most of the leaf litter input (Modenutti et al. 1998, Albariño & Balseiro 2002). The input timing and breakdown rates of *Nothofagus pumilio* (P. et E.) Krasser leaf litter might be key drivers in the functioning of small canopied streams (Albariño & Balseiro 2002). Shredders, mainly large nymphs of Plecoptera, contribute substantially to leaf litter breakdown (Albariño 2001, Albariño & Balseiro 1998, 2002). The Plecoptera are a fairly old group of lotic freshwater insects with an extremely high degree of endemism in this region (Illies 1977). The selective feeding behaviour of trout raises the possibility that this visual predator could affect large shredders or active-swimmer invertebrates such as Plecoptera and Ephemeroptera. We hypothesise that the impact of salmonid fish on preferred dietary components belonging to particular functional feeding groups, such as large shredders or swimmer grazers, would drive the community to a novel structure and functioning. To test this hypothesis we analysed the effects of an alien fish predator on invertebrate size, taxonomic and functional structure in Andean Patagonian headwater streams.

Methods

Study site

This study was carried out in three low order streams of the Nahuel Huapi basin: Challhuaco, Cascada and Pescadero streams. The area is located in the Nahuel Huapi National Park, Northwestern Patagonia (Argentina) and corresponds to the deciduous forest district of the Subantarctic province. Challhuaco and Cascada streams flow through a deciduous *N. pumilio* forest ("lenga") while the canopy of Pescadero stream is mixed, composed of both *N. pumilio* and the evergreen *N. dombeyi* (Mirb.) Blume ("coihue"). The climate is cold temperate, with a mean annual temperature of 8 °C and rainfall around 1700 mm/year mainly falling in autumn.

The streams contain a series of waterfalls that act as physical barriers for salmonid movements allowing us to identify fishless and fish sites in neighbouring reaches (above and below of natural barriers, respectively). In Challhuaco stream, we established a fishless site called UBCh (Up-Barrier Challhuaco) and an immediately continuous trout reach called DBCh (Down-Barrier Challhuaco). Cascada stream joins Challhuaco downstream after a high waterfall allowing us to replicate the fishless site (Up-Barrier Cascada; UBCa). Down-Barrier Challhuaco was considered a common site for both fishless upper barrier sections. Pescadero stream has two close waterfalls that determine three contiguous reaches with different trout abundances as determined in a preliminary survey. The uppermost section has no fish (Up-Barrier Pescadero; UBPe), and the middle (Inter-Barrier Pescadero, IBPe) and lower (Down-Barrier Pescadero; DBPe) reaches have low and high abundance trout, respectively. DBCh and DBPe resulted in similar fish abundance (see results).

The different study sites are very similar in physical and chemical features. Sampling sites were located in sections with ~1.6 m width and ~0.36 m depth (*t*-test comparing fishless and fish sites $P > 0.05$). The substrate was a mixture of boulders and cobbles averaging 0.22 m in diameter (*t*-test comparing fishless and fish sites $P > 0.05$). Streams have diluted waters dominated by calcium, bicarbonate and dissolved silica (Pedrozo et al. 1993). Water pH was circumneutral, and dissolved oxygen concentration was always at saturation. Water temperature varied during the year, from 11 °C in summer to 2 °C in winter. Conductivity was low, varying between 40–45 $\mu\text{S cm}^{-1}$ (autumn–winter) and 45–64 $\mu\text{S cm}^{-1}$ (spring–summer) (*t*-test comparing fishless and fish sites $P > 0.05$). Water velocity ranged from 27 cm s^{-1} (summer) to 114 cm s^{-1} (winter) (*t*-test comparing fishless and fish sites $P > 0.05$). All study sites are canopied by *Nothofagus* forest that prevents direct sunshine reaching the stream surface. In spring–summer, noon sunny days irradiance varies between 8–25 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$.

Macroinvertebrate and fish sampling

From May 2003 to June 2004 stream benthic invertebrates were collected with a Surber sampler (0.09 m², 250 μm mesh size). Ten randomly collected replicates were taken at each site in winter 2004 (UBCh, UBCa, UBPe, IBPe, DBCh and

DBPe). In addition, we carried out seasonal sampling in spring, summer, and autumn 2003–2004 in UBCh, UBCa and DBCh (10 replicate Surber samples at each date).

Samples were preserved in 5% formalin until processing. In the laboratory all invertebrates were sorted, identified to the lowest possible taxonomic level, and counted. Additionally, invertebrates were assigned to functional feeding groups (FFGs) (Merritt & Cummins 1996, Albariño & Balseiro 2002, Velázquez & Miserendino 2003). Measurements of total body length of each individual, excluding antennae and terminal cerci, were made with an ocular micrometer (at the nearest 0.1 mm). Biomass was estimated from length-weight regressions (Miserendino 2001). When not available, regressions were obtained from our own data. Specimens were measured, dried at 80 °C for 24 h, weighed to the nearest 0.01 mg and used to estimate length-weight relationships.

On each sampling occasion (carried out between 11 and 15 h) fish abundance was obtained by electrofishing. A stream section of 50–75 m² was enclosed with ballasted nets (5 mm mesh size) to prevent fish escapes. Then, the entire section was scanned three times with a backpack electroshocker, and all fish collected. The absence of fish in the upper barrier sections of Challhuaco, Cascada and Pescadero streams was confirmed by extensive electrofishing (covering over 300 m²) and visual inspection.

All fishes caught were identified and, fork length, maximum mouth width and mouth height, were measured. In order to evaluate trout diet, 20 randomly selected fish from each section were killed immediately after capture to avoid post-capture digestion of prey items, and individuals were preserved in 5% formalin. All fishes not used in stomach content analysis were released immediately after measurement. In the laboratory, gut analysis was performed under a stereomicroscope identifying and measuring each prey item. Prey identification was achieved by comparing digestion-resistant body parts (head capsules, mouthparts, tergal plates, etc.) with reference material. Measurements of resistant parts were used to estimate total prey body size.

Data analysis

Numerical and gravimetric analyses of stomach content were performed. The numerical importance (%N) of each food prey category was calculated estimating the numeric percentage of individuals in all 20 stomachs on each sampling date. The relative importance of a food item in the diet was expressed as a percentage of dry weight relative to total dry weight of all foods found in the gut (%D). The Ivlev electivity index (Ivlev 1961) was calculated to estimate trout selectivity for each single size class (independently of taxonomic identification).

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

where r_i and p_i are the proportions of i^{th} size class in the gut content and in the environment, respectively. This index varies from -1 (complete rejection) to +1 (complete selection), with values around zero indicating that feeding is proportional to item abundance in the environment.

Differences in fish size and macroinvertebrate abundance and biomass were tested with ANOVA, and when necessary a Tukey's test was performed for *a posteriori* multiple comparisons. Invertebrate size class frequency distributions between fish and no fish sites were compared using Chi-square goodness of fit test (χ^2). The size frequency distributions of fishless and fish sites were used as the expected and observed distribution, respectively. Statistical differences in the biomass of the different Functional Feeding Groups (FFGs) between fish and fishless sites for winter or other seasons were assessed by t-test. Data were log-transformed to achieved normality and/or homoscedasticity when necessary. Macroinvertebrate community differences in fishless, low and high fish abundance sites were analysed by a detrended correspondence analysis (DCA) using the CANOCO software (Ter Braak & Smilauer 1998). Species with abundances < 1% of total macroinvertebrate abundance were not considered in this analysis. Additionally, significant differences among communities from different sites were tested based on the difference between the average of all dissimilarities between samples between groups and the average of all dissimilarities between samples within groups (Quinn & Keough 2002). For this purpose we used the software ANOSIM of the package Primer (Plymouth Marine laboratory, Plymouth, USA).

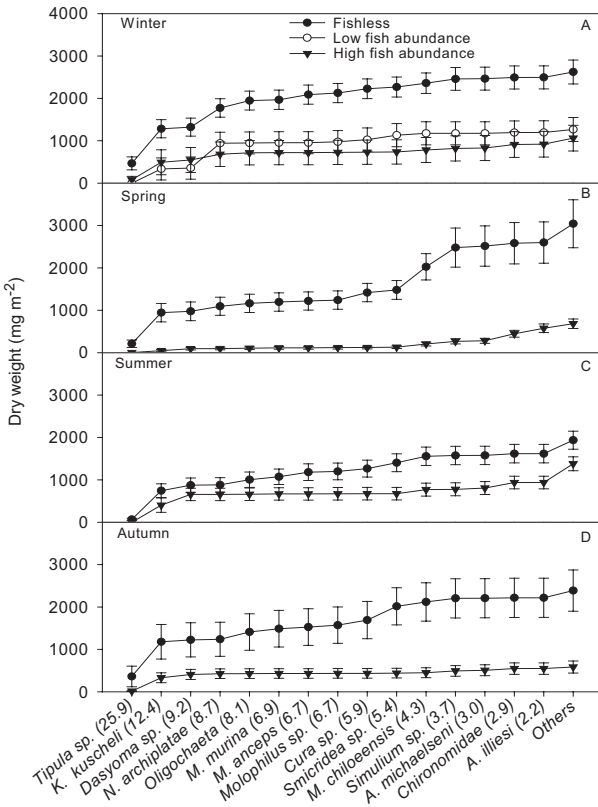
Results

Electrofishing revealed the complete absence of fish in the upper sections of streams (UBCh, UBCa and UBPe). On the other hand, the lower sections, DBCh and DBPe, have very similar fish abundance (Table 1). These two sites were considered, in this study, as the high abundance sections. The intermediate section at Pescadero stream (IBPe) presented very low fish abundance, around one fifth of that found in the lower sections (Table 1). In all fish sites, rainbow trout (*Oncorhynchus mykiss*, Walbaum) comprised 98% of all fish collected while brook trout (*Salvelinus fontinalis*, Mitchill) made up the remaining 2% and no native fishes were recorded. The few specimens of brook trout were only recorded at the DBPe section in Pescadero stream. Fish morphometry (fork size and mouth width and height) attained values very similar among reaches; however, fishes at the low abundance IBPe section were slightly larger although no significant differences were observed (ANOVA $F_{5,114} = 1.42$, $P = 0.220$) (Table 1).

We recorded a total of 34 taxa of benthic macroinvertebrates, although only 15 taxa accounted for 79–89% and 82–95% of total abundance and biomass, respectively. In winter, total invertebrate biomass differed between fish and fishless sections (ANOVA, $F_{2,45} = 20.372$, $P < 0.001$) (Fig. 1A). High abundance fish reaches presented significantly lower total bio-

Table 1. Fish morphometry (cm) and abundance (Ind m⁻²) recorded in the different study sites (Challhuaco and Pescadero). Values are means ± 1 SE.

	IBPe	Winter DBPe	DBCh	Summer DBCh	Autumn DBCh	Spring DBCh
Mean fork size	13.1 ± 2.5	9.2 ± 1.1	9.6 ± 0.7	10.7 ± 0.5	11.2 ± 0.4	11.6 ± 0.3
Mean mouth width	1.1 ± 0.2	0.6 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	1.0 ± 0.1
Mean mouth height	1.3 ± 0.2	0.9 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.3 ± 0.1
Abundance	0.12	0.54	0.47	0.44	0.53	–

**Fig. 1.** Cumulative biomass (mean ± SE) of benthic macroinvertebrate in fishless (UBCh, UBCa, UBPe); low abundance (IBPe) and high abundance trout sites (DBCh, DBPe). The 15 main taxa are ordered by mean body length (mm) indicated in brackets. **A:** Winter, **B:** Spring, **C:** Summer and **D:** Autumn. A: all streams, B, C and D: Challhuaco valley.

mass than fishless sites (Tukey test, $P < 0.001$), and the patterns of cumulative community biomass distribution differed mainly by changes in the biomass of the four largest invertebrates (Fig. 1A). The IBPe section showed intermediate values. Overall, total biomass was reduced near 50% (IBPe) and 75% (DBCh and DBPe) of that found in fishless sites (Fig. 1A). The persistence of the large scraper *Notoperla archiplatae* (Illies) in IBPe made the difference between this section and DBPe (Fig. 1A). Similar patterns were found in summer, spring and autumn, in Chall-

huaco-Cascada streams between fishless and high abundance fish sections (Fig. 1B, C and D). Smaller taxa (body length ≤ 3 mm) increased in abundance at fish sites and compensated for the losses of large, more vulnerable taxa. In consequence, total invertebrate abundance was similar in fish and fishless sites in winter (ANOVA $F_{2,45} = 2.317$, $P = 0.11$), spring (ANOVA $F_{1,22} = 1,182$, $P = 0,289$) and autumn (ANOVA $F_{1,19} = 0.0602$, $P = 0,809$) (abundance ~ 3000 ind. m⁻²). However, in summer invertebrate abundance in fish sites was higher than in fishless ones (ANOVA, $F_{1,22} = 13,586$, $P = 0.001$), due to an increase of the small-bodied taxa (abundance ~ 4000 ind. m⁻² in fishless to ~ 7000 ind. m⁻² in fish sites).

The abundance of the different macroinvertebrate species was strongly affected by fish presence. The multivariate DCA analysis showed that samples were grouped according to the presence of fish along a gradient of fish abundance regardless of the stream (Cascada, Challhuaco and Pescadero) (Fig. 2). The two first axes explained 32.5% of total variance. The statistical analysis showed that benthic communities grouped in the DCA differed significantly (ANOSIM, global $\rho = 0.424$, $P = 0.001$), and the *post hoc* pairwise comparison also showed differences between each pair of groups ($\rho_{\text{fishless vs low fish}} = 0.360$, $P = 0.001$; $\rho_{\text{fishless vs. high fish}} = 0.402$, $P = 0.001$; $\rho_{\text{low fish vs. high fish}} = 0.611$, $P = 0.001$).

Considering the whole dataset, we observed that there are species consistently affected by the presence of fish. On the one hand, trout negatively affected nine taxa of which six (*Cura* sp., *Klapopteryx kuscheli* Illies, *Hyalella curvispina* Shoemaker, *Metamonius anceps* (Lestage), scirtids and *Smicridea* sp.) showed strong reductions (Fig. 3A). *Cura* sp. and *Smicridea* sp. were only negatively affected in high abundance trout sites (Fig. 3A). The others were reduced in both high and low abundance fish sites (Fig. 3A). *Hyalella curvispina*, the scirtid and *M. anceps* were practically excluded in the presence of fish. On the other hand, five taxa (Chironomidae, Oligochaeta, *Aubertoperla illiesi* (Froehlich), *Antarcto-*

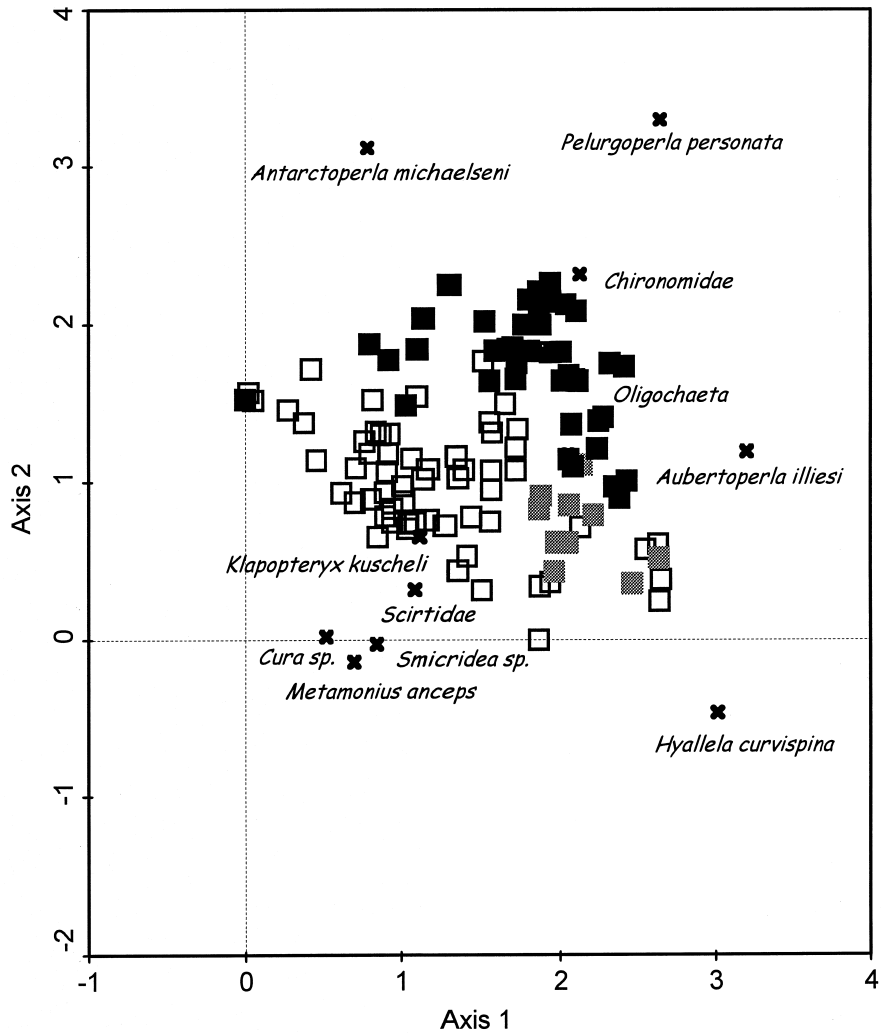


Fig. 2. Detrended correspondence analysis (DCA) of the complete sample-by-species abundance matrix in the study sites of Challhuaco, Cascada and Pescadero streams. Empty squares: Fishless sites; Gray filled squares: Low fish abundance sites and Black filled squares: High fish abundance sites. Only selected taxa (i. e. those that were reduced or enhanced in number and are shown in Fig. 3) are displayed with symbol X.

perla michaelsoni (Klapalek), and *Pelurgoperla personata* Illies) presented important differences at trout sites compared to the fishless ones (Fig. 3B). All taxa, except Oligochaeta, tended to increase their abundance in high abundance fish sites (Fig. 3B). Chironomids seemed to benefit most in the presence of trout since their numbers were up to four times higher than at sites without trout. Moreover, all but *A. illiesi* had higher numbers at high fish abundance sites than at low abundance sites (Fig. 3B).

As a consequence of these changes, the size frequency distribution of the invertebrate community in fish sections was displaced towards smaller size classes compared to fishless sites. We found significant differences when we compared pooled winter data of fishless-low abundance ($\chi^2_{(18)} = 39.75$; $P < 0.001$), fishless-high abundance ($\chi^2_{(18)} = 318.35$; $P < 0.001$) and low-high abundance ($\chi^2_{(18)} = 203.56$; $P < 0.001$). Only the upper barrier sections (fishless sites) pre-

sented individuals larger than 35 mm (Fig. 4). The smallest size categories (from 1 to 3 mm) increased from 58 % in fishless sites to 68 % and 74 % in the low and high abundance trout reaches, respectively (Fig. 4). In the other seasons, only studied in the Challhuaco-Cascada systems, we found a similar pattern where small size classes increased from 37–56 % at fishless sites to 47–72 % at the fish site ($\chi^2_{(18)} = 1003.43$; $P < 0.001$ in summer; $\chi^2_{(18)} = 667.48$; $P < 0.001$ in autumn and $\chi^2_{(18)} = 1027.16$; $P < 0.001$ in spring). As macroinvertebrate size changed seasonally, we observed peaks of high frequencies displaced towards smaller size classes from spring to autumn in Challhuaco-Cascada streams probably associated with adult emergence and offspring increase during late spring to early autumn.

Rainbow trout diet was dominated by aquatic macroinvertebrates (Table 2). In guts, prey size classes larger than 3 mm represented 74 % of total prey.

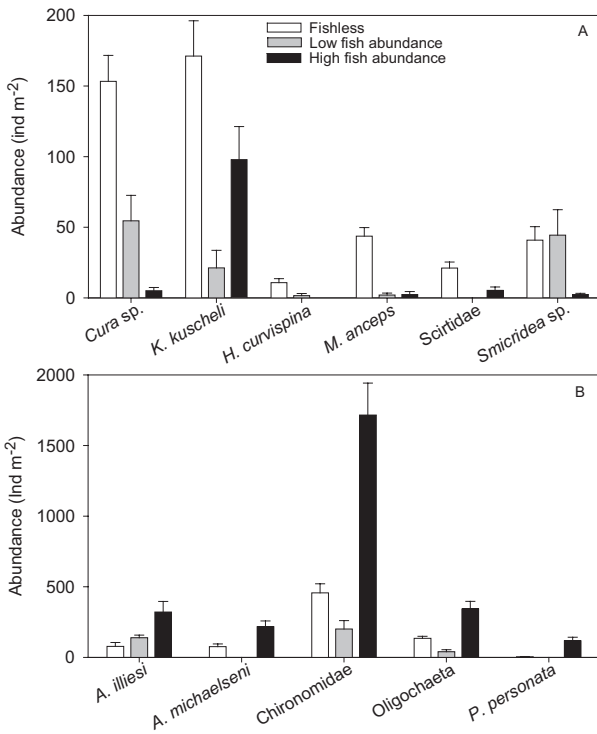


Fig. 3. Mean annual abundance (\pm SE) of selected benthic macroinvertebrates at fishless, low fish abundance and high fish abundance sites. **A:** Species negatively affected in the presence of trout. **B:** Species positively affected in the presence of trout.

Those prey smaller than 3 mm were less important in guts compared to the composition of stream benthos (Fig. 4). Our analysis indicated that large invertebrates (mean body size > 8.5 mm) represented between 50–60 % of fish gut content. In high abundance trout sites, four taxa (mean size < 4 mm) comprised nearly 50 % of the gut content (Table 2). In contrast, in the low abundance trout section three taxa of intermediate size (mean body size 4–7 mm) dominated fish diets surpassing 50 % of gut content and remarkably, the mayfly *M. anceps* accounted for 22 % of the diet.

The Ivlev's index (E) obtained for each prey size class confirmed trout selectivity for specimens larger than 5 mm on any sampling date and fish site (Fig. 5). Maximal positive selection occurred on the intermediate and large size classes. Prey size selection varied seasonally from smaller prey items in autumn-winter (prey selected > 3 mm) to larger ones in spring-summer (prey > 5 mm) (Fig. 5).

Macroinvertebrate community composition changed substantially since trout predation did significantly affect the biomass of the different FFGs (see *t*-test results in Fig. 6). Fishless sections were domi-

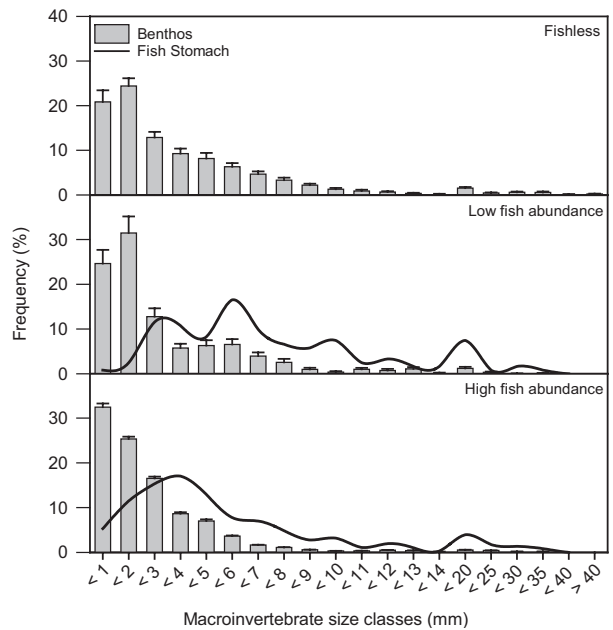


Fig. 4. Winter Pooled data of size class frequency distribution (mean \pm SE) of benthic macroinvertebrates in fishless, low abundance trout and high abundance trout stream sections. Prey in trout gut content indicated with solid line.

nated by shredders followed by grazers and collector feeders. In contrast, sections with fish showed in all cases a significant decrease of shredders (–68 %) (Fig. 6). These reductions were also observed for scrapers (–31 %) and filtering-collectors (–20 %). Predators and gathering-collectors did not show substantial changes in biomass (–7 % and +1 %, respectively). As a result of these shifts in biomass, the functional trophic structure of the community changed in the presence of fish towards a community dominated by small shredders and collectors.

Discussion

In our study, aquatic macroinvertebrate size distribution differed between stream sections with and without fish. In the fish sections we observed a dominance of smaller individuals (\leq 3 mm) and the scarcity or absence of large specimens that were found in the above barrier fishless sites. As a consequence, taxonomic composition, total biomass and functional structure differed greatly among sections.

Predation has long been viewed as an important force in structuring ecological communities, influencing the abundance and species composition of prey assemblages (Crowder & Cooper 1982). Fish, as visual predators, can exert strong control on the prey

Table 2. Relative abundance (%N), and relative dry biomass (%D) of the most important aquatic and terrestrial items in the gut of rainbow trout (*Oncorhynchus mykiss*) in low and high abundance sections during winter (Challhuaco and Pescadero streams) and the other seasons (Challhuaco system). Values <0.1 or absence are indicated with dash. Food items are sorted by size (larger to smaller). Values are based on 20 individual fish examined in each season and sampling occasion (n = 120 individual).

Class/Order	Winter		Winter		Spring, summer and autumn		
	Low abundance		High abundance		High abundance		
	%N	%D	%N	%D	%N	%D	
Aquatic items							
<i>Tipula</i> sp.	Diptera	0.8	4.0	1.5	23.5	0.7	16.5
<i>Klapopteryx kuscheli</i> Illies	Plecoptera	5.7	22.4	4.2	14.2	1.9	14.2
<i>Dasyoma</i> sp.	Diptera	1.6	0.4	3.9	2.7	5.3	5.8
<i>Notoperla archiplatae</i> (Illies)	Plecoptera	6.5	37.4	2.9	22.3	1.3	12.8
Oligochaeta	Oligochaeta	–	–	1.0	0.2	0.8	0.2
<i>Myotrichia murina</i> (Schmid)	Trichoptera	3.3	0.8	2.4	2.3	3.1	3.5
<i>Metamonius anceps</i> (Lestage)	Ephemeroptera	22.0	14.0	3.7	1.6	0.8	1.4
<i>Molophilus</i> sp.	Diptera	2.4	0.1	1.0	0.2	1.4	0.5
<i>Cura</i> sp.	Turbellaria	–	–	–	–	0.1	–
<i>Smicridea</i> sp.	Trichoptera	11.4	5.7	2.5	0.8	–	–
<i>Meridialaris chiloeensis</i> (Demoulin)	Ephemeroptera	11.4	1.8	4.4	2.7	6.7	8.4
<i>Simulium</i> sp.	Diptera	0.8	0.1	19.0	10.6	13.8	7.6
<i>Antarctoperla michaelsoni</i> (Klapalek)	Plecoptera	–	–	3.9	0.4	10.6	3.3
Chironomidae	Diptera	1.6	0.1	10.0	2.8	15.9	2.0
<i>Aubertoperla illiesi</i> (Froehlich)	Plecoptera	0.8	–	16.9	3.1	10.0	3.5
Others		24.5	9.1	20.4	10.1	23.2	19.4
Terrestrial items							
Coleoptera	Coleoptera	0.8	–	0.5	–	1.2	–
Diptera	Diptera	0.8	–	0.1	–	0.7	–
Homoptera	Homoptera	2.4	–	1.6	–	1.3	–

community by drastically reducing total community biomass. Flecker & Townsend (1994) reported reductions of up to 50% in macroinvertebrate biomass in stream channels stocked with brown trout (*Salmo trutta* L.). In other streams with both alien and native fish, a shift towards an invertebrate community dominated by smaller size-classes has resulted in biomass decline (Gilliam et al. 1989, Wilzbach et al. 1986, Bechara et al. 1993). Our study in Andean forested headwaters suggested that rainbow trout affect the biomass of invertebrates through the selective elimination of large macroinvertebrates. At the same time, as predation acts directly on prey populations, indirect facilitation can take place through release from competitors and intermediate predators (Shurin 2001). The reduction of large invertebrates caused by fish predation has been suggested as an indirect reason for small invertebrate numerical increase (Power 1992, Bechara et al. 1992, Usio & Townsend 2000). In our field study, species that benefited from trout presence (e.g. chironomids) compensated for the loss of species that were depressed by predation (e.g. *Tipula* sp., *K. kuscheli*); thus, trout caused shifts in spe-

cies composition and size frequency distribution but had no great effect on total invertebrate abundance.

Body size mediates the outcome of predator-prey interactions; insect small sizes may result as an effective refuge against fish predation (Bechara et al. 1993, Huryn 1998). Our findings on the impact of trout on the macroinvertebrate community were also supported by the analysis of gut contents. These showed selectivity towards macroinvertebrates larger than 3 mm.

Although body size was observed to be a reason in prey vulnerability to trout predation, other traits can also be important. Two abundant taxa in fishless sites, the mayfly grazer *Metamonius anceps* and the gammarid shredder *Hyaella curvispina*, were scarce or absent in fish reaches, suggesting that individuals were consumed as soon as they colonized trout sites from above barrier fishless sites through drift. Both species are active swimmers and this feature in addition to their size (mean size: 6.8 mm) would increase their vulnerability to size-selective drift-feeders such as trout. Population reduction of large active swimming species such as the mayfly *Nesameletus ornatus*

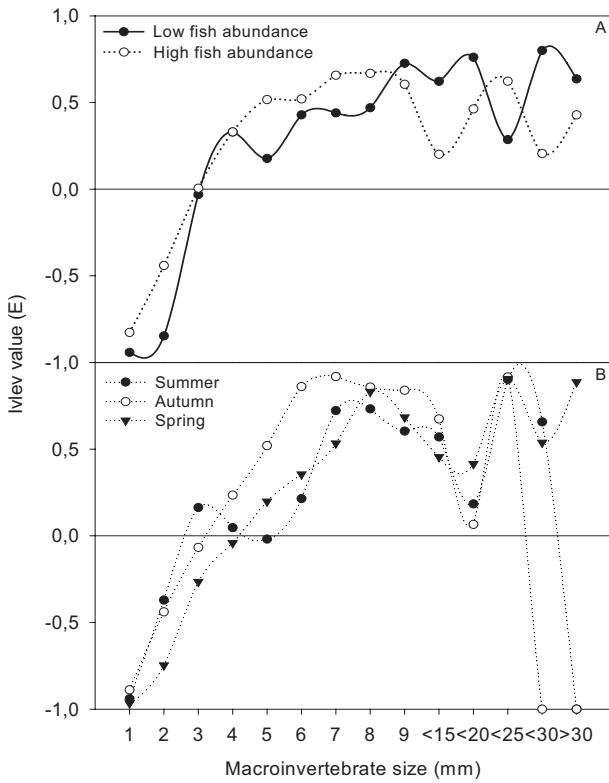


Fig. 5. Ivlev electivity index based on prey size classes in diets and in streams. **A:** winter and **B:** other seasons. Values above zero mean positive selection of a single size class.

(Eaton) and amphipods as a consequence of trout predation were also reported in New Zealand and USA streams (Newman & Waters 1984, McIntosh & Townsend 1994). On the other hand, the presence of spatial refuges such as interstitial habitats may also account for differences in prey vulnerability (Culp

1986, Bechara et al. 1992). For instance, in our stream sections with fish, the abundance of large oligochaetes (8.1 mm) increased. Although large invertebrates displayed contrasting vulnerabilities to fish predation, total community biomass was reduced in relation to fish abundance: total biomass was reduced near 50 % in IBPe to 75 % in DBPe of that found in fishless site (UBPe). The same reduction (75 % from fishless sites) was observed in the Challhuaco system under very similar trout abundances.

Although Andean headwaters are detritus-based systems in which shredders play an important role in processing coarse organic matter coming from the *Nothofagus* forest (Albariño & Balseiro 2002), they also support an important benthic algal community that serve as food resource for grazers (Albariño & Díaz Villanueva 2006). As expected and supporting our hypothesis, the biomass of large shredders and grazers was reduced in the presence of trout. Cascading effects of fish predators in streams have been already shown in both detritus-shredder (Ruetz et al. 2002, Greig & McIntosh 2006) and periphyton-grazer (Power 1992, Brönmark et al. 1997, Townsend 2003) three-trophic systems. Therefore, the significant reduction found in shredder and grazer biomasses as a consequence of fish predation is likely to alter ecosystem processes (i. e. reduction in detritus breakdown rates and increase in primary production) in those small Andean streams.

Our study provides evidence that trout in Patagonian streams may influence size frequency distribution, total biomass, and taxonomic and functional composition of benthic macroinvertebrates. In our study we have documented biodiversity loss in re-

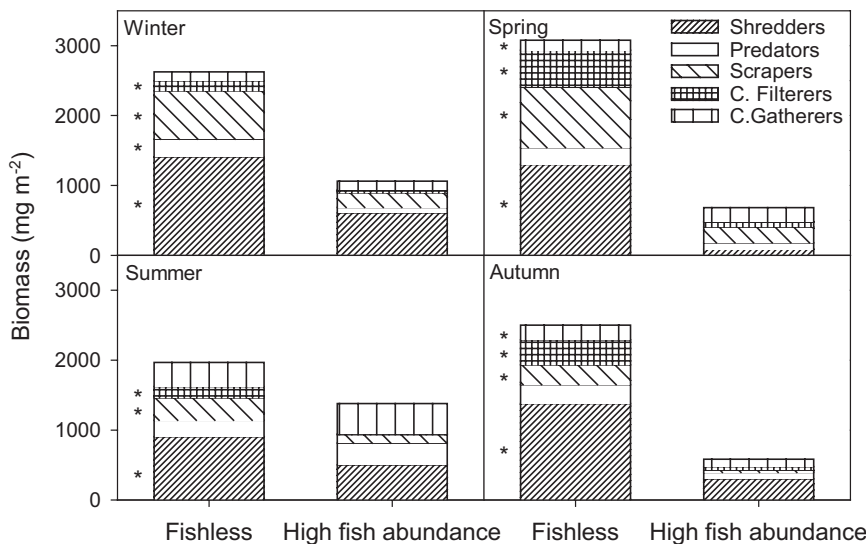


Fig. 6. Biomass of macroinvertebrates in functional feeding groups in winter samples (Challhuaco, Cascada and Pescadero) and other seasons (Challhuaco system) in fishless and high fish abundance sites. * indicates that the FFG has significant difference between sites (t-test, P < 0.05).

sponse to fish presence, but natural barriers mitigated such effects. On the other hand, upstream fishless reaches (i.e. small streams) have been recently seen as important sources of food supply to downstream fish population (Wipfli & Gregovich 2002). Although our study agrees with this statement, it also highlights the importance of fishless upper stream sections as refuges for populations of vulnerable species.

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References

- Albariño, R. J., 2001: Food habit and mouthpart morphology of a South Andes population of *Klapopteryx kuscheli* (Plecoptera: Austroperlidae). – Aquat. Insects **23**: 171–181.
- Albariño, R. J. & Balseiro, E. G., 1998: Larval size and leaf conditioning in the breakdown of *Nothofagus pumilio* leaves by *Klapopteryx kuscheli* (Insecta, Plecoptera) in a South Andean stream. – Internat. Rev. Hydrobiol. **83**: 397–404.
- 2002: Leaf litter breakdown in Patagonian streams: native vs. exotic trees and the effect of invertebrate size. – Aquat. Conserv. Mar. Freshwat. Ecosyst. **12**: 181–192.
- Albariño, R. J. & Díaz Villanueva, V., 2006: Feeding Ecology of Two Plecopterans in Low Order Andean-Patagonian Streams. – Internat. Rev. Hydrobiol. **91**: 122–135.
- Bechara, J. A., Moreau, G. & Planas, D., 1992: Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. – Can. J. Fish. Aquat. Sci. **49**: 2093–2103.
- Bechara, J. A., Moreau, G. & Hare, L., 1993: The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. – J. Anim. Ecol. **62**: 451–464.
- Brönmark, C., Dahl, J. & Greenberg, L. A., 1997: Complex trophic interactions in freshwaters benthic food chains. – In: Streit, B., Städler, T., Lively, C. M. (eds): *Evolutionary Ecology of Freshwater Animals: Concepts and Case Studies*. – Birkhäuser Verlag, Berlin, pp. 55–88.
- Crowder, L. B. & Cooper, W. E., 1982: Habitat structural complexity and the interaction between bluegills and their prey. – Ecology **63**: 1802–1313.
- Culp, J. M., 1986: Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. – J. N. Amer. Benthol. Soc. **5**: 140–149.
- Flecker, A. S. & Townsend, C. R., 1994: Community-wide consequences of trout introductions in New Zealand streams. – Ecol. Appl. **4**: 798–807.
- Gilliam, J. F., Fraser, D. F. & Sabat, A. M., 1989: Strong effects of foraging minnows on a stream benthic invertebrate community. – Ecology **70**: 445–452.
- Greig, H. S. & McIntosh, A. R., 2006: Indirect effects of predatory trout on organic matter processing in detritus-based stream food webs. – Oikos **112**: 31–40.
- Huryñ, A. D., 1998: Ecosystem level evidence for top-down and bottom-up control of production in a grassland stream system. – Oecologia **115**: 173–183.
- Illies, J., 1977: Plecoptera. – In: Hulbert S. H. (ed.): *Biota Acuática de Sudamérica Austral*. – San Diego State University Press, San Diego, pp. 185–186.
- Ivlev, V. S., 1961: *Experimental Ecology of the Feeding of Fishes*. – Yale University Press, New Haven & London.
- Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. & Bazzaz, F. A., 2000: Biotic invasions: causes, epidemiology, global consequences, and control. – Ecol. Appl. **10**: 689–710.
- McIntosh, A. R., 2000: Habitat and size-related variations in exotic trout impacts on native galaxiid fishes in New Zealand streams. – Can. J. Fish. Aquat. Sci. **57**: 2140–2151.
- McIntosh, A. R. & Townsend, C. R., 1994: Inter population variation in mayfly anti-predator tactics: differential effects of contrasting predatory fish. – Ecology **75**: 2078–2090.
- Merritt, R. W. & Cummins, K. W., 1996: *An Introduction to the Aquatic Insects of North America*. – Kendall/Hunt Publishing Company, Dubuque.
- Miserendino, M. L., 2001: Length-mass relationships for macroinvertebrates in freshwater environments of Patagonia (Argentina). – Ecología Austral **11**: 3–8.
- Modenutti, B. E., Balseiro, E. G., Queimaliños, C. P., Añón Suárez, D. A., Diéguez, M. C. & Albariño, R. J., 1998: Structure and dynamics of food webs in Andean lakes. – Lakes Reserv. Res. Manage. **3**: 179–186.
- Modenutti, B. E. & Balseiro, E. G., 1994: Zooplankton size spectrum in four lakes of the Patagonian Plateau. – Limnológica **24**: 51–56.
- Newman, R. M. & Waters, T. F., 1984: Size-selective predation on *Gammarus pseudolimnaeus* by trout and sculpins. – Ecology **65**: 1535–1545.
- Nyström, P., Svensson, O., Lardner, B., Brönmark, C. & Granéli, W., 2001: The influence of multiple introduced predators on a littoral pond community. – Ecology **82**: 1023–1039.
- Pascual, M., Macchi, P., Urbanski, J., Marcos, F., Rossi, C. R., Novara, M. & Arciprete, P., 2002: Evaluating potential effects of exotic freshwater fish from incomplete species presence-absence data. – Biol. Invasions **4**: 101–113.
- Peckarsky, B. L., 1982: Aquatic insect predator-prey relations. – Bioscience **32**: 261–266.
- Pedrozo, F. L., Chillrud, S., Temporetti, P. & Díaz, M. M., 1993: Chemical composition and nutrient limitation in rivers and lakes of northern Patagonian Andes (39° 5′–42° S; 71° W) (Rep. Argentina). – Verh. Internat. Verein. Limnol. **25**: 207–214.
- Power, M. E., 1992: Habitat heterogeneity and the functional significance of fish in river food webs. – Ecology **73**: 1675–1688.
- Quinn, G. P. & Keough, M. J., 2002: *Experimental design and data analysis for biologists*. – Cambridge University Press, Cambridge, pp. 1–537.

- Ruetz, C. R., Newman, R. M. & Vondracek, B., 2002: Top-down control in a detritus-based food web: fish, shredders, and leaf breakdown. – *Oecologia* **132**: 307–315.
- Shurin, J. B., 2001: Interactive effects of predation and dispersal on zooplankton communities. – *Ecology* **82**: 3404–3416.
- Ter Braak, C. J. F. & Smilauer, P., 1998: CANOCO Reference manual and User's guide to Canoco for Windows: software for Canonical Community Ordination (version 4). – Microcomputer power, Ithaca, New York 352 pp.
- Townsend, C. R., 1996: Concepts in river ecology: pattern and process in the catchment hierarchy. – *Arch. Hydrobiol. Suppl.* **113**: 3–21.
- 2003: Individual, population, community and ecosystem consequences of a fish invader in New Zealand streams. – *Conserv. Biol.* **17**: 38–47.
- Townsend, C. R. & Hildrew, A. G., 1984: Longitudinal pattern in detritivore communities of acid streams – a consideration of alternative hypotheses. – *Verh. Internat. Verein. Limnol.* **22**: 1953–1958.
- Usio, N. & Townsend, C. R., 2000: Distribution of the New Zealand crayfish *Paranephrops zealandicus* in relation to stream physical chemistry, predator fish and invertebrate prey. – *N. Z. J. Mar. Freshwat. Sci.* **34**: 557–567.
- Velázquez, S. M. & Miserendino, M. L., 2003: Habitat type and macroinvertebrate assemblage in low order Patagonian streams. – *Arch. Hydrobiol.* **158**: 461–483.
- Vitousek, P. M., 1990: Biological invasions and ecosystem process towards an integration of biology and ecosystem studies. – *Oikos* **57**: 7–13.
- Wipfli, M. S. & Gregovich, D. P., 2002: Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. – *Freshwat. Biol.* **47**: 957–969.
- Wilzbach, M. A., Cummins, K. W. & Hall, J. D., 1986: Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. – *Ecology* **67**: 898–911.

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