



## Experimental assessment of predation by native and exotic fish on stream invertebrates in Northern Patagonia



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### ABSTRACT

During the last decades invasive species became a matter of concern all over the world. Established salmonid populations make sport fishery in Patagonia one of the top in the world, but there is increasing evidence that these populations have negative impacts on native ecosystems. Predation rates and feeding preferences of native catfish *Hatcheria macraei* and invasive trout *Oncorhynchus mykiss* were compared by exposing three stream benthic invertebrate species with contrasting ecological roles to direct predation. Secondly, feeding and escaping behaviours of the mayfly *Meridialaris chiloeensis* belonging to either non-naive or naive populations to predators were investigated in the presence of predation chemical cues, i.e. non direct predator access. Total predation by trout was 2–3 times higher than by native catfish. Trout had clear prey preferences while catfish changed its preferences with shifting prey composition. Invertebrate species showed different responses to predation by native and exotic fish due to the different strategies of fish and invertebrates which resulted from the combination of predator efficiency and prey vulnerability. Feeding activity of non-naive nymphs was significantly lower than that of naive nymphs. In addition, mayfly nymphs from both populations showed higher emigration rates in presence of trout chemical cues than in presence of catfish cues or in fishless treatment. Consequently, the reduced feeding activity observed in non-naive mayflies exposed to rainbow trout cues resulted from their inactivity in channels, as both nymph populations had similar emigration rates. Due to high predation rates, prey preferences (i.e. high potential to exploit prey resources) and induced strong predation avoidance behaviour of prey, invasive trout may have a stronger influence on the abundance and species composition of native macroinvertebrates than native catfish. In just about one century, invertebrate species such as the ubiquitous *M. chiloeensis* show behavioural adaptations to this exotic predator.

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### Introduction

During a period of just about two centuries, worldwide introduction of non-native species has increased immensely (Ricciardi, 2007) causing irreparable or highly expensive damages to the environment and human welfare (Simon and Townsend, 2003; Pascual et al., 2009). Salmonids, originating from the cool-temperate Northern Hemisphere, were spread nearly across the whole Southern Hemisphere during late 19th- and early 20th century (Pascual et al., 2009; Garcia de Leaniz et al., 2010). Introductions in Argentina began in 1904 and within just about 30 years salmonids were established throughout most regions of Patagonia, creating a valuable trophy sport fishery and also developing the aquaculture industry

(Macchi et al., 2008; Pascual et al., 2009; Garcia de Leaniz et al., 2010). Seven salmonid species have established self-sustaining populations while rainbow trout became the most widely distributed (Macchi et al., 2008). In Patagonia only very few native fish species have certain sport fishing value (Pascual et al., 2007), but salmonids make sport fishery to be one of the top in the world with revenues of over US\$42 million recorded in 2005 (Pascual et al., 2009).

From an ecological point of view, invasive trout have caused local extinctions of vulnerable native species changing community composition and consequently altering stream functioning (McIntosh, 2000; Herbst et al., 2009). In New Zealand, trout is believed to be responsible for the decline (McDowall, 2006) and fragmentation (Townsend, 2003) of native fish populations, for shifts in the organization of whole stream communities and even for impacts on terrestrial organisms (Korsu et al., 2008). Entire annual stream insect production has been shown to be consumed by trout (Huryn, 1996) and shifts in body size of invertebrate

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populations have already been found in Patagonian streams (Buria et al., 2007).

Predation has long been considered a major selective force in the evolution of several morphological and behavioural characteristics of animals (Lima and Dill, 1990). In a co-evolutionary process, each adaptation of one species generates an advantage and must thus be compensated by a reciprocal step of the other species. Even though, there is an uneven selective pressure as the predator is in risk to lose its food, but the prey is in risk to lose its life (Brodie and Brodie, 1999; Ferrari et al., 2010). Aquatic prey has the ability of using chemical signals to receive or transmit information and avoid encounters with predators. In particular, invertebrate prey with relatively poor visual capabilities, are also able to detect predators by hydrodynamic signals (Dodson et al., 1994). Chemical signals may induce strong predation avoidance behaviour such as avoidance of risky areas, increase of shelter use, reduction in feeding activity, etc. (Åbjörnsson et al., 2004; Ferrari et al., 2010). Such avoidance behaviour entails fitness costs for prey and leads to reduced growth and reproduction, which forces prey to evaluate actual predation risk. In addition, prey species may display different anti-predator behaviours regarding the identity of a predator or even do not respond to the presence of a novel predator (Brönmark and Hansson, 2000; Ferrari et al., 2010; Wisenden, 2000).

This experimental study compares the effects of predation by an invasive salmonid and a native fish on the benthic macroinvertebrates fauna of Northern Patagonian streams in Argentina. We aimed to compare, by stream-fed channel experiments, predation rates and feeding preferences of the native catfish *Hatcheria macraei* and the exotic trout *Oncorhynchus mykiss* on three ecologically contrasting stream invertebrates. We hypothesized that predation by rainbow trout will have a stronger effect on benthic invertebrate abundance and composition than predation by the catfish. Secondly, we tested the feeding activity and escaping rate of stream mayflies, which were either naive- or non-naive- to predation, by exposing them only to chemical cues (i.e. kairomones) from distinct predators. Considering the involved predation pressure of a native and an exotic fish predator, we hypothesized that macroinvertebrates from fishless streams (naive population) will not be able to interpret predation cues as a risk, contrastingly, those from streams cohabiting with both fish species (non-naive population) will recognize chemical cues belonging to native fish but not those of the exotic trout (Sih et al., 2010), introduced just a century ago.

## Methods

### Study populations

Fish were collected in Pichi Leufu River, fifth order (41°06'23.70" S, 70°50'22.20" W). For logistic reasons invertebrates were collected in Ñirihuau River, fourth order (41°05'25.15" S, 71°08'34.87" W) and a second order fishless stream in the Challhuaco Valley (41°15'34.06" S, 71°17'14.96" W) which were located closer to the experimental facilities. Non-naive invertebrates were collected in Ñirihuau River where both fish and invertebrate species cohabit, thus invertebrates were assumed to have already been exposed to chemical cues of both fish. In particular for the second experiment, naive nymphs came from the mentioned stream at Challhuaco Valley. Streams were all well oxygenated, cold and oligotrophic with low conductivity and low nutrient concentrations (Díaz et al., 2007). They were inhabited by the same core assemblage of invertebrates and fish (except of the fishless stream) (Buria et al., 2007; Barriga et al., 2013). Invertebrates were selected to represent widespread and abundant species of the major taxonomical groups of Northern Patagonian benthic communities with three contrasting feeding modes. The scraper

*Meridialaris chiloeensis* (Ephemeroptera), the shredder *Antarctoperla michaelsoni* (Plecoptera) and the filtering-collector *Smicridea annulicornis* (Trichoptera) were chosen as they are important items of both fish diets (Buria et al., 2009; Barriga et al., 2013). Since rainbow trout is the most abundant exotic fish, catfish is the most abundant native fish (Navone, G. *unpublished results*) and they have a similar diet, which include our target invertebrates (Barriga and Battini, 2009; Ferriz, 2012), these both fish species were selected as predators. In the experiments, specimens of *H. macraei* had a mean total length of  $9.27 \pm 1.00$  cm (mean  $\pm$  SE) and a mean wet mass of  $3.94 \pm 1.32$  g. Specimens of *O. mykiss* had a mean total length of  $9.39 \pm 0.66$  cm and a mean wet mass of  $7.35 \pm 1.29$  g. Invertebrates had mean body lengths of  $7.07 \pm 0.07$  mm (*M. chiloeensis*),  $10.09 \pm 0.61$  mm (*A. michaelsoni*), and  $9.38 \pm 0.77$  mm (*S. annulicornis*; animal stretched but hind legs not included). From all the experimental possibilities (similar body mass, similar ontogenetic stages, etc.) we chose to compare fish specimens of similar body length in order to compare the effects of predation on similar invertebrate body sizes belonging to an idealized benthic invertebrate assemblage.

### General experimental setup

Experiments were carried out during November and December 2011 in artificial channels in Aquaculture Centre of Universidad Nacional del Comahue, near San Carlos de Bariloche, Northwestern Patagonia, Argentina. Channels were fed by water of the Gutiérrez stream 4 km after draining the ultra-oligotrophic Gutiérrez Lake (DIN: 4.6  $\mu$ g/L, SRP: 3.4  $\mu$ g/L, Na: 1.7 mg/L, a Chl-a: 0.4  $\mu$ g/L, pH: 6.7, conductivity: 58.1  $\mu$ S/cm; Díaz et al., 2007). Experimental channels were 3 m long, 0.29 m wide, 0.17 m deep, and had a mean water influx of 25 L/min with water velocities of  $\sim 1.0$  cm/s. Incoming water was filtered by a 200  $\mu$ m mesh to avoid immigration of aquatic insects and seston from the main stream. At the outlet, channels were confined by a 1 mm mesh to avoid escaping of invertebrates. Three control channels (without fish), three channels for *H. macraei* and three channels for *O. mykiss* were selected randomly out of 9 channels. Fish specimens to be used in experimental trials were kept in separate spare channels (one channel per species) and were fed every day with the same invertebrate species used in the experiment. Two days before each experiment started, fish were starved. Invertebrates were placed in channels and channels were left overnight until fish were added.

### Predation experiment

In a first experiment, predation rates and feeding preferences of native catfish *H. macraei* and the exotic trout *O. mykiss* were measured. Each channel was divided in three by placing two plastic screens (5 mm mesh size): an upstream area of 0.25 m, a downstream area of 0.25 m and a central area of 2.50 m. The central area (experimental arena) was chosen larger, as the main experimental settings were arranged here and invertebrates were exposed to fish predation. Mesh screens permitted invertebrates but not fish to pass and allowed us to measure invertebrate emigration from the experimental arena. The central area of each channel was provided with four substrate patches, each consisted of cobbles, representing refuge and food resource for invertebrates. Leaf litter and fine sand were spread within the patches before starting the experiment to provide food for *A. michaelsoni* and construction material for *S. annulicornis* retreats. Fish shelter was provided by a black PVC tube (8  $\times$  25 cm diameter and length). In each channel 15 nymphs of *M. chiloeensis*, 15 nymphs of *A. michaelsoni* and 15 larvae of *S. annulicornis* were placed. Regarding the surface of the provided stone patches, the number of 15 individuals represented an abundance of 167 ind./m<sup>2</sup> for each species and a total

density of 500 ind./m<sup>2</sup>. These densities were within the range of natural abundance in Patagonian streams like the Pichi Leufu River (Navone, G. *unpublished results*). The equal number of individuals per species was meant to prevent a density-dependent predation by fish and to simplify statistical analyses. At the beginning of the experiments ( $t_0$ ), three channels were provided with one individual of *H. macraei*, three channels with one individual of *O. mykiss* and three channels were remained fishless. Fish density per channel (~1.3 ind./m<sup>2</sup>) was within the natural occurrence of rainbow trout and catfish in medium sized Patagonian rivers like the Pichi Leufu River, but exceeded the density of small streams in Challhuaco catchment (Buria et al., 2007; Barriga et al., 2013). Every single day at the same hour, invertebrates outside the central area were recorded as emigrated and removed from the experiment. On the second day ( $t_2$ ) and the last day ( $t_4$ ) all remaining invertebrates in the whole channel were counted and individuals outside the central area were recorded as emigrated. This whole experiment was repeated four days later and data from both experimental runs were pooled for analyses. Death and emergence of invertebrates were minimal factors, therefore were eliminated from the analysis.

To compare prey preferences of catfish and trout, a prey preference index (PI) for each prey species was created. For prey species  $a$ , the index was calculated by dividing the proportional consumption ( $P_c$ ) upon the species  $a$  based on its availability at the beginning of period  $t_0$  or  $t_2$ , by the sum of the proportional consumptions ( $P$ ) upon all prey species.

$$PI(a) = \frac{P_c(a)}{\sum_a^n(a, \dots, n)}$$

#### Indirect effects experiment

A second experiment was implemented to compare feeding activity and emigration of non-naive and naive benthic invertebrates, in presence of predation chemical cues of native and exotic fish. This experiment was carried out with 25 non-naive nymphs of *M. chiloeensis* per channel and repeated one week later with 25 naive nymphs of the same species. This species was selected because it represents a widely distributed and abundant invertebrate in fish and fishless streams. For the experiment, each channel was subdivided into two areas by a 1 mm mesh to avoid fish and invertebrates exchanges. The experimental arena for invertebrates was located at the downstream end of the channel (last 65 cm) and the area for the fish was located upstream, so the chemical cues of fish were carried into the experimental arena by water current. Three channels were provided with individuals of *H. macraei*, three channels with individuals of *O. mykiss* and three channels were remained fishless. The experimental arena of each channel contained five stones (cobble size) of which two had been previously colonized with biofilm under controlled conditions to offer similar initial periphyton abundances to invertebrates and therefore served as experimental units (experimental stones); the other three stones provided additional refuge for invertebrates. In each channel without fish, two experimental stones (control) were placed in the upstream channel area (i.e. no invertebrates, no fish). These stones were not exposed to biofilm consumption by invertebrates and served to correct biofilm changes in experimental arenas with invertebrate presence. To obtain a higher chemical signal, two fish were provided in each channel. During the experiment, fish were fed every day with nymphs of *M. chiloeensis*. Thus, behaviour of experimental invertebrates might have been affected not only by fish kairomones, but also by chemical cues from digested prey that were released with predator faeces (Ferrari et al., 2010). Rainbow trout is present in the fish community of Gutiérrez stream, thus water that fed our experimental channels likely contained fish

kairomones. Because water reservoir for feeding channel system has filters for organic matter and sediments that precludes fish entering the reservoir, we assumed that basal fish kairomones (i.e. concentration in control channels) was low. Regarding the stone patch surface, densities of *M. chiloeensis* were 400 ind./m<sup>2</sup>, which is within the range of natural abundance in Patagonian streams. On the last day ( $t_4$ ), all invertebrates were collected and counted (to quantify nymph escaping, i.e. emigration from the arena) and biofilm consumption by invertebrates was calculated.

To calculate biofilm consumption by invertebrates, initial ( $t_0$ ) periphyton ash free dry mass (AFDM) and final AFDM ( $t_4$ ) were measured in pre-cultured experimental stones. Stones were brushed vigorously and washed with distilled water to take off all organic matter. The resulting slurry was homogenized and two subsamples of 10 ml each were filtered separately in micro-glass fibre filters (Muntkell), which were later averaged. Filters were dried, weighted, combusted in a furnace and reweighted to obtain AFDM of the biofilm subsamples. The surface of each brushed stone was calculated by the formula: stone surface [cm<sup>2</sup>] = 1.59 + 0.811 (XY + YZ + XZ). This formula puts out the fraction of stone surface which is available to be colonized by periphyton (approx. 65% of the total surface). X, Y and Z are the lengths of the three main axes in cm (Biggs and Kilroy, 2000). Feeding activity rate of invertebrates during the experiment was determined by the difference between initial ( $t_0$ ) and final ( $t_4$ ) periphyton AFDM per square centimetre of stone surface. The term feeding activity is used instead of consumption as it is recognized that invertebrate movement on substrates detaches biofilm and may lead to overestimated periphyton consumption rates (Albariño and Díaz Villanueva, 2006). To correct feeding activity in treatment channels (with invertebrate access) for periphyton growth during the experiment, initial and final periphyton AFDM data of experimental control stones (without invertebrate and fish access) were used.

#### Statistical analyses

Differences in invertebrate assemblages among predation treatments were analyzed graphically by non-multidimensional scaling (nMDS) analysis and statistically by one-way ANOSIM (Clarke, 1993; Clarke and Warwick, 2001), after creating a Bray Curtis resemblance matrix. Data was previously square-root transformed. The nMDS attempts to depict samples in a low-dimensional graphical representation regarding their similarities, and this adjustment is measured by a stress value. If stress is between 0.05 and 0.2 the graphical arrangement is good, if values are greater than 0.3 the representation may be due to chance (Clarke and Warwick, 2001).

One-way ANOSIM performs a permutation analysis of differences between replicates within groups contrasted with differences between groups, computing a Global  $R$  statistic under the null hypothesis of no differences in sample composition between predation groups. Global  $R$  falls between  $-1$  and  $1$ , so Global  $R$  is  $=0$  if the null hypothesis is true and Global  $R$   $=1$  if all replicates within groups are more similar to each other than any replicates from different groups. Pairwise ANOSIMs ( $R$  values) between all pairs of groups were provided as a post hoc test.

To compare total predation of catfish and trout in the period  $t_0$ – $t_4$ , a One-way ANOVA was performed. Total predation during period  $t_0$ – $t_2$  and  $t_2$ – $t_4$  was compared by two-way repeated measures ANOVA, using predation treatment and time as factors. Percentages of total preyed invertebrates in the time period  $t_2$ – $t_4$  were calculated on the basis of available prey at  $t_2$ . Prey preferences were tested by Hotelling's  $T^2$  tests for each fish and experimental period, following modifications by Manly (1993) and Lockwood (1998). For each statistic value (i.e. the mean difference between two prey items), a 95% Bonferroni confidence interval was calculated;

pairwise differences were assumed to be significant if the confidence intervals did not contain zero. Total migration among predation treatments was analyzed by one-way ANOVA, specific migration of invertebrate species within and among predation treatments were tested by two-way ANOVAs.

In the second experiment, differences in removed biofilm AFDM by *M. chiloensis* were analyzed by a two-way ANOVA, using origin of prey and predator chemical cues as factors. We found significantly different feeding activity between naive and non-naive mayfly populations, particularly between control treatments (two-way ANOVA,  $F_{1,12} = 5.682$ ,  $P = 0.038$ ). This significant difference indicated that non-naive nymphs fed less than the naive ones, which might in part have been caused by previous experience with predators in nature (e.g. individuals did not relax after predation risk was removed and displayed a fixed anti-predator behaviour and/or it was a slight basal chemical cues concentration in water that fed experimental channels and affected controls) or by other biological reasons differentiating populations. As this precluded us to interpret feeding differences due to the condition of predation, we further analyzed results by a one-way ANOVA for each origin of prey population. Differences in *M. chiloensis* emigration were also analyzed by a two-way ANOVA, using origin of prey and predator chemical cues presence as factors. A posteriori multiple comparisons were performed with post hoc tests. If assumptions of normality or homogeneity of variance were not satisfied, data were square-root transformed (Quinn and Keough, 2002).

## Results

### Predation experiment

Abundance of invertebrates changed during the experiment, not only due to predation itself but also due to emigration behaviour. After four days of experiment, invertebrates assemblages differed significantly among predation treatments when considering the combined effects of direct predation and emigration in channels (one-way ANOSIM, Global  $R = 0.566$ ,  $P = 0.001$ ; Fig. 1a). After excluding prey emigration in the analysis, to emphasize the direct events of predation on assemblage composition, differences among assemblages were larger (Global  $R = 0.395$ ,  $P = 0.001$ ; Fig. 1b). In both cases, assemblages in fishless channels were more similar to each other's than assemblages in catfish or trout channels. Including the emigration events to the nMDS analysis (Fig. 1a), differences between catfish and trout assemblages were just marginally significant ( $R = 0.193$ ,  $P = 0.050$ ), but when removing migration events, to weight the direct effect of predation events (Fig. 1b), the difference between assemblages of catfish and trout treatments became highly significant ( $R = 0.552$ ,  $P = 0.002$ ). These results clearly illustrate the higher predation pressure of trout than of catfish and emphasize the relatively high migration in catfish channels.

In general, trout consumed significantly more invertebrates than catfish (one-way ANOVA,  $F_{1,10} = 17.062$ ,  $P = 0.002$ ; Fig. 2a). Catfish caught 18% of total invertebrates in the channels, while trout captured nearly half of the present resources (47%), representing a predation intensity 2.6 times higher than catfish. However, fish predation varied with time (two-way RM ANOVA, predator species  $\times$  time:  $F_{1,10} = 5.075$ ,  $P = 0.048$ ). During the first two days of experiment, catfish preyed significantly less invertebrates (10%) than trout did (37%; Holm–Sidak test,  $P = 0.001$ ). In average, one catfish consumed 2–3 invertebrates per day while trout fed on ~8 individuals per day, which comes to a predation rate for trout of 3.7 times higher than for catfish. From day 2 on, trout reduced its predation intensity and consumed during the next two days 24% of the invertebrates still available at  $t_2$ , which were 1.7 times more invertebrates than catfish consumed (14%). Predation rates of

trout and catfish were not significantly different during this period (Holm–Sidak test,  $P = 0.121$ ).

Trout preferred feeding significantly more on *A. michaelseni* than *S. annulicornis* in the first two days of the experiment (Hotelling's  $T^2 = 39.704$ ,  $P = 0.012$ ; Bonferroni CI,  $P < 0.05$ ). Although trout displayed a trend to prey more *A. michaelseni* than *M. chiloensis* and more *M. chiloensis* than *S. annulicornis*, differences were not significant (Bonferroni CI,  $P > 0.05$ ). The same pattern of preferences was maintained during the second experimental period ( $t_2-t_4$ ), even after relative prey availability had changed, but no significant differences were detected (Hotelling's  $T^2 = 3.733$ ,  $P = 0.328$ ). For catfish, we did not find significant preferences among the different prey ( $t_0-t_2$ : Hotelling's  $T^2 = 3.684$ ,  $P = 0.332$ ), however catfish showed a trend to change its preference during the experiment. During period  $t_0-t_2$ , there was a trend of preference for *M. chiloensis* over *S. annulicornis* and *A. michaelseni*, while during  $t_2-t_4$  catfish fed relatively much more on *S. annulicornis*. Catfish clearly preferred *S. annulicornis* over *A. michaelseni* in that second period, but as no *A. michaelseni* specimens were consumed, a Hotelling's  $T^2$  test could not be performed. Besides the different prey preferences of catfish and trout, distinct foraging patterns of the two fish species were observed. Catfish actively foraged between and beneath stones and even removed well-placed sand from the stone patches, while rainbow trout just passed the patches like on a patrol.

Total emigration of invertebrates was different among predation treatments (one-way ANOVA,  $F_{2,51} = 3.822$ ,  $P = 0.028$ ; Fig. 3a). In presence of trout significantly less invertebrates (12.6%; Holm–Sidak test,  $P = 0.017$ ) emigrated from the experimental areas than in the presence of catfish (35.6%). However, emigration of invertebrates was significantly affected by both, predation and the species of invertebrate (two-way ANOVA,  $F_{4,45} = 3.413$ ,  $P = 0.016$ ; Fig. 3b). In particular, *A. michaelseni* was very active during the experiment; significantly more specimens left the experimental arena than specimens of *M. chiloensis* (Holm–Sidak test,  $P < 0.001$ ) or *S. annulicornis* ( $P < 0.001$ ) in fishless and catfish channels. In trout treatments, emigration of *A. michaelseni* was reduced considerably. It was significantly higher than emigration of *S. annulicornis* (Holm–Sidak test,  $P = 0.005$ ), but not higher than emigration of *M. chiloensis* ( $P = 0.164$ ). Trichopteran *S. annulicornis* showed the lowest emigration, independently of predation treatment.

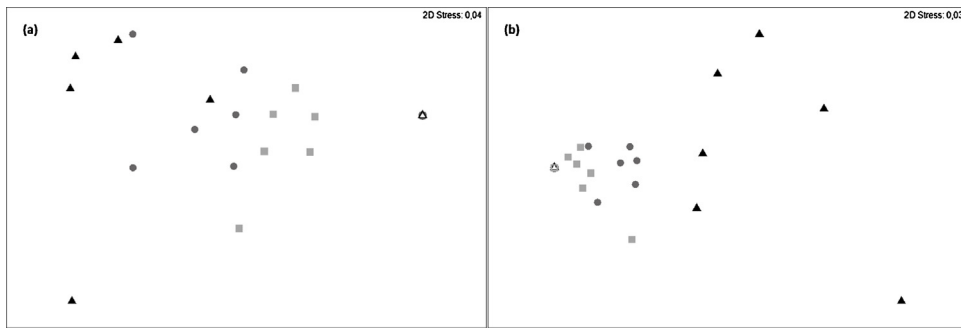
### Indirect effects experiment

Non-naive nymphs of *M. chiloensis* showed significantly different feeding activity among predation treatments (one-way ANOVA,  $F_{2,6} = 12.51$ ,  $P = 0.019$ ). Nymphs under the influence of trout cues removed much less biofilm than nymphs in the fishless treatment (Fisher's LSD test,  $P = 0.008$ ) and nymphs under catfish cues had an intermediate feeding activity (Fig. 4a, left). In contrast, naive nymphs showed no significant differences in feeding activity (one-way ANOVA,  $F_{2,6} = 0.22$ ,  $P = 0.806$ ) among predation treatments (Fig. 4a, right).

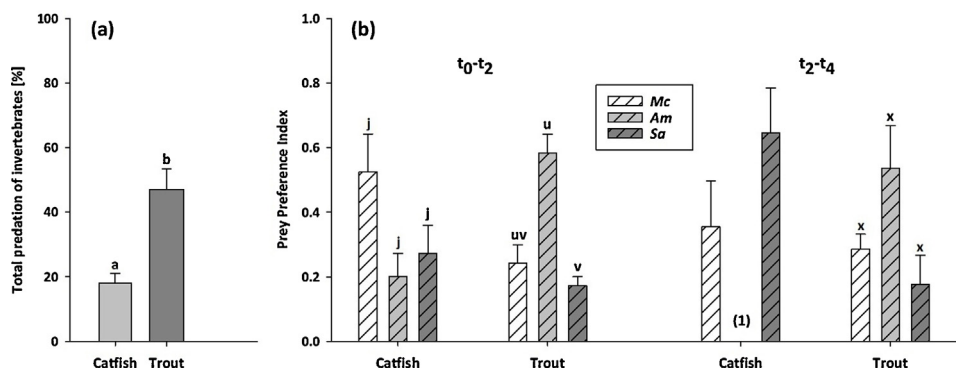
Nymphs escaped from the experimental arenas independently of their population origin (two-way ANOVA,  $F_{1,12} = 0.32$ ,  $P = 0.580$ ) but were affected by distinct predator's chemical cues (two-way ANOVA,  $F_{2,12} = 8.071$ ,  $P = 0.006$ ). While catfish cues did not affect mayfly escaping behaviour compared to that in control channels (Fisher's LSD test,  $P = 0.638$ ), significantly more *M. chiloensis* escaped in presence of rainbow trout cues (Trout vs. Control,  $P = 0.003$ ; Trout vs. Catfish,  $P = 0.007$ ; Fig. 4b).

## Discussion

Our study aimed to compare the influence of invasive rainbow trout and a native fish on Argentina Patagonian stream



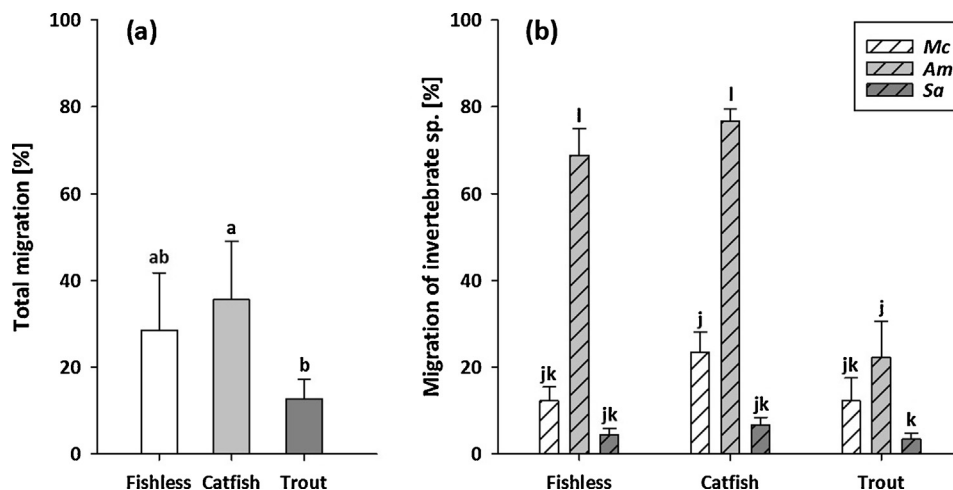
**Fig. 1.** nMDS-plots of Bray-Curtis similarity indices of invertebrate assemblage under different predation treatments (square: fishless, circle: catfish, triangle: trout) at the beginning of the experiment (open symbol:  $t_0$ ) and the end of the experiment (filled symbol:  $t_4$ ), with direct predation and prey emigration taken into account (a) and with factor emigration excluded from the analysis (b).



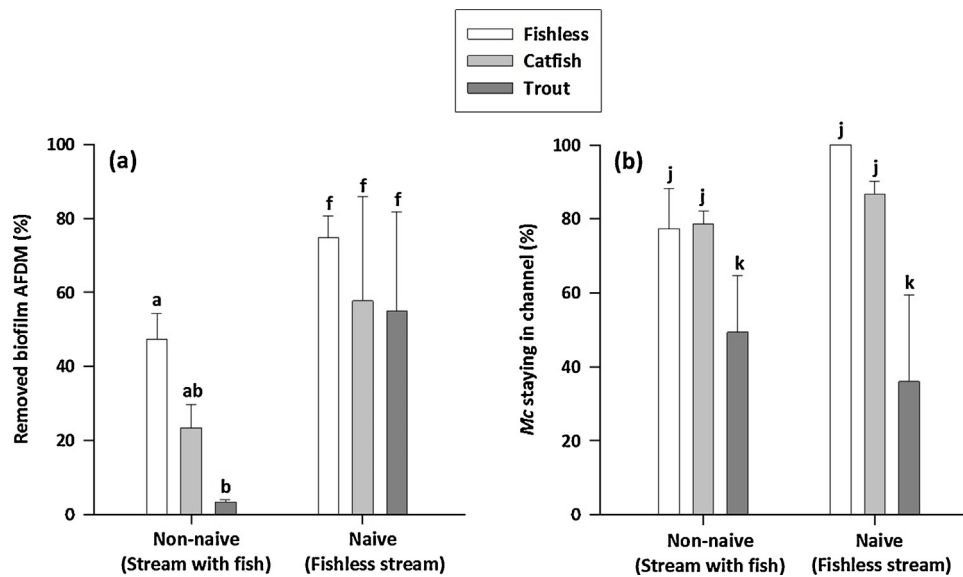
**Fig. 2.** Total predation of catfish and trout during the time period  $t_0-t_4$  (a) and prey preferences of both fish in period  $t_0-t_2$  and  $t_2-t_4$  (b). Prey preferences were calculated on basis of prey availability of *M. chiloensis* (Mc), *A. michaelseni* (Am) and *S. annulicornis* (Sa) at the beginning of each period. Letters display post hoc test results and indicate significant differences if they are not the same, or if letter combinations do not share letters, within a tested group. (1) = because of zero predation events of Am in channels with catfish from  $t_2-t_4$ , a Hotelling's  $T^2$  test could not be performed.

invertebrates at two different levels, direct predation and induced changes in behaviour under predator presence. We assumed that predation by rainbow trout will have a stronger effect on benthic invertebrate abundance and composition than predation by the native catfish. Furthermore we hypothesized that the presence of exotic rainbow trout (in the form of fish chemical cues) would not affect behaviour of invertebrates either naive- or non-naive to predation, while the presence of catfish would have an influence on the behaviour of non-naive invertebrates, but not on the behaviour of naive ones.

The exotic rainbow trout had a stronger predation effect on three common Patagonian stream invertebrates, consuming nearly 3 times more prey than the native catfish. Although specimens of both fish species had similar body sizes they had different body masses and different developmental stages (trout were juveniles while catfish were already mature) which might determine different energy demands (Townsend and Simon, 2006). This surely contributed to the observed higher predation pressure in trout channels. Nevertheless the average trout predation rate in the experiments might have been higher, but trout reduced its



**Fig. 3.** Total emigrated invertebrates (a) and specific migration of *M. chiloensis* (Mc), *A. michaelseni* (Am) and *S. annulicornis* (Sa) in fishless, catfish or trout treatments (b). Letters display post hoc test results and indicate significant differences if they are not the same, or if letter combinations do not share letters, within a tested group.



**Fig. 4.** Removed biofilm AFDM (a) and percentage of *M. chiloeensis* (*Mc*) nymphs originating from stream with fish (non-naive) or fishless stream (naive), still in control- (fishless), catfish- or trout-channels at the final day of the experiment (b). Percentage of removed biofilm AFDM was interpreted as “feeding activity” (high percentage of removed AFDM = high feeding activity and vice versa). Letters display post hoc test results and indicate significant differences if they are not the same within a tested group.

predation rate at the end of the experiment probably as a matter of resource limitation. In the first experimental period, its predation rate was 3.7 times higher than that of catfish, but it was just 1.7 times higher in the second period. At  $t_2$ , only 13.3% of the initially provided *A. michaelsoni* nymphs remained, probably causing trout to consume less. Our result may well reflect what happens in nature. As trout is an opportunistic feeder it might have maintained a high predation rate if more vulnerable prey individuals from one or more species were available. In contrast, after depletion of more vulnerable individuals (what accounted at the end of the first part of the experiment) trout had to have shifted its target to less conspicuous prey with a consequent reduction in predation rate.

High predation pressure by invasive trout has been already shown to significantly reduce invertebrate abundances. In New Zealand streams, Hury (1998) demonstrated that brown trout consumed almost the total annual invertebrate secondary production while the native *Galaxias eldoni* consumed about 20%. More recently, Buria et al. (2007) surveyed three Patagonian fishless streams where stream reaches downstream waterfalls were inhabited by rainbow trout (the only fish species). Compared to fishless reaches, total invertebrate community abundance was significantly reduced in downstream trout reaches. However, in a similar study design conducted in 21 fishless streams in Sierra Nevada, California, Herbst et al. (2009) found that total community abundance did not differ to that of 21 invaded-trout streams.

Fish top predators are known to exert strong control on the structure of their prey community (McPeck, 1998). Fish usually prey selectively on the most vulnerable species regarding prey size and habits (Wootton, 1990), but may also alter prey behaviour resulting in differential prey strategies, e.g. emigration or occultation (Meissner and Muotka, 2006). In our study, the structure of invertebrate assemblages was influenced by fish presence but fish identity was also a critical factor. The stronger effect that trout had in shaping invertebrate composition became apparent after removing the effect associated with invertebrate emigration. Trout predation resulted in assemblages that differed from those in fishless or catfish channels.

The trajectory of invertebrate assemblages set in this experiment underlines the importance of selective fish predation in shaping community structure (Buria et al., 2007; Herbst et al.,

2009). Rainbow trout maintained a preference pattern for the plecopteran shredder *A. michaelsoni* and the scraper *M. chiloeensis* over the filtering-collector *S. annulicornis*, while catfish preferred to feed on the scraper at the initial experimental stage and changed to feed on *S. annulicornis* when the former prey became scarce. Observed prey preference patterns probably occurred due to an interaction of the different habitat use of invertebrates and the distinct feeding strategies of the predatory fish (Lima and Dill, 1990; Allan, 1995). Trout is a visual forager (McIntosh, 2000; Novales Flamarique and Browman, 2001), whereas catfish depends on its tactile perception (Barriga and Battini, 2009; Ferriz, 2012). Irrespective of fish presence (i.e. fishless channels), the plecopteran shredder presented a vagile behaviour, emigrating significantly more than the other invertebrates. It is likely that its emigration behaviour caused them to be the most vulnerable prey to trout. In contrast, the trichopteran filtering-collector emigrated very little, rapidly building their retreats beneath stones. Similarly, the mayfly scraper tended to move little and remained mostly attached to stones, making it more vulnerable to catfish. It is worth noting that our experimental channels reproduced a water flow closer to that of pool habitats where invertebrate drift is less likely to occur than in riffle habitats. Higher flow conditions might have stimulated emigration by drift enhancing trout predation efficiency, increasing differences in predation intensity between rainbow trout and the benthic feeder catfish. Considering the contrasting behavioural traits of predators and prey, a gradient of prey vulnerability was revealed; trout fed most on more vagile and visually exposed invertebrates and catfish preyed most on more concealed invertebrates which were vulnerable to tactile-based detection. While studies on the diet of the native catfish *H. macraei* in Patagonian streams have shown that chironomids, mayflies and caddisflies (i.e. collectors and scrapers) were the most consumed items (Ferriz, 1994; Barriga and Battini, 2009; Ferriz, 2012), in other streams in the same region, rainbow trout positively selected large size classes of benthic invertebrates, being shredders the feeding group most negatively affected followed by scrapers (Buria et al., 2007). Interestingly, shredders were the most important item in rainbow trout stomachs (% biomass) and were consumed according to natural abundance, while scrapers, which were overrepresented regarding benthic abundance, were the second functional group in the diet (Buria et al., 2009).

Considering that predation is a significant mortality factor, it is not surprising that prey have developed multiple defensive behaviours to avoid being detected and attacked by predators (Brönmark and Hansson, 2000). We had assumed that naive invertebrates from fishless streams would not react to predator's kairomones and in consequence would not show response to predation risk. In contrast, non-naive invertebrates would react to these chemical cues from native predators but not to the cues of the exotic ones (Sih et al., 2010) as these were introduced to Patagonia just about a hundred years ago. Although we were not able to test it statistically, it may be seen that the origin of mayfly populations resulted in contrasting feeding activity. On one hand, our prediction for naive nymphs was met as prey did not alter feeding activity relative to predation cues. However individuals originating from the stream with fish predators unexpectedly responded relatively strong to trout cues. Regarding escaping behaviour, our expectations were not met, as mayflies emigrated more under the influence of trout cues than in other treatments, independently of the origin of their populations. It is worth noting that the reduced feeding activity in our experiments did not result from mayfly diminished abundance as a consequence of emigration but from nymph inactivity. Mayflies from both origin populations exposed to rainbow trout cues, similarly remained in the channels but only non-naive ones reduced feeding activity. As mentioned above, though naive specimens displayed similar feeding activities under different predation risks, they emigrated from channels with trout cues similarly to their non-naive conspecifics. It is possible, as well, that naive individuals had reacted to prey cues from conspecifics that were released with predator faeces (Ferrari et al., 2010). Because trout was the most effective predator in our first experiment, the concentration of predation-related cues would have been higher under trout presence.

Additional factors might have acted in concert to explain mayfly behaviour in our experiments. Because non-naive nymphs were collected from the wild, having experienced predation risks, we can not be sure to what extent their responses to fish cues were innate or learned. In addition, the distance between sites with and without fish in Challhuaco stream may be short enough to allow gene flow between invertebrate populations (i.e. adult mayfly mating). The same mechanism (i.e. gene flow) was used to explain genetically anchored predation avoidance behaviour in naive populations not differing from that of non-naive populations in other mayflies (*Baetis* spp), and was consistent with the hypothesis that traits associated with environments with contrasting risks are phenotypically plastic (Peckarsky et al., 2005). The predation avoidance behaviour of non-naive invertebrates towards invasive trout may also be explained by a rapid genetic adaptation to the exotic predator. Responses to changing predation pressures may evolve quickly if the selection pressure is strong (Laurila, 2000; Åbjörnsson et al., 2004). Assuming that rainbow trout exerts a strong predation pressure on native freshwater fauna in Patagonia (Macchi et al., 1999; Buria et al., 2007; Vigliano et al., 2009; and our first experiments), it is likely that some invertebrate species have adapted to cohabit with this predator within just one century. A similar evidence comes from New Zealand where another invasive fish, brown trout, having one century of introduction history, has been shown to exert strong changes in mayfly behaviour (feeding, moving and drifting) when compared with changes associated to native galaxiids (Townsend and Simon, 2006). Individuals are known to be sensitive to the current level of predation risk in nature which allows them to balance their behavioural decision-making to feed, move, and avoid being preyed (Lima and Dill, 1990). Interestingly, the non-naive specimens of the scraper *M. chiloeensis* under no risk of predation (control channels) displayed low emigration activity (~20%) in our two experiments. Similarly, when catfish predation risk was present either as visual and chemical or only chemical

cues they took in average the same behavioural decision; 25% or 20%, respectively, emigrated from channels (see Figs. 3b and 4b). However, individuals had a contrasting antipredator behaviour exclusively when exposed to rainbow trout chemical cues (second experiment); more than twice of individuals emigrated from these channels compared to channels with trout presence (50% vs. 18%). These results indicate that this common scraper was able to distinguish different levels of predation risks from the direct presence of a predator, deciding to be inactive, to the sole presence of chemical cues in the nearby where they chose escaping. Similarly, different mayfly species of the genus *Baetis* change drift intensity as avoidance behaviour according to the relative risk of predation (McIntosh et al., 1999; Huhta et al., 2000).

The characteristic of being a strong predator of benthic invertebrates makes trout not only a hazardous predator for native invertebrates, but also a potentially strong competitor of native fish like *H. macraei*. In particular, despite of the morphological and behavioural differences between rainbow trout and *H. macraei*, both fish use very similar invertebrate food resources (Barriga and Battini, 2009; Ferriz, 2012;) and significant diet overlap exists (Di Prinzio and Casaux, 2012). In a recent study in Pichileufu River, Barriga et al. (2013) showed that the exotic salmonids *O. mykiss* and *S. trutta* prefer pools and runs with intermediate water velocity while *H. macraei* mostly use habitats with faster water velocity, such as runs and riffles. These findings indicate differences in habitat use but they may also reflect predation/competition avoidance among species. Evidence for this statement was found by Penaluna et al. (2009) for three native fish, including another catfish species, in Chilean Patagonia rivers. All three native species changed their mesohabitat use after a manipulation that reduced invasive salmonid abundance in river segments.

The present study represents the first evidence to understand the contrasting predation effects between an invasive salmonid and a native fish on benthic invertebrates in Northern Patagonian streams. The observed individual and assemblage-level effects are likely to occur in natural systems and affect invertebrate's population dynamics and communities (McIntosh et al., 2004; Townsend and Simon, 2006; Buria et al., 2007). Moreover, our study was focused on certain prey and fish sizes in order to make comparative results regarding predation events, but streams and rivers in Patagonia support a range of fish sizes. Introduced trout, like rainbow and brown trout, have been reported to hold more abundant populations with larger size ranges and larger individuals than native fish when natives are present (Soto et al., 2006; Barriga et al., 2007; Habit et al., 2010; Di Prinzio and Casaux, 2012). Those fish patterns in presence, sizes and abundances are likely to determine contrasting and even stronger impacts of trout on community's taxonomic and size structure and also result in diminished secondary production of such benthic prey communities (see Huryn, 1996). Recreational fisheries of introduced salmonids in Patagonia are unarguably a significant ecosystem service (Lara et al., 2009; Pascual et al., 2009), whereas the economical values of native species and their roles in ecosystem functioning are difficult to calculate because their values are not direct to human welfare. However, managers in Patagonia need to protect upstream refuges for native fauna above migration barriers making landowners and anglers fully aware of the impact of trout on vulnerable native species, and of the need to prevent their further spread.

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## References

- Åbjörnsson, K., Hansson, L.A., Brönmark, C., 2004. Responses of prey from habitats with different predator regimes: local adaptation and heritability. *Ecology* 85, 1859–1866.
- Albariño, R., Díaz Villanueva, V., 2006. Feeding ecology of two plecopterans in low order Andean-Patagonian Streams. *Int. Rev. Hydrobiol.* 91, 122–135.
- Allan, J.D., 1995. Predation and its consequences. In: *Stream Ecology: Structure and Function of Running Waters*. Chapman and Hall, London, UK, pp. 163–185.
- Barriga, J.P., Battini, M.A., Cussac, V.E., 2007. Annual dynamic variation of a land-locked *Galaxias maculatus* (Jenyns 1842) population in a Northern Patagonian river: occurrence of juvenile upstream migration. *J. Appl. Ichthyol.* 23, 1–8.
- Barriga, J.P., Battini, M.A., 2009. Ecological significances of ontogenetic shifts in the stream-dwelling catfish, *Hatcheria macraei* (Siluriformes, Trichomycteridae), in a Patagonian river. *Ecol. Freshw. Fish* 18, 395–405.
- Barriga, J.P., Espinós, N.A., Chiarello-Sosa, J.M., Battini, M.A., 2013. The importance of substrate size and interstitial space in the microhabitat selection by the stream-dwelling catfish *Hatcheria macraei* (Actinopterygii, Trichomycteridae). *Hydrobiologia* 705, 191–206.
- Biggs, B.J.F., Kilroy, C., 2000. *Stream Periphyton Monitoring Manual*. NIWA, Christchurch, New Zealand.
- Brodie III, E.D., Brodie Jr., E.D., 1999. Predator-prey arms races, asymmetrical selection on predators and prey may be reduced when prey are dangerous. *Bioscience* 49, 557–568.
- Brönmark, C., Hansson, L.A., 2000. Chemical communication in aquatic systems: an introduction. *Oikos* 88, 103–109.
- Buria, L., Albariño, R., Díaz Villanueva, V., Modenutti, B., Balseiro, E., 2007. Impact of exotic rainbow trout on the benthic macroinvertebrate community from Andean-Patagonian headwater streams. *Hydrobiologie* 168, 145–154.
- Buria, L., Albariño, R., Modenutti, B., Balseiro, E., 2009. Temporal variations in the diet of the exotic rainbow trout (*Oncorhynchus mykiss*) in an Andean-Patagonian canopied stream. *Rev. Chil. de Hist. Nat.* 82, 3–15.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 2nd ed. PRIMER-E, Plymouth.
- Di Prinzio, C.Y., Casaux, R.J., 2012. Dietary overlap among native and non-native fish in Patagonian low-order streams. *Annales de Limnologie – Int. J. Limnol.* 48, 21–30.
- Díaz, M., Pedrozo, F., Reynolds, C., Temporetti, P., 2007. Chemical composition and the nitrogen-regulated trophic state of Patagonian lakes. *Limnologia* 37, 17–27.
- Dodson, S.I., Crowl, T.A., Peckarsky, B.L., Kats, L.B., Covich, A.P., Culp, J.M., 1994. Non-volitional communication in freshwater benthos: an overview. *J. N. Am. Benthol. Soc.* 13, 268–282.
- Ferrari, M.C.O., Wisenden, B.D., Chivers, D.P., 2010. Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. *Can. J. Zool.* 88, 698–724.
- Ferriz, R., 1994. Alimentación de *Olivaichthys vielmensis* (Mac Donagh, 1932) y *Hatcheria macraei* (Girard, 1855) (Teleostei: Saluriformes) en el Río Limay, Alicurá, Argentina. *Nat. Patagón.* 2, 83–88.
- Ferriz, R., 2012. Dieta de *Hatcheria macraei* (Girard, 1855) (Teleostei, Siluriformes, Trichomycteridae) en el río Chubut, Argentina. *Latin Am. J. Aquat. Res.* 40, 248–252.
- García de Leaniz, C., Gajardo, G., Consuegra, S., 2010. From best to pest: changing perspectives on the impact of exotic salmonids in the southern hemisphere. *Syst. Biodivers.* 8, 447–459.
- Habit, E., Piedra, P., Ruzzante, D.E., Walde, S.J., Belk, M.C., Cussac, V.E., Gonzalez, J., Colin, N., 2010. Changes in the distribution of native fishes in response to introduced species and other anthropogenic effects. *Global Ecol. Biogeogr.* 19, 697–710.
- Herbst, D., Silldorff, E., Cooper, S., 2009. The influence of introduced trout on the benthic communities of paired headwater streams in the Sierra Nevada of California. *Freshw. Biol.* 54, 1324–1342.
- Huhta, A., Muotka, T., Tikkanen, P., 2000. Nocturnal drift of mayfly nymphs as a post-contact antipredator mechanism. *Freshw. Biol.* 45, 33–42.
- Huryn, A., 1996. An appraisal of the Allen paradox in a New Zealand trout stream. *Limnol. Oceanogr.* 41, 243–252.
- Huryn, A.D., 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream. *Oecologia* 115, 173–183.
- Korsu, K., Huusko, A., Muotka, T., 2008. Ecology of alien species with special reference to stream salmonids. *Boreal Environ. Res.* 13, 43–52.
- Lara, A., Little, C., Urrutia, R., McPhee, J., Álvarez-Garretón, C., Oyarzún, C., Soto, D., Donoso, P., Nahuelhual, L., Pino, M., Arismendi, I., 2009. Assessment of ecosystem services as an opportunity for the conservation and management of native forests in Chile. *Forest Ecol. Manag.* 258, 415–424.
- Laurila, A., 2000. Behavioural responses to predator chemical cues and local variation in antipredator performance in *Rana temporaria* tadpoles. *Oikos* 88, 159–168.
- Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 69, 619–640.
- Lockwood, J.R., 1998. On the statistical analysis of multiple-choice feeding preference experiments. *Oecologia* 116, 475–481.
- Macchi, P., Cussac, V., Alonso, M., Denegri, M., 1999. Predation relationships between introduced salmonids and native fish fauna in lakes and reservoirs of northern Patagonia. *Ecol. Freshw. Fish* 8, 227–236.
- Macchi, P., Vigliano, P., Pascual, M., Alonso, M., Denegri, M., Milano, D., Lippolt, G., 2008. Historical policy goals for fish management in northern continental Patagonia Argentina: a structuring force of actual fish assemblages? *Am. Fisheries Soc. Symp.* 49, 331–348.
- Manly, B.F.J., 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. *Oecologia* 93, 149–152.
- McDowall, R.M., 2006. Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Fish Biol. Fisheries* 16, 233–422.
- McIntosh, A.R., 2000. Aquatic predator-prey interactions. In: Collier, K.J., Winterbourn, M.J. (Eds.), *New Zealand Stream Invertebrates: Ecology and Implications for Management*. New Zealand Limnological Society, Christchurch, pp. 125–156.
- McIntosh, A.R., Peckarsky, B.L., Taylor, B.W., 1999. Rapid size-specific changes in the drift of *Baetis bicaudatus* (Ephemeroptera) caused by alteration in fish odour concentration. *Oecologia* 118, 256–264.
- McIntosh, A.R., Peckarsky, B.L., Taylor, B.W., 2004. Predator-induced resource heterogeneity in a stream food web. *Ecology* 85, 2279–2290.
- McPeck, M., 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecol. Monogr.* 68, 1–23.
- Meissner, K., Muotka, T., 2006. The role of trout in streams food web: integrating evidence from field surveys and experiments. *J. Anim. Ecol.* 75, 421–433.
- Novalés Flamarique, I., Browman, H.I., 2001. Foraging and prey-search behaviour of small juvenile rainbow trout *Oncorhynchus mykiss* under polarized light. *J. Exp. Biol.* 204, 2415–2422.
- Pascual, M., Cussac, V., Dyer, B., Soto, D., Vigliano, P., Ortubay, S., Macchi, P., 2007. Freshwater fishes of Patagonia in the 21st Century after a hundred years of human settlement, species introductions, and environmental change. *Aquat. Ecosyst. Health Manag.* 10, 212–227.
- Pascual, M.A., Lancelotti, J.L., Ernst, B., Ciancio, J.E., Aedo, E., García-Asorey, M., 2009. Scale, connectivity, and incentives in the introduction and management of non-native species: the case of exotic salmonids in Patagonia. *Front. Ecol. Environ.* 7, 533–540.
- Peckarsky, B., Hughes, J., Mather, P., Hillyer, M., Encalada, A., 2005. Are populations of mayflies living in adjacent fish and fishless streams genetically differentiated? *Freshw. Biol.* 50, 42–51.
- Penaluna, B.E., Arismendi, I., Soto, D., 2009. Evidence of interactive segregation between introduced trout and native fishes in Northern Patagonian Rivers, Chile. *Trans. Am. Fisheries Soc.* 138, 839–845.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.
- Ricciardi, A., 2007. Are modern biological invasions an unprecedented form of global change? *Conserv. Biol.* 21, 329–336.
- Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S., Vonesh, J.R., 2010. Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119, 610–621.
- Simon, K.S., Townsend, C.R., 2003. Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshw. Biol.* 48, 982–994.
- Soto, D., Arosamendi, I., Gonzalez, J., Sanzana, J., Jara, F., Guzman, E., Lara, A., 2006. Southern Chile, trout and salmon country: invasion patterns and threats for native species. *Rev. Chil. de Hist. Nat.* 79, 97–117.
- Townsend, C.R., 2003. Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams. *Conserv. Biol.* 17, 38–47.
- Townsend, C.R., Simon, K.S., 2006. Consequences of brown trout invasion for stream ecosystems. In: Allen, R.B., Lee, W.G. (Eds.), *Biological Invasions in New Zealand*. Springer-Verlag, Berlin, Heidelberg, pp. 213–225.
- Vigliano, P.H., Beauchamp, D.A., Milano, D., Macchi, P.J., Alonso, M.F., García Asorey, M.I., Denegri, M.A., Ciancio, J.E., Lippolt, G.E., Rechenq, M., Barriga, J.P., 2009. Quantifying predation on galaxiids and other native organisms by introduced rainbow trout in an ultraoligotrophic lake in northern Patagonia, Argentina: a bioenergetics modeling approach. *Trans. Am. Fisheries Soc.* 138, 1405–1419.
- Wisenden, B.D., 2000. Olfactory assessment of predation risk in the aquatic environment. *Philos. Trans. R. Soc. B: Biol. Sci.* 355, 1205–1208.
- Wootton, R.J., 1990. *Ecology of Teleost Fishes*. Kluwer Academic Publications, London.