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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.

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 michaelseni* (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 ± 1.00 cm (mean ± SE) and a mean wet mass of 3.94 ± 1.32 g. Specimens of *O. mykiss* had a mean total length of 9.39 ± 0.66 cm and a mean wet mass of 7.35 ± 1.29 g. Invertebrates had mean body lengths of 7.07 ± 0.07 mm (*M. chiloeensis*), 10.09 ± 0.61 mm (*A. michaelseni*), and 9.38 ± 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 μg/L, SRP: 3.4 μg/L, Na: 1.7 mg/L, a Chl-a: 0.4 μg/L, pH: 6.7, conductivity: 58.1 μS/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 ~1.0 cm/s. Incoming water was filtered by a 200 μm 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. michaelseni* and construction material for *S. annulicornis* retreats. Fish shelter was provided by a black PVC tube (8 × 25 cm diameter and length). In each channel 15 nymphs of *M. chiloeensis*, 15 nymphs of *A. michaelseni* 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^2 for each species and a total