

A trial of two trouts: comparing the impacts of rainbow and brown trout on a native galaxiid

K. A. Young¹, J. B. Dunham², J. F. Stephenson³, A. Terreau¹, A. F. Thailly¹, G. Gajardo⁴ & C. Garcia de Leaniz⁵

¹ Universidad de Los Lagos, Puerto Montt, Chile

² U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis Research Group, Corvallis, OR, USA

³ Department of Biological Sciences, University of Bristol, Bristol, UK

⁴ Laboratorio de Genética y Acuicultura, Universidad de Los Lagos, Osorno, Chile

⁵ School of the Environment and Society, Department of Biological Sciences, Swansea University, Swansea, UK

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Correspondence

Kyle A. Young, Environment Agency, Lutra House, Walton Summit, Preston PR5 8BX, UK. Tel: +44 01 772 714 093; Fax: +44 01 772 311 936

Email: kyle.young@environment-agency.gov.uk

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Abstract

Rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* are the world's two most widespread exotic fishes, dominate the fish communities of most cold-temperate waters in the southern hemisphere and are implicated in the decline and extirpation of native fish species. Here, we provide the first direct comparison of the impacts of rainbow and brown trout on populations of a native fish by quantifying three components of exotic species impact: range, abundance and effect. We surveyed 54 small streams on the island of Chiloé in Chilean Patagonia and found that the rainbow trout has colonized significantly more streams and has a wider geographic range than brown trout. The two species had similar post-yearling abundances in allopatry and sympatry, and their abundances depended similarly on reach-level variation in the physical habitat. The species appeared to have dramatically different effects on native drift-feeding *Aplocheilichthys* spp., which were virtually absent from streams invaded by brown trout but shared a broad sympatric range with rainbow trout. Within this range, the species' post-yearling abundances varied independently before and after controlling for variation in the physical habitat. In the north of the island, *Aplocheilichthys* spp. inhabited streams uninvaded by exotic trouts. Our results provide a context for investigating the mechanisms responsible for apparent differences in rainbow and brown trout invasion biology and can help inform conservation strategies for native fishes in Chiloé and elsewhere.

Introduction

Exotic fishes are a principal threat to global freshwater biodiversity (Allan & Flecker, 1993; Leprieur *et al.*, 2008) that can harm native fishes directly through predation and competition, and indirectly by altering the behaviour and abundance of prey, and disturbing food web dynamics (Flecker & Townsend, 1994; Nyström, McIntosh & Winterbourn, 2003; Baxter *et al.*, 2004). Although progress has been made in identifying which traits characterize particularly invasive (Kolar & Lodge, 2001; Marchetti, Moyle & Levine, 2004; Ricciardi & Mottiar, 2006; Olden, Poff & Bestgen, 2006; Ribeiro *et al.*, 2008) and harmful exotic fish (Kolar & Lodge, 2002; Ricciardi & Atkinson, 2004), such generalizations are taxonomically and geographically restricted. The challenge of protecting native species will continue to benefit from detailed studies on the impacts of particularly damaging exotic species. Parker *et al.* (1999) introduced a conceptual framework for such studies by recognizing that the impact of an exotic species is the

cumulative result of three distinct and potentially unrelated components: the range of the species, the abundance of individuals within that range, and the per-capita effect of the species on individuals, populations and communities of native species. Here, we apply this framework to compare the impacts of two of the world's most notorious exotic fishes on populations of a native fish.

Rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* have large, non-overlapping native ranges spanning from temperate to near-arctic watersheds of the north Pacific and north-east Atlantic, respectively (Fishbase, 2009). Principally due to their popularity as sport fish, both species have been introduced to cold-water rivers and lakes on every continent except Antarctica, and are now two of the most widely distributed and damaging exotic fish in the world (MacCrimmon & Marshall, 1968; MacCrimmon, 1971; Cambray, 2003; Lowe, Browne, & Boudjelas, 2004; Fishbase, 2009). Their invasion biology has been best studied in Australia and New Zealand. Both species have been unequivocally implicated in the decline of the native

galaxiid fishes through predation, competition and food web alteration (reviewed by Crowl, Townsend & McIntosh, 1992; Townsend, 1996, 2003; McDowall, 2003, 2006). The qualitative consensus on the relative impacts of rainbow and brown trout on southern hemisphere galaxiids is reflected by the first conclusion of Crowl *et al.* (1992): 'brown trout appear to be more damaging than rainbow trout due to strong interactions, particularly involving predation'. McDowall (2006) suggests that this perception may be due to brown trout being more widespread in New Zealand and, in the absence of any quantitative comparison of their impacts, correctly concludes that 'the jury is still out on this question'.

The rivers of Chilean Patagonia are the biogeographic equivalent of an archipelago of islands isolated from South America by the Andes Mountains and the Pacific Ocean. These migration barriers combined with repeated Quaternary glaciations have resulted in freshwater fish communities with few native species that are dominated by introduced rainbow and brown trout (Dyer, 2000; Cussac *et al.*, 2004; Soto *et al.*, 2006; Leprieur *et al.*, 2008). Compared with the mature literature from Australia and New Zealand, salmonid invasion biology remains poorly studied in South America (reviewed by Pascual *et al.*, 2002, 2007), and we know of no study demonstrating population-level impacts of rainbow or brown trout on a native fish in Patagonia. Macchi *et al.* (1999) and Macchi, Pascual & Vigliano (2007) have shown that both rainbow and brown trout prey on native fish in Patagonian lakes. Soto *et al.* (2006) found evidence of a negative relationship between the abundance of native fishes and exotic salmonids in 115 third- to fourth-order streams in southern Chile (39°–54°S). Unfortunately, they combined data across climatic and ichthyogeographic regions without controlling for the effects of variation in the physical habitat, making it impossible to implicate interspecific interactions, much less those between salmonids and native fishes, as the cause of variation in relative abundance (Dyer, 2000). Regarding the impacts of rainbow and brown trout on native fish, if in New Zealand the jury is still out, in Patagonia it has yet to be convened.

Given their wide distribution, popularity as sport fish and obvious threat to native biodiversity, quantitatively comparing the impacts of rainbow and brown trout on native fishes is a global conservation priority. To begin meeting this challenge, we apply the framework of Parker *et al.* (1999) to compare the ranges, abundances and effects of rainbow and brown trout on populations of native *Aplocheilichthys* spp. in southern Chile.

Methods

Study area

The Grand Island of Chiloé (41°45'–42°45'S) lies at the north-western border of the Patagonian ichthyogeographic province and was roughly bisected by the last glaciation (Dyer, 2000; Cussac *et al.*, 2004). The east side of the island is ideal for studying the invasion biology of anadromous

salmonids for two reasons. First, there are hundreds of small streams draining directly into the ocean. For native and exotic diadromous fishes these streams represent independent habitat patches connected via marine dispersal. Second, the native fish communities are simple, making it easier to attribute the variation in population-level indices to the presence and abundance of exotic salmonids. In our surveys of island streams, we have encountered five native species: four galaxiids – *Galaxias maculatus* (ubiquitous and abundant in intertidal zones), *Brachygalaxias bullocki* (rare and scarce), *Aplocheilichthys zebra* (variable), *Aplocheilichthys taeniatus* (rare and scarce), and a native lamprey – *Geotria australis* (rare with juveniles locally common). Our study compares the impacts of rainbow and brown trout on *Aplocheilichthys* spp., two diadromous drift feeders whose life histories, ecologies and conservation status remain poorly understood (McDowall & Nakaya, 1988; Dyer, 2000; Cussac *et al.*, 2004; McDowall, 2006; Lattuca *et al.* 2008; Young *et al.* 2009).

Sampling

During the southern summer of 2007–08, we sampled the fish communities and physical habitat of 54 first- to third-order streams beginning at high tide and extending upstream an average of 138 m (Appendix S1a). We studied small streams for two reasons. First, we were able to effectively sample all habitat types using electrofishing. Second, small streams are less likely to have been intentionally stocked with exotic trout, making it more likely that patterns of presence/absence are the result of natural colonization/extinction dynamics.

Fish communities were sampled using upstream, single-pass electrofishing without block nets. All *Aplocheilichthys* spp., rainbow and brown trout were measured for total length (mm), and for analysis separated into two age classes using size-class histograms: young-of-year (YOY) and post-yearling (all fish born before the year of the survey). Because we were unable to distinguish between YOY *A. zebra* and *A. taeniatus* and their riverine ecologies are poorly studied, we included 35 suspected post-yearling *A. taeniatus* (4% of the total) and hereafter use *Aplocheilichthys* to describe the two species. Environmental variation was quantified using two categorical and eleven continuous watershed/reach scale habitat variables (Appendix S1; watershed variables were taken from maps and reach scale habitat variables were visually estimated by a single experienced observer, K. A. Y.): disturbance (1 = evidence of channel erosion/modification from cattle, 0 = no such evidence); riparian type (1 = closed/mixed canopy forest, 0 = meadow, pasture, grassland); stream mouth latitude; watershed area (km²); watershed highpoint (m); average channel width (m); channel gradient (%); valley width index (VWI = valley bottom width/channel width); pool percentage (proportion of the wetted channel with pool habitat); fish cover (proportion of the wetted channel with large/small woody debris, undercut bank, aquatic vegetation and overhanging vegetation), and three substrate scores: PC1, PC2 and PC3. Substrate scores were calculated using principal components analysis (PCA)

on the correlation matrix of the proportions of substrate in four classes: boulder (*c.* >40 cm diameter), cobble (10–40 cm), gravel (1–10 cm) and fines (<1 cm). For analyses using subsets of streams, PCA was repeated using only those streams included in the analysis.

Our analyses of range, abundance and effect were complicated by the number of correlated environmental variables and the requirement that the different hypotheses be tested using different subsets of the 54 streams. We describe all analyses but present only the key results (full results are available in online Appendices).

Range

Using all streams, we first tested the hypothesis that rainbow and brown trout have colonized the same number of streams with a two-tailed proportions parameter test, which uses a χ^2 distribution to compare the proportions of 'successes' for two categories of a common sample (S-Plus, 1999). We then used forward stepwise logistic regressions (entry/removal condition $P = 0.05$) with a constant to determine if the presence/absence of the two exotic trout species were predicted by the two categorical and eleven continuous variables. We tested the selected model's significance using the difference in log-likelihood ratio (LLR) between the final and constant only models. We measured each model's explanatory ability as the percentage of streams for which the model successfully predicted the presence/absence of the species (SYSTAT, 2000).

Abundance

For every colonized stream (43 of 54; Appendix S1), we estimated the YOY and post-yearling abundance of both exotic species as the number of fish captured per square metre (survey length \times average wetted width). We first compared post-yearling abundances of rainbow ($n = 28$) and brown trout ($n = 10$) in streams colonized by only one species using a two-sample *t*-test. Because *Aplochiton* was rare in streams colonized by brown trout (see 'Results'), we repeated the comparison using rainbow trout abundance estimates only from streams with no post-yearling *Aplochiton* ($n = 7$). For the five streams colonized by both trout species, we compared post-yearling abundances using a paired *t*-test.

We tested how post-yearling trout abundance in the 38 single species streams depended on species identity and variation in physical habitat as follows. First, we used forward and backward stepwise ANCOVA (entry/removal criteria of $P = 0.05$) with three class variables (species, disturbance and riparian type), 10 continuous variables (latitude was not included in these models) and all one-way interactions involving species, for a total of 25 terms. Terms retained by both stepwise models were used to construct a final model. We next conducted PCA on the correlation matrix of the seven watershed/reach level habitat variables, retained the three axes with eigenvalues > 1, and repeated the model building procedure with three class and six

continuous variables (17 terms). Finally, we conducted PCA on the correlation matrix of the seven reach level habitat variables and four substrate proportions together, and used the scores of the first four axes as continuous habitat variables (13 terms). We present results from models for which forward and backward stepwise procedures converged (Appendix S2).

We also considered body size, which may influence the impact of exotic trout. We used a 100-mm-long cutoff, which roughly corresponds to the size at which trout become piscivorous (Mittelbach & Persson, 1998; Arismendi, 2009). Asymptotic Kolmogorov–Smirnov tests were used to test for differences in the length distributions of small (<100 mm) and large (>100 mm) rainbow and brown trout (Zar, 1996).

Effect

We first compared the population-level effects of rainbow and brown trout on *Aplochiton* using Fisher's exact test to determine if the presence/absence of *Aplochiton* in the 38 colonized streams depended on exotic trout identity. In the 39 streams north of 42.8° (where brown trout is not present, see Fig. 1), we tested for effects of rainbow trout on *Aplochiton* as follows. First, we compared the abundances (calculated as above) of post-yearling *Aplochiton* in streams with (21) and without (11) rainbow trout using a two sample *t*-test. To control for the effects of habitat variation, we built stepwise ANCOVA models for post-yearling *Aplochiton* abundance as described above. We then tested whether the residuals from the final models differed between streams with and without rainbow trout using a two sample *t*-test. We next considered the 21 streams with post-yearling fish of both species, first testing whether the abundances of *Aplochiton* and rainbow trout were different (paired *t*-test) or negatively related (parametric correlation). To control for the effects of habitat variation, we built ANCOVA models as before for each species independently and tested whether the residual abundances from these models were negatively correlated (parametric correlation).

Results

We observed all seven possible community types and highlight three general patterns (Appendix S1, Fig. 1). First, *Aplochiton* has an island-wide distribution. Second, brown trout was present in every stream south of, and no stream north of, latitude 42.8°. Third, north of 42.8°, there was a gradual change in community type from allopatric rainbow trout, to rainbow trout and *Aplochiton* in sympatry, to allopatric *Aplochiton*.

Range

Rainbow trout had a larger geographic range and has colonized a significantly higher proportion ($33/54 = 0.61$) of streams than brown trout ($15/54 = 0.28$) ($\chi^2 = 10.8$, $P = 0.001$; 95% CI of difference, 0.14–0.53) (Fig. 1). For brown trout, latitude (*t*-ratio = 54.2, $P < 0.001$) was the only

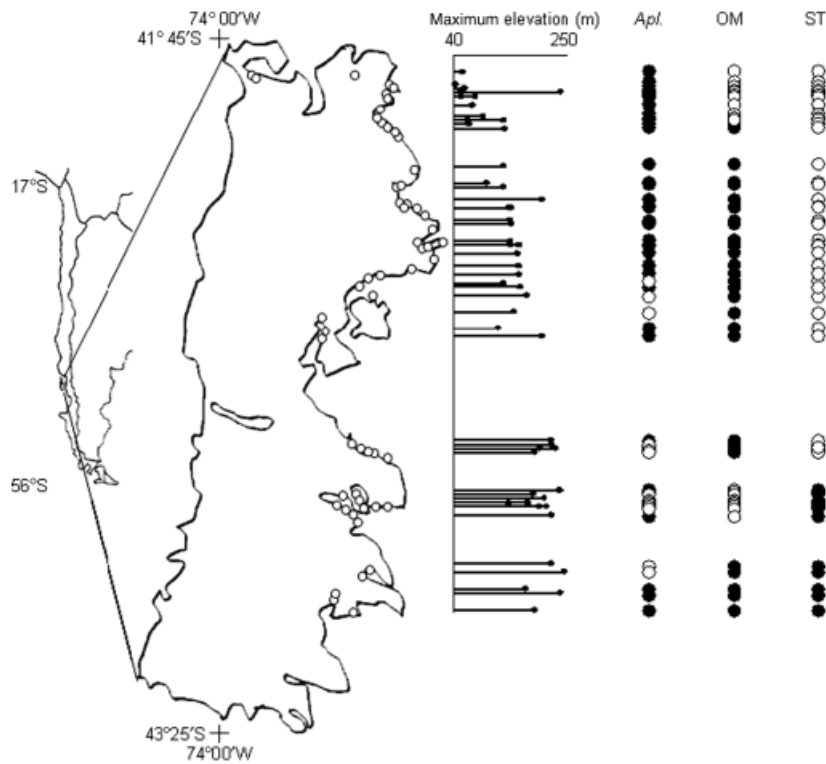


Figure 1 Southern South America with the locations and maximum watershed elevations (metres) of the 54 study streams on Chiloé Island, Patagonia, Chile. The presence (●) or absence (○) of three fish species is shown for each stream. *Apl.* = *Aplochiton* spp., *OM* = *Oncorhynchus mykiss*, *ST* = *Salmo trutta*. Note that many smaller islands off the east coast of the main island have been removed from this figure for clarity.

variable to enter a highly significant logistic model (LLR = 63.8, $P < 0.0001$) that predicted the presence/absence with 100% accuracy. Considering all 54 streams, rainbow trout was more likely to be present in valley bottom streams (VWI, t -ratio = 2.7, $P = 0.006$) and large watersheds (watershed area, t -ratio = 2.1, $P < 0.05$), two variables that were uncorrelated in our sample ($r_p = -0.12$, $P = 0.37$). This model (LLR = 20.4, $P < 0.001$) predicted the presence/absence of rainbow trout with 73 and 58% accuracy, respectively. Considering only the 39 streams north of 42.8°, latitude alone entered a highly significant model (LLR = 46.4, $P < 0.0001$), which predicted rainbow trout presence/absence with 100% accuracy (Fig. 1). Among those same 39 streams watershed highpoint increases significantly with latitude ($r_p = 0.76$, $P < 0.001$) and alone produced a significant (LLR = 17.1, $P < 0.001$) but less accurate model (correct presence/absence, 86 and 64%, respectively).

Abundance

In the 38 streams with only one trout species, post-yearling brown trout were twice as abundant as rainbow trout [0.1 (0.09) vs. 0.04 (0.03), mean (SD); $t_{36} = 3.5$, $P = 0.001$]. In the 17 of these streams without post-yearling *Aplochiton*, the species were equally abundant [0.1 (0.09)-v-0.06 (0.04); $t_{15} = 1.2$, $P = 0.24$]. In the five streams with both trout

species, their post-yearling abundances did not differ ($t_4 = 0.7$, $P = 0.5$). The stepwise ANCOVA models on post-yearling abundance converged only for the analysis using PCA on the combined habitat–substrate data (Appendix S2). The final model explained 78% of the variation in post-yearling trout abundance and was dominated by the relationship between abundance and PC2 ($F_{1,33} = 68.1$, $P < 0.0001$), which explained 18% of variation in physical habitat. Post-yearling abundance was higher in narrow, steep streams with high amounts of cover (Fig. 2), a pattern that was more pronounced for brown than rainbow trout (species \times PC2, $F_{1,33} = 15.1$, $P < 0.001$). This model also revealed that controlling for the effects of physical habitat, brown trout was significantly more abundant than rainbow trout (species, $F_{1,33} = 12.7$, $P = 0.001$).

The distributions of rainbow and brown trout lengths were not different for larger (> 100 mm) fish, but for small fish (< 100 mm) rainbow trout (mean 74 mm) were significantly larger than brown trout (mean = 66 mm) ($K_{sa} = 4.03$, $P < 0.001$).

Effect

Aplochiton was less likely to be present in streams colonized by brown trout (3/10) than in streams colonized by rainbow trout (23/28) (Fisher's exact test, $P = 0.005$). This pattern was more pronounced considering only post-yearling

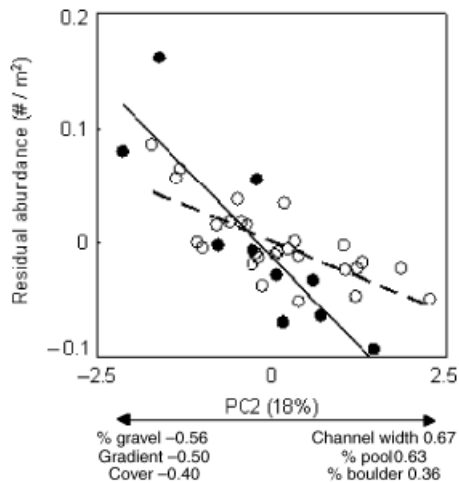


Figure 2 Variation in the abundance of post-yearling rainbow trout *Oncorhynchus mykiss* (○, dashed line) and brown trout *Salmo trutta* (●, solid line) in 38 single trout species streams in relation to variation in the scores along the second principal component axis summarizing variation in watershed/reach level habitat. The y-axis shows the residuals from the final ANCOVA model (Appendix S2) with PC2 removed. The x-axis shows the score along PC2 (summarizing 18% of the variation in physical habitat) and the habitat variables with the three most positive and negative loadings.

Aplochiton (0/10 vs. 21/28) ($P < 0.0001$); in total, only three *Aplochiton* YOY were found in the 10 streams colonized by brown trout.

North of 42.8°, the relative abundance of post-yearling *Aplochiton* and rainbow trout varied systematically with latitude (Fig. 3a; $r_s = -0.80$; $P < 0.0001$) and watershed highpoint (Fig. 3b; $r_s = 0.76$; $P < 0.0001$). The abundance of post-yearling *Aplochiton* did not differ between streams with (21) and without (11) rainbow trout ($t_{30} = 0.68$, $P = 0.5$), whereas rainbow trout was significantly more abundant in allopatry (7) than in sympatry (21) ($t_{26} = 0.68$, $P = 0.02$). For *Aplochiton*, stream gradient was the only habitat variable retained by the first pair of stepwise ANCOVA models and none were retained by the latter two pairs (Appendix S3). The residual *Aplochiton* abundances from the first model and two forced models including all available terms did not differ between streams with and without rainbow trout (all $t_{30} < 0.3$, $P > 0.5$).

In the 21 streams with post-yearling rainbow trout and *Aplochiton*, their abundances were similar ($t_{20} = 0.76$, $P = 0.5$) and unrelated to one another (Fig. 4a), latitude or watershed highpoint (all $|r_p| < 0.22$, $P > 0.3$). For the models using principal component scores of reach/watershed variables (Appendix S4), *Aplochiton* abundance increased in streams with low percentages of fines in their substrate (Substrate PC1, $F_{1,19} = 5.9$, $P < 0.05$) and rainbow trout abundance was higher in small, high-gradient streams with large amounts of cover (Habitat PC2, $F_{1,19} = 8.7$, $P < 0.01$). In models built from terms summarizing variation in all habitat and substrate variables, *Aplochiton* abundance was

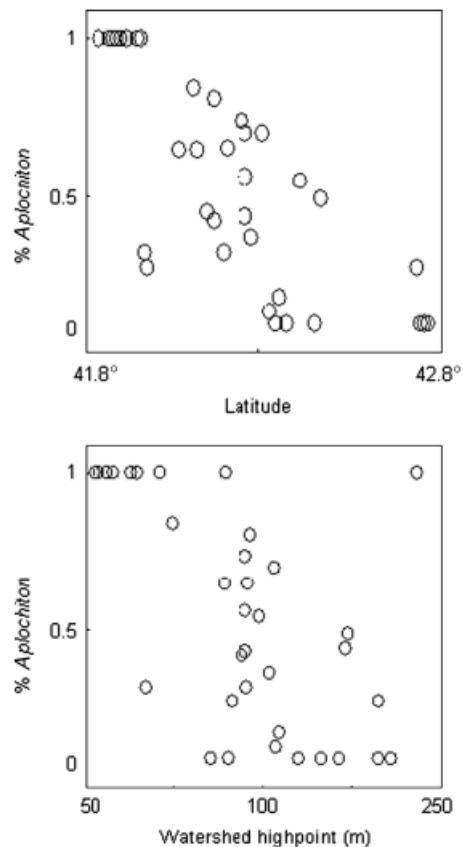


Figure 3 Variation in the proportion (# *Aplochiton*/(# *Aplochiton* + # rainbow trout)) of native *Aplochiton* among post-yearling fish captured in 39 streams north of 42.8°.

higher in steep, cobble substrate streams with low pool percentages, little cover and few fines (Fig. 4c; Total PC1, $F_{1,19} = 5.9$, $P < 0.05$), whereas rainbow trout abundance was higher in narrow, steep streams draining high elevation watersheds (Fig. 4d; Total PC4, $F_{1,19} = 7.1$, $P < 0.01$). The residuals from both pairs of models were negatively, but not significantly correlated (Fig. 4b; $|r_p| < 0.16$, $P > 0.4$).

Discussion

In small streams on the east side Chiloé island, the invasion biology of rainbow and brown trout differed in each of the three components of impact. Rainbow trout had colonized more streams over a wider latitudinal range, whereas brown trout appeared to be more abundant and have a stronger population-level effect on native *Aplochiton*.

Comparing the invasiveness of exotic species is facilitated by recognizing that a species' range depends on three ecological processes that link metapopulation dynamics with classic Grinnellian and Eltonian niche concepts (Pulliam, 2000; Guisan & Thuiller, 2005; Falk-Petersen, Bøhn & Sanderlund, 2006; Soberón, 2007). First, a species' dispersal ability determines the number of individuals arriving at habitat patches. Second, a species' physiology determines

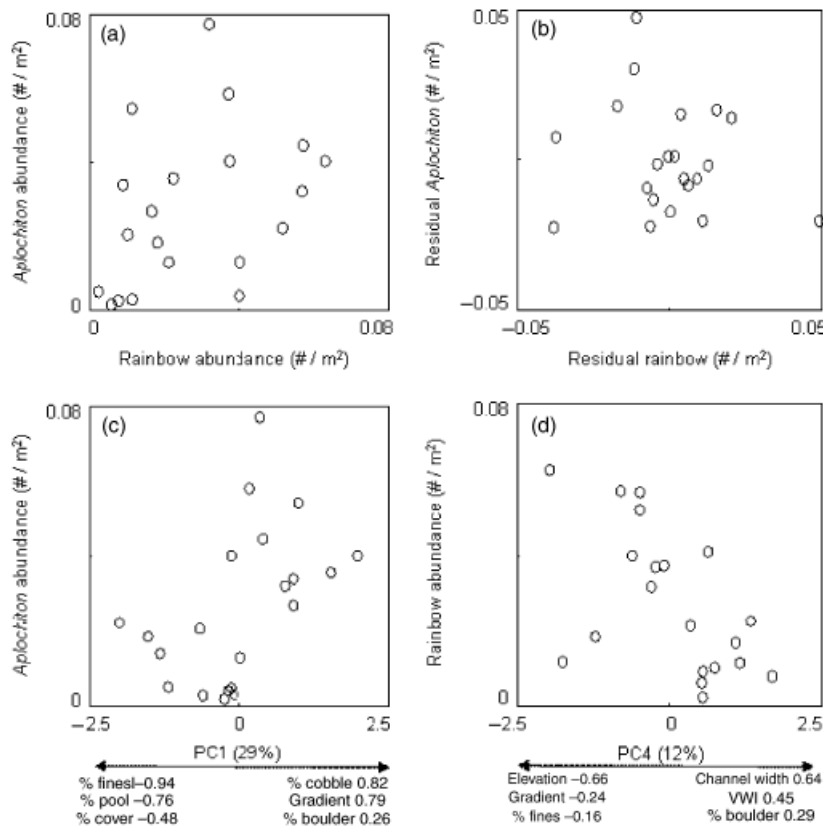


Figure 4 (a) Relationship between post-yearling rainbow trout *Oncorhynchus mykiss* and *Aplochiton* abundance in 21 sympatric streams north of 42.8°. (b) Relationship between the residual post-yearling abundances of rainbow trout and *Aplochiton* abundance in 21 sympatric streams north of 42.8° after accounting for the effects of watershed/reach level environmental variation on each species' abundance independently. (c) Relationship between post-yearling *Aplochiton* abundance and scores along the first principal component summarizing 29% of the variation in watershed/reach level environmental variation. Variables with the three most positive and negative loadings are shown below the axis. (d) Relationship between post-yearling rainbow trout abundance and scores along the fourth principal component summarizing 12% of the variation in watershed/reach level environmental variation. Variables with the three most positive and negative loadings are shown below the axis.

which patches have the environmental conditions (physical, thermal, chemical, etc.) that allow it to survive and reproduce (Grinnell, 1917). Finally, a species' ability to maintain a positive population growth rate depends in part on interactions with consumable resources, competitors, and predators (Elton, 1927).

Rainbow trout may be more invasive on Chiloé because it has dispersed to more streams than brown trout. Both species are facultatively anadromous in their native ranges and South America (L'Abée-Lund *et al.*, 1989; Pascual *et al.*, 2001; Quinn & Myers, 2004; O'Neal, 2008). In their native ranges, anadromous rainbow trout undertakes long-distance, multi-year migrations in the open ocean (Quinn & Myers, 2004), whereas anadromous brown trout migrations are limited to estuaries and coastal waters (Knutsen *et al.*, 2001; Rikardsen & Amundsen, 2005). If this pattern holds in Chiloé, brown trout might be less likely to colonize new (distant) streams via marine dispersal. The northern limit of brown trout on Chiloé is not associated with an abrupt change in any measured physical variable (Appendix S1a). It

does, however, coincide with an abrupt change from protected coast in the south to an open, unprotected coast to the north, a pattern consistent with brown trout being stocked in large southern rivers and colonizing small, nearby streams via estuarine/near-shore migration (Fig. 1).

Without information on historic stocking effort, we cannot rule out the possibility that rainbow trout is more widespread because of anthropogenic propagule pressure (i.e. a stocking bias favouring rainbow trout) (Lockwood, Cassey & Blackburn, 2005). Three observations lead us to believe that stocking bias alone is an insufficient explanation for our results. First, we sampled small, often remote, streams unlikely to be targeted for stocking (Appendix S1a). Second, north of 42.8° within and beyond our study area, brown trout occur in large rivers draining both west into the open ocean and east into the protected sea (unpubl. data). This observation suggests that it is unlikely that there was a cultural stocking bias against brown trout on the island. Third, in larger streams of mainland Patagonia, the species have similar ranges (Soto *et al.*, 2006), suggesting

that rainbow trout has not been favoured by a cultural stocking bias in Chile. Finally, we note that while our data cannot quantify the relative contributions of natural and anthropogenic propagule pressure to the observed range difference of rainbow and brown trout, their present ranges nevertheless contribute to their overall impact and provide a context for strategies to conserve native species.

Rainbow trout may be more invasive because it has a wider Grinnellian niche than brown trout. We consider it unlikely that differences in thermal tolerance explain the smaller range of brown trout. First, the species' thermal tolerances are similar (Beitinger, Bennett & McCauley, 2000). Second, there is no abrupt change in maximum elevation (which should affect the summer water temperature) at the brown trout range limit (Fig. 1, Appendix S1a). A decline in maximum elevation is, however, clearly related to the gradual transition from rainbow-dominated to *Aplochiton*-dominated communities north of 42.8° (Figs 1 and 3). The small, troutless streams of northern Chiloé drain low-elevation watersheds with upland peat bogs, suggesting some combination of high temperature, low pH and water chemistry places these streams outside the Grinnellian niche of salmonids (Olsson *et al.*, 2006).

Finally, it is possible that biotic interactions contribute to the observed range difference. First, there may be a colonization 'priority effect', whereby the presence of one species (rainbow trout) reduces the likelihood that heterospecific individuals will enter the stream. It is well documented that salmonids and other fishes are attracted to conspecific odour (Quinn, 1993; Baker & Hicks, 2003), but the degree to which they are repelled by heterospecific odour is unknown. Second, interspecific interactions may prevent one species from maintaining a positive population growth rate. Studies of competitive interactions between rainbow and brown trout have yielded mixed results, but suggest competitive exclusion by rainbow trout is an unlikely explanation for the restricted range of brown trout in Chiloé (Gatz, Sale & Loar, 1987; Hayes, 1989; Kocik & Taylor, 1994, 1995, 1996; Blanchet *et al.*, 2007).

That post-yearling abundances of both exotic species were higher in steep, narrow streams with abundant cover is consistent with decades of research on stream-rearing salmonids. Steeper channels have more habitat units per linear metre, and thus a higher percentage optimal habitat (i.e. heads of pools), and narrower channels have a higher proportion of habitat with bank cover. We suggest the finding that brown trout was more abundant after controlling for variation in physical habitat is the result of its narrower range. Overall rainbow trout abundance may be lower because it has invaded increasingly suboptimal habitat patches in the north of the island where it shares the physical habitat and consumable resources with *Aplochiton*. This explanation is consistent with the fact that the abundances of the exotic trout were the same in sympatry, and in allopatry for streams without post-yearling *Aplochiton*.

Our results suggest that brown trout has a more negative effect on *Aplochiton* populations and quantitatively confirm a longstanding qualitative consensus among salmonid inva-

sion biologists. McDowall, Allibone & Chadderton (2001) documented a similar pattern in the Falkland Islands, where *A. zebra* rarely occurred in streams colonized by brown trout (rainbow trout is absent in the Falklands). Given brown trout's proclivity for piscivory and that competition with exotics is rarely implicated in native animal extinctions (Gurevitch & Padilla, 2004; Sax & Gaines, 2008), it is logical to credit predation for the near absence of *Aplochiton* in streams colonized by brown trout. Brown trout is consistently more piscivorous than rainbow trout in Patagonian lakes (Macchi *et al.*, 1999; Milano *et al.*, 2002), but we know of no similar data for streams. Potentially piscivorous (>100) brown trout were no larger than rainbow trout, suggesting a size-dependent difference in piscivory is an unlikely explanation for the apparent difference in effect. Competitive interactions may also contribute to the difference in the effect observed. Hasegawa *et al.* (2004) studied pair-wise interactions in the laboratory and found that brown trout outcompeted two native charr (*Salvelinus* spp.) species while rainbow trout outcompeted only one.

Our conclusion that brown trout has a more negative effect depends on the mechanism responsible for the rainbow trout–*Aplochiton* abundance gradient north of 42.8° (Figs 1 and 3). If the gradient reflects a slowly advancing rainbow invasion front from the south, streams at the southern end may reflect the eventual fate of *Aplochiton* in streams invaded by rainbow trout – local extirpation. Alternatively, the gradient may be temporally stable, with relative abundances of each patch fluctuating around a value determined by an environmentally mediated combination of demographic stochasticity, intraspecific density dependence, interspecific interactions, immigration and emigration (With, 2002; Adler, HilleRisLambers & Levine, 2007). Identifying the processes responsible for the pattern we observed will require monitoring the population vital rates of both species in multiple streams along the gradient (Peterson & Fausch, 2003; Peterson, Fausch & White, 2004).

Given that the processes responsible for the patterns we observed are incompletely understood, how can our results inform conservation strategies for native fishes in Chiloé and elsewhere? Our most striking finding is that in small streams *Aplochiton* appears more able to coexist with rainbow than brown trout. The immediate priority should be to prevent introductions, particularly of brown trout, to uninvaded streams (in Chile, stocking exotic trout into troutless waters is prohibited by a poorly communicated and weakly enforced law). It may also be possible to remove exotic trout from some streams (e.g. Peterson *et al.*, 2004), providing source populations from which *Aplochiton* might recolonize neighbouring patches. Surveys of fish communities above migration barriers, in larger streams, and in lakes will provide a broader perspective on where *Aplochiton* and other native species persist on the island. Finally, more observational and experimental work on the autecology of native species is needed. There is little information on the dispersal ability of native species or how physical and biological conditions, particularly the presence of exotic trout, affect the chance of colonization and persistence.

We conclude by encouraging those working on invasive salmonids to conduct similar comparative studies of impact in other areas, and those studying other exotic species to adopt the framework of Parker *et al.* (1999) and collect and analyse data to distinguish between the different components of impact.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1a. Means (standard deviations) of survey lengths and eleven habitat variables measured for each of the 54 study streams. For disturbance we give the proportion of streams with visible evidence of riparian disturbance (mostly cattle). For riparian it is the proportion of streams with closed/partial canopy riparian zones rather than pasture/grassland. The final three columns 'Sub. PC1-3' summarize variation in the scores along the first three axes of a principal components analysis conducted on the correlation matrix of the percent substrate in each of four categories: fines, gravel, cobble and boulder.

Appendix S1b. Bivariate Pearson correlation coefficients among the 11 continuous variables measured in the 54 study streams. Those significant at the uncorrected $\alpha = 0.05$ are in bold. The final three columns 'Sub. PC1-3' summarize variation in the scores along the first three axes

of a principal components analysis conducted on the correlation matrix of the percent substrate in each of four categories: fines, gravel, cobble and boulder.

Table S2a. Analysis of Covariance on the abundance of **post-yearling trout** captured per square metre surveyed for 38 streams where rainbow and brown trout occurred in allopatry. The table shows the final model selected following the forward and backward stepwise (entry/removal $P = 0.05$) assessment of 25 terms: three class (species (rainbow, brown), disturbance (cattle/erosion, none), riparian (forest, grassland)), ten continuous environmental variables (watershed area, watershed high point, channel width, channel gradient, valley width index (= valley width/channel width), pool percentage, total fish cover, PC1-3 scores summarizing variation in substrate), and all twelve first order interaction terms involving species. The final model includes terms that were retained by both forward and backward stepwise models.

Table S2b. Analysis of Covariance on the abundance of **post-yearling trout** captured per square metre surveyed for 38 streams where rainbow and brown trout occurred in allopatry. The table shows the final model selected following the forward and backward stepwise (entry/removal $P = 0.05$) assessment of 25 terms: three class (species (rainbow, brown), disturbance (cattle/erosion, none), riparian (forest, grassland)), ten continuous environmental variables (watershed area, watershed high point, channel width, channel gradient, valley width index (= valley width/channel width), pool percentage, total fish cover, PC1-3 scores summarizing variation in substrate), and all twelve first order interaction terms involving species. The final model selected by including terms that were retained by both forward and backward stepwise models.

Table S2c. Analysis of Covariance on the total number of **post-yearling trout** captured per square metre surveyed for 38 streams where rainbow and brown trout occurred in allopatry. The table shows the final model selected following the forward/backward stepwise (entry/removal $P = 0.05$) assessment of 13 terms: three class (species (rainbow, brown), disturbance (cattle/erosion, none), riparian (forest, grassland)), four continuous (scores of four PC axes summarizing variation in reach level habitat and substrate), and all six first order interaction terms involving species. The same model was selected using a backward stepwise procedure, so this is also the final overall model.

Table S3a. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 32 streams north of latitude 42.8° S. The table shows the final model selected following forward and backward stepwise (entry/removal $P = 0.05$) assessment of 12 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)), and ten continuous environmental variables (watershed area, watershed high point, channel width, channel gradient, valley width index (= valley width/channel width), pool percentage, total fish cover, PC1-3 scores summarizing variation in substrate). The table shows the final model selected by including terms that were retained by both stepwise models.

Table S3b. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 32 streams north of latitude 42.8° S. The table shows the final model selected following forward and backward stepwise (entry/removal $P = 0.05$) assessment of 9 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)), and seven continuous (scores of four PC axes summarizing variation in reach level habitat, PC1-3 scores summarizing variation in substrate). No terms were retained by either stepwise procedure. The table shows the model including all the terms available to enter.

Table S3c. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 32 streams north of latitude 42.8° S. The table shows the final model selected following forward and backward stepwise (entry/removal $P = 0.05$) assessment of 6 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)) and four continuous (scores of four PC axes summarizing variation in reach level habitat and substrate) variables. No terms were retained by either stepwise procedure. The table shows the model including all the terms available to enter.

Table S4a. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The table shows the final model selected following the **forward stepwise** (entry/removal $P = 0.05$) assessment of 12 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)), and ten continuous environmental variables (watershed area, watershed high point, channel width, channel gradient, valley width index (= valley width/channel width), pool percentage, total fish cover, PC1-3 scores summarizing variation in substrate).

Table S4b. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The table shows the final model selected following the **backward stepwise** (entry/removal $P = 0.05$) assessment of 12 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)), and ten continuous environmental variables (watershed area, watershed high point, channel width, channel gradient, valley width index (= valley width/channel width), pool percentage, total fish cover, PC1-3 scores summarizing variation in substrate).

Table S4c. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The step-wise models retained no term in common.

Table S4d. Analysis of Covariance on the total number of **post-yearling rainbow** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The table shows the final model selected following the **forward stepwise** (entry/removal $P = 0.05$) assessment of 12 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)), and ten

continuous environmental variables (watershed area, watershed high point, channel width, channel gradient, valley width index (= valley width/channel width), pool percentage, total fish cover, PC1-3 scores summarizing variation in substrate).

Table S4e. Analysis of Covariance on the total number of **post-yearling rainbow** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The table shows the final model selected following the **backward** (entry/removal $P = 0.05$) assessment of 12 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)), and ten continuous environmental variables (watershed area, watershed high point, channel width, channel gradient, valley width index (= valley width/channel width), pool percentage, total fish cover, PC1-3 scores summarizing variation in substrate).

Table S4f. Analysis of Covariance on the abundance of **post-yearling peladilla** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The step-wise models retained no term in common.

Table S4g. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The table shows the final model selected following forward and backward stepwise models (entry/removal $P = 0.05$) assessment of 9 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)) and seven continuous (scores of four PC axes summarizing variation in reach level habitat, PC1-3 scores summarizing variation in substrate) variables. The same model was selected by both stepwise procedures.

Table S4h. Analysis of Covariance on the total number of **post-yearling rainbow** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The table shows the final model selected following forward and backward stepwise models (entry/removal $P = 0.05$) assessment of 9 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)) and seven continuous (scores of four PC axes summarizing variation in reach level habitat, PC1-3 scores summarizing variation in substrate) variables. The same model was selected by both stepwise procedures.

Table S4i. Analysis of Covariance on the total number of **post-yearling peladilla** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling peladilla and rainbow trout. The table shows the final model selected following forward and backward stepwise models (entry/removal $P = 0.05$) assessment of 7 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)) and scores of five PC axes summarizing variation in reach level habitat and substrate. The same model was selected by both stepwise procedures.

Table S4j. Analysis of Covariance on the total number of **post-yearling rainbow** captured per square metre surveyed for 21 streams north of latitude 42.8° S with post-yearling

peladilla and rainbow trout. The table shows the final model selected following forward and backward stepwise models (entry/removal $P = 0.05$) assessment of 7 terms: two class (disturbance (cattle/erosion, none), riparian (forest, grassland)) and scores of five PC axes summarizing variation in reach level habitat and substrate. The same model was selected by both stepwise procedures.

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