

The diversity of juvenile salmonids does not affect their competitive impact on a native galaxiid

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Abstract We used an invaded stream fish community in southern Chile to experimentally test whether the diversity of exotic species affects their competitive impact on a native species. In artificial enclosures an established invasive, rainbow trout, *Oncorhynchus mykiss*, and a potential invader, Atlantic salmon, *Salmo salar*, reduced the growth rate of native peladilla, *Aplochiton zebra*, by the same amount. In enclosures

with both exotic salmonids, the growth rates of all three species were the same as in single exotic treatments. While neither species identity nor diversity appeared to affect competitive interactions in this experiment, the impact of salmonid diversity may vary with the type of interspecific interaction and/or the species identity of the exotics. Our experiment links two prominent concepts in invasion biology by testing whether the result of invasional meltdown, an increase in the diversity of exotic species, affects their impact through interspecific competition, the mechanism invoked by the biotic resistance hypothesis.

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Introduction

In his classic text Elton (1958) proposed that a community's resistance to invasion should increase with native species diversity. Motivated primarily by the observation that species poor island communities appear particularly susceptible to invasion, this prediction formally linked the science of invasion biology to community ecology, niche theory and the emerging principles of limiting similarity and competitive exclusion (MacArthur and Levins 1967; Roughgarden 1983; Case 1990; Chesson 2000). Fifty

years later this connection serves to highlight a complimentary and conceptually identical prediction: an increase in the diversity of exotic species should increase their negative impact on native species. Regardless of a species' identity as exotic or native, persistence in a community requires maintaining a positive population growth rate when rare, a condition which should become increasingly difficult as the number of ecologically similar competitors increases (Shea and Chesson 2002).

Despite evidence from a range of competitive communities that native species diversity can impede invasion (Fridley et al. 2007), how the diversity of exotic species affects their competitive impact on native species remains less well studied (Simberloff 2006). Moreover, the relationship between exotic diversity and competitive impact may not be as clear as it first appears. Consider an idealized community of two species, one native and one exotic, where competitive interactions affect the populations' vital rates. If the species are competing for limiting consumable resources and/or habitat, the establishment of a second ecologically similar exotic species will by requirement reduce the population growth rate of the native and/or established exotic. If not, the new exotic species would be sufficiently different from the two existing members that competition theory does apply and the prediction is irrelevant. Because competition theory assumes no two species are ecologically identical, the addition of a second exotic will likely increase the number of total individuals in the community, making it difficult to isolate the effect of diversity per se. The more precise question from the perspective of a rare native species is whether, for a fixed number of exotic individuals, the competitive impact of exotic organisms varies with their species diversity? Depending on the strength of density dependent intra- and inter-specific interactions, and potentially positive indirect effects, increasing exotic diversity may have a negative, positive or no impact on the native species (Levine 1976; Stone and Roberts 1991).

Motivated by this uncertainty and the need to obtain data on the potential impacts of exotic salmonid aquaculture on native fishes, we conducted an experiment using an invaded stream fish community in southern Chile to test the hypothesis that the diversity of exotic species affects their competitive impact on a native species.

Methods

Study system

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 containing a handful of native species and two widespread exotic salmonids, rainbow trout, *Oncorhynchus mykiss*, from western North America and brown trout, *Salmo trutta*, from Europe (Cussac et al. 2004; Soto et al. 2006; Leprieur et al. 2008). There is compelling evidence these same two exotic species have negatively impacted native fish communities in Australasia directly through competition and predation, and indirectly through altering stream food webs (McDowall 2006). In Patagonia, however, interactions between exotic salmonids and native fish remain poorly studied (Pascual et al. 2002, 2007; Soto et al. 2006). In the past 20 years marine net pen aquaculture of exotic salmonids has grown exponentially in southern Chile (Munoz 2006). The industry is based principally on Atlantic salmon, *S. salar*, with coho salmon, *O. kisutch*, and *O. mykiss* together accounting for less than half of production. Escapees from freshwater and marine facilities can breed in the wild and have the potential to establish populations in communities already containing one or more exotic salmonid (Volpe et al. 2000; Naylor et al. 2005; Thorstad et al. 2008).

On the central east coast of the Grand Island of Chiloé (S 41°45'–42°45') the communities of first to third order streams draining into the ocean are dominated by *O. mykiss* (*S. trutta* is absent) and peladilla, *Aplocheilichthys zebra*. *A. zebra* is a native galaxiid drift feeder whose life history, population biology, and geographic distribution are poorly understood (McDowall and Nakaya 1988; Cussac et al. 2004). The two species have similar body shapes and follow the typical ontogenetic niche shifts of stream rearing salmonids: newly hatched fry use shallow/low-velocity edge water, young-of-year (YOY) and 1-year-old (1+) fish predominate in shallow riffles, and older fish occupy deeper runs and pools (Young et al. unpublished data). The protected waters of the Chiloé archipelago have one of the highest concentrations of

marine net pen aquaculture facilities in Chile (Munoz 2006) and we have found adult escapees of all three farmed species in area streams.

Experimental design and analysis

We designed an experiment to test if the species identity and diversity of exotic salmonids affect their competitive impact on *A. zebra* during the juvenile stage. The experiment was conducted in a gravel-cobble (gradient 1.5%) reach of an unnamed second order stream with sympatric populations of *O. mykiss* and *A. zebra* (42°09' S, 73°28' W). We placed twenty enclosures (1" PVC frame, 1 m², 80 cm height, 6 mm mesh size) in riffles and shallow runs in the first 200 m of the stream above high tide. Zimmerman and Vondracek (2006) showed that such enclosures do not significantly reduce invertebrate drift rates or growth rates of YOY salmonids. Enclosures were installed on 25 January, 2008 by securing a 1 m² PVC template with one corner upstream and removing the gravel/cobble substrate to create a flat surface on which to place the enclosure. We filled the enclosures with natural substrate to the same level as the adjacent channel, making sure each had sufficient cobble to provide cover for juvenile fish. We measured the five largest substrate particles (cm), and the depth (cm) and velocity (m/s) at the same five locations within each enclosure and quantified physical habitat using

the means and coefficients of variation of these three variables (Table 1).

Fish were placed in the enclosures on 1 February. We collected 1+ *A. zebra* and YOY *O. mykiss* from a nearby stream (10 km) with sympatric populations. There are as yet no documented breeding populations of *S. salar* in Chile so we collected juveniles from below an aquaculture hatchery in a different nearby stream (2 km). Given their location and high density, we suspect these fish were escapees from the hatchery. Fish were transported periodically to the experimental site and held in live wells until being placed in the enclosures. The experiment had four treatments: two *A. zebra*, two *A. zebra* plus four *O. mykiss*, two *A. zebra* plus four *S. salar*, two *A. zebra* plus two *O. mykiss* and two *S. salar*. Canopy cover decreased and water temperature increased (by a maximum of 2°C in the afternoon on clear days) from the top to bottom of the experimental reach. The treatments were thus randomly assigned to enclosures in five groups of four beginning at the river mouth.

Fish were individually marked using adipose or small pelvic fin clips (*A. zebra* has an adipose fin) and their fork length (mm) and weight (0.1 g) recorded. At the beginning of the experiment *O. mykiss* were significantly smaller than *A. zebra* and *S. salar*, but the lengths and weights of each species were similar across the four (*A. zebra*) or two (*O. mykiss* and *S. salar*) treatments (Table 1). The size difference

Table 1 Means and 95% CIs for habitat variables (all $F_{3,16} < 2$, $P > 0.15$) and initial fish lengths and weights in the four experimental treatments

	Treatment			
	2 <i>A. zebra</i>	2 <i>A. zebra</i> + 4 <i>O. mykiss</i>	2 <i>A. zebra</i> + 4 <i>S. salar</i>	2 <i>A. zebra</i> + 2 <i>O.m.</i> + 2 <i>S.s.</i>
Substrate size (cm)	19.9 (19.1–20.6)	19.9 (19.0–20.7)	19.9 (19.3–20.5)	19.8 (18.9–20.7)
C.V. of substrate size	0.19 (0.12–0.26)	0.17 (0.11–0.23)	0.15 (0.09–0.21)	0.15 (0.10–0.19)
Depth (cm)	11.2 (8.7–13.7)	11.4 (9.9–12.8)	11.0 (9.1–12.9)	12.0 (11.1–12.9)
C.V. of depth	0.14 (0.08–0.20)	0.20 (0.09–0.31)	0.16 (0.08–0.24)	0.15 (0.10–0.20)
Velocity (m/s)	0.17 (0.12–0.21)	0.16 (0.08–0.23)	0.18 (0.14–0.22)	0.14 (0.13–0.16)
C.V. of velocity	0.37 (0.26–0.49)	0.44 (0.08–0.81)	0.39 (0.22–0.56)	0.43 (0.33–0.54)
<i>A. zebra</i> length (mm)	65.5 (62.1–68.9)	66.4 (63.9–68.8)	67.3 (64.6–69.9)	66.2 (62.6–69.8)
<i>A. zebra</i> weight (g)	3.1 (2.4–3.7)	2.9 (2.4–3.5)	2.9 (2.5–3.5)	2.9 (2.4–3.5)
<i>O. mykiss</i> length (mm)	NA	58.8 (56.5–60.9)	NA	61.2 (58.4–63.9)
<i>O. mykiss</i> weight (g)	NA	2.4 (2.2–2.7)	NA	2.8 (2.4–3.3)
<i>S. salar</i> length (mm)	NA	NA	64.0 (61.7–66.3)	68.3 (66.0–70.6)
<i>S. salar</i> weight (g)	NA	NA	3.2 (2.8–3.6)	3.9 (3.5–4.4)

NA, not applicable

between 1+ *A. zebra* and YOY *O. mykiss* was typical for area streams and that between *S. salar* and *O. mykiss* in the direction expected because the species spawn in the fall and spring, respectively, so *S. salar* fry would emerge earlier and have a size advantage in sympatry (Volpe et al. 2000; Bisson 2006). During the experiment we cleaned the enclosures and checked for mortalities 3–6 times per week depending on flow and litter loads. Five *A. zebra* died during the experiment (one in a two *A. zebra* treatment and four in exotic treatments, similar to the 1:3 ratio of the treatments) and were replaced using similar sized fish with the same mark. Fish were removed from the enclosures after 39 days. For each fish we calculated two measures of specific daily growth rate: final length(weight) – initial length(weight)/(number of days in enclosure). We present results based on length but conducted all statistical tests using both measures of growth. The independent unit of observation in this experiment is the mean specific daily growth rate of each species in each enclosure. For enclosures where fish were replaced, we use the average growth rate of the original and replacement. Seven days before the end of the experiment a high flow event moved one enclosure onto a gravel bar; this enclosure was emptied a week early and growth rates calculated accordingly. Two enclosures (four *O. mykiss* and four *S. salar* treatments) apparently suffered from bird predation, leaving 18 enclosures for analysis.

Our experiment was not designed to test whether exotic salmonids compete with *A. zebra*. Our goal was to induce competitive interactions between *A. zebra* and salmonids in order to test whether the identity and/or diversity of exotic species affect their impact on *A. zebra*. By holding *A. zebra* density constant, variation in its growth rate across treatments can be attributed to the presence, identity and diversity of exotic salmonids. We confirmed that the presence of salmonids induced a competitive impact by comparing the growth rate of *A. zebra* alone ($n = 5$) and in the presence of salmonids ($n = 13$). To test the hypothesis that exotic identity affected this impact we compared the growth rate of *A. zebra* in the presence of *O. mykiss* ($n = 4$) and *S. salar* ($n = 4$). We tested the hypothesis that exotic diversity affected competitive impact by comparing the growth rate of *A. zebra* in the presence of one ($n = 8$) and two salmonid species ($n = 5$). We used two tailed t -tests for all comparisons.

Results

The presence of salmonids reduced the growth rate of *A. zebra* by over 50% (length: $t_{16} = 4.1$, $P = 0.001$; weight: $t_{16} = 2.4$, $P = 0.03$), confirming that our exotic treatments successfully induced a negative impact from interspecific competition (Fig. 1). This impact did not, however, depend on the identity (length: $t_6 = 0.29$, $P = 0.78$; weight: $t_6 = 0.75$; $P = 0.48$) or diversity (length: $t_{11} = 0.84$, $P = 0.42$; weight: $t_{11} = 0.82$, $P = 0.41$) of exotic salmonids. Despite being stocked at twice the density of *A. zebra* in the exotic treatments, *O. mykiss* grew three times, and *S. salar* twice, as fast as did *A. zebra* in the absence of salmonids. The growth rates of the salmonids did not differ between the single and two species exotic treatments (length: $t_7 < 0.4$, $P > 0.7$; weight: $t_7 < 0.9$; $P > 0.4$). Together, these results suggest neither exotic species identity nor diversity affected the impact of competition on the growth of any of the three species in our experimental enclosures.

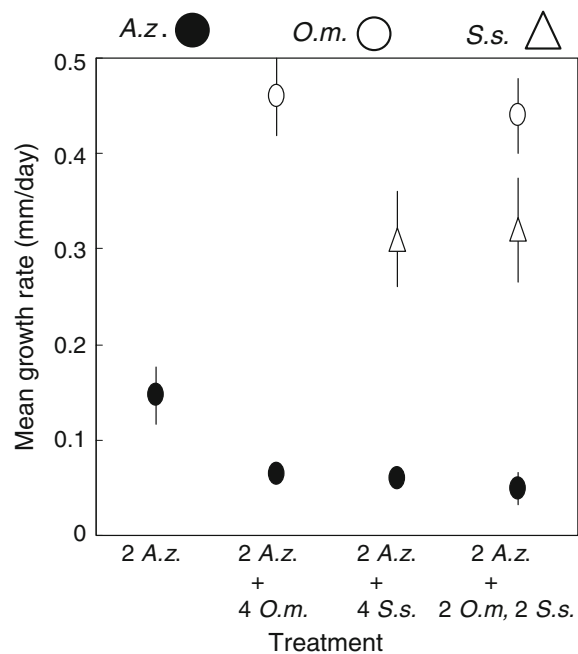


Fig. 1 Growth rates (\pm SE) of the three species in the four experimental treatments. Each point is the mean of the cage means of individually marked fish. A.z.—*Aplochiton zebra*, O.m.—*Oncorhynchus mykiss*, S.s.—*Salmo salar*

Discussion

Experimentally induced competition with exotic salmonids reduced the growth rate of *A. zebra*, but neither exotic species identity nor diversity affected the magnitude of this impact. Furthermore, the growth rates of salmonids were not affected by the replacement of conspecific by heterospecific competitors across the three exotic treatments. To the degree variation in juvenile growth affects individual survival and population growth rates of *A. zebra* in streams with *O. mykiss* populations, our results suggest increasing exotic species diversity through the partial replacement of *O. mykiss* by *S. salar* may have little impact on native *A. zebra*.

Extending the results of controlled experiments to natural conditions is inherently uncertain and we highlight two caveats. The first is that our experiment tested how exotic diversity impacts a native species through a single mechanism during a single life stage; competition among juveniles. Obviously, the impact of exotic diversity may differ with life stage and/or mechanism. For example, the presence of *S. salar* juveniles may provide a prey subsidy to adult *O. mykiss*, increasing their density, and thus their predation rate and impact on *A. zebra*. Second, our experiment controlled for exotic abundance while increasing exotic diversity. While it is unrealistic to expect that the addition of ecologically similar exotic will not reduce the density of existing community members, it is also unlikely that any two species will be perfectly replaceable at the population level. As a result, an increase in exotic diversity would be accompanied by an increase in the total number of exotic individuals. An alternative diversity treatment, for example three *O. mykiss* and three *S. salar*, may have elicited an effect, but the confounding increase in exotic density would make it impossible to attribute that effect to exotic diversity.

In addition to testing the compliment of Elton's biotic resistance hypothesis, our results are relevant to two other outstanding hypotheses in invasion biology. The first is the prediction that an exotics' impact should increase with its taxonomic distinctiveness relative to the invaded community (Diamond and Case 1986; Riccardi and Atkinson 2004). This prediction is based on two basic evolutionary principals: that interacting species co-evolve to reduce to negative impacts of interspecific competition

(Futuyma and Slatkin 1983), and that taxonomic proximity is related to ecological similarity (Webb et al. 2002). Extended to multiple invasions, these principles predict the impact of an additional exotic should increase with its taxonomic distance from established exotics. This extension ignores, however, the coevolutionary history of the exotics. In our experiment the heterogeneric exotics do not share a recent co-evolutionary history and have broadly similar habitat preferences as subyearlings (Hearn and Kynard 1988). Despite behavioral differences between the species (Volpe et al. 2001) in our experiment juvenile *O. mykiss* and *S. salar* appeared replaceable in their competitive impact on each other and a native species.

We used *O. mykiss* and *S. salar* because the former is widespread throughout Chilean Patagonia and the latter is the most common species used in aquaculture. From the perspective of stream fish communities, the colonization by *S. salar* of streams containing *O. mykiss* represents one likely result of exotic aquaculture. It is possible that replacing *S. salar* with *O. kisutch* or *S. trutta*, which use different microhabitats and behave differently than the congenics with which they have co-evolved (Hartman 1965; Armstrong et al. 2003; Young 2003, 2004), may differentially affect the competitive impact of exotic species diversity on *A. zebra*. The fact that competitive co-evolution can make taxonomic proximity a poor predictor of ecological similarity (Losos et al. 2003) highlights the need to consider both factors when predicting the impact of multiple invasions. With two widespread invasive salmonids and the possibility that exotic aquaculture will drive additional invasions by species from both genera, the fish communities of Chilean Patagonia provide an ideal system to investigate how taxonomic proximity and coevolutionary history interact to influence the impact of exotic species diversity on native species.

In an influential paper Simberloff and Von Holle (1999) conducted a literature review to introduce the idea of 'invasional meltdown', the process by which facilitative and mutualistic interactions between established and new exotic species facilitate further invasions. The hypothesis has been made popular as an alternative to the biotic resistance hypothesis originally proposed by Elton (Riccardi 2001). We suggest our experiment bridges this conceptual dichotomy by highlighting the distinction between

invasion, the establishment and spread of an exotic, and the per-capita effect of that exotic on native species (Parker et al. 1999). The invasional meltdown hypothesis proposes that exotic diversity increases invasibility but makes no mechanistic prediction about how the diversity of exotics affects their impact on native species (Simberloff and Von Holle 1999; Simberloff 2006). Though the concept of biotic resistance is commonly framed in the context of a community's resistance to invasion, because it invokes competitive interactions between native and exotic species, its prediction implicitly extends to the impact of exotic species on members of the native community (Shea and Chesson 2002). Our experiment thus bridges these two concepts by testing whether the result of invasional meltdown, an increase in the diversity of exotic species, affects their impact through competition, the same mechanism invoked by the biotic resistance hypothesis.

Considerable progress has been made in generalizing how the traits of exotic fish and the characteristics of aquatic ecosystems interact to regulate the establishment and spread of exotic species (Moyle and Light 1996; Kolar and Lodge 2001; Marchetti et al. 2004; Olden et al. 2006). This progress has been possible because that invasion success is necessarily determined first by interactions between introduced species and the physical characteristics of the receiving environment (Mack et al. 2000). It is more difficult to predict the impacts of invasive species because they will typically result from various types of ecological interactions between numerous species. Using controlled experiments like the one reported here is one promising approach for identifying how different mechanisms affect the relationship between exotic species diversity and impact on native species.

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