Impacts of invasive stream salmonids on native fish: using meta-analysis to summarize four decades of research

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Salmonid fishes are among the most frequently introduced organisms. We included 58 papers to meta-analysis to assess the effects of introduced stream salmonids on native salmonids. We also explored whether the responses of native species depended on the type of study. Introduced salmonids had negative effects on the foraging rate, abundance and survival of native salmonids, which also altered their habitat use in the presence of invaders. Brown trout appeared to be the ‘worst’ alien species (strongest impact on native fish). Negative effects were most pronounced when several introduced species were present. Moreover, the magnitude of the impact was related to the study type: the observed impacts were stronger in laboratory streams than in field enclosures or in natural streams. Our results indicate that introduced salmonid species may have little effect on native fish in some areas, but may have substantial effects in other parts of their range.

Introduction

Introduction and establishment of species beyond their natural ranges is one of the major threats to biodiversity, being second only to habitat loss and fragmentation (Sala et al. 2000). Although the impacts of alien species on recipient ecosystems and native organisms are often negative, not all introductions are detrimental; in fact, Williamson (2006) suggested that only a minor portion of species introductions are likely to cause detectable changes to native ecosystems. Exotic species also provide a unique opportunity to understand ecological and evolutionary processes at relevant spatial and temporal scales (Sax et al. 2007). It is therefore a great challenge to conservation biologists to distinguish \textit{a priori} introductions that are likely to be detrimental to native biodiversity.

Because of their economical and societal value, stream-dwelling salmonids are among the most frequently introduced fish species, being now established on many continents (Rahel 2007). Outside their native ranges, salmonids have had harmful effects on native ecosystems, including agonistic behaviour towards, and hybridization with, the native species, and population fragmentation and decline of the natives. Furthermore, community-wide impact of introduced salmonids that alter not only freshwater,
but also riparian ecosystems, have been reported (Simon and Townsend 2003, Baxter et al. 2004). Due to multiple adverse effects, two of the salmonid species — brown trout (Salmo trutta) and rainbow trout (Oncorhynchus mykiss) — rank among the eight fish species included in the list of 100 of the world’s worst invasive alien species (Lowe et al. 2000). Therefore, fisheries managers around the world have launched extensive management programs to control salmonid invasions, and possibly eradicate already established populations, with the aim of conserving native fish populations (Novinger and Rahel 2003, Jackson et al. 2004, Finlayson et al. 2005).

The impacts of alien salmonids on native fish have a long history of scientific documentation, yet only a few papers have attempted to identify general patterns in salmonid invasions (but see Krueger and May 1991, Dunham et al. 2002, Fausch 2008, Korsu et al. 2008). Even these few are narrative and somewhat case-specific, and are not focused on the detection of general impacts of alien salmonids on native fish, particularly other salmonids. Therefore, the mechanisms facilitating invasions, and potentially resulting in the reduction of regional distinctiveness and loss of native biota, are not well understood. Two major mechanisms that have been proposed are: (i) niche pre-adaptations facilitates invaders’ establishment in their introduced ranges (e.g. Fausch et al. 2001, Korsu et al. 2007); and (ii) invaders displace native salmonids through aggressive behaviour (e.g. DeWald and Wilzbach 1992, Wang and White 1994).

Here, we use a meta-analysis to quantify the impacts of alien salmonids on their native counterparts. We summarize the effects of introduced salmonids on the behaviour, habitat use, foraging, growth, survival, and abundance of native salmonids, comparing the responses of native species in allopatri to those in sympatry with the introduced species. Because the presence of multiple invaders tends to weaken the biotic resistance of the recipient system (Hewitt and Huxell 2002), we also examined whether the magnitude of the impact was greater when several species were introduced. Moreover, we examined whether the three most extensively introduced salmonids — brown trout, brook trout (Salvelinus fontinalis) and rainbow trout — differ in their impacts on native salmonids. Finally, because patterns may be greatly modified by the scale of observations (e.g. Underwood et al. 2005), we explored whether the responses of the native species to invader presence differed between studies conducted at widely variable spatial scales and using different methodological approaches (laboratory channels, fish enclosure designs and field studies). We hypothesized that studies forced to restricted spatial scales could intensify interspecific interactions, reducing the native species’ performance and potentially resulting in stronger effect sizes.

Material and methods

We used a meta-analysis to assess the general effects of introduced stream salmonids on the vital rates, behaviour and habitat use of native salmonids. We conducted a thorough literature search on studies published between 1970 and January 2008 using ASFA (Aquatic Sciences and Fisheries Abstracts) and Google Scholar™, supplemented with our own reference collections. We also added our own unpublished material to this data set which thus comprised 58 studies (Table 1). We divided the studies in six groups based on the response variables measured: aggression, habitat use, foraging, growth, survival, and abundance. We further divided the habitat use data according to the five most frequently measured responses: use of stream pools, focal position (vertical distance from stream bed), and use of cover, depth, and water velocity. In a majority of experimental studies, fishes were of similar size and age (mostly age-0 or age-1) or reflected the size structure in the field during the experiment (e.g. Taniguchi et al. 2002). Since a preliminary analysis indicated no age-related differences in response variables, we did not consider fish age in further analyses.

We included all studies that provided (i) an estimate of the mean and (ii) the number of replicates in both sympatric and allopatri situations. The number of aggression was usually measured only in sympatric (alien vs. native) trials to test whether agonistic acts were targeted mainly toward the native species. In this subset,
Table 1. The list of studies included in the meta-analysis. Shown are the species involved and the geographical area of each study. Species are: arctic grayling (AG, *Thymallus arcticus*), Atlantic salmon (AS, *Salmo salar*), brook trout (BKT, *Salvelinus fontinalis*), bull trout (BLT, *Salvelinus confluentus*), brown trout (BRW, *Salmo trutta*), chinook salmon (CKS, *Oncorhynchus tshawytscha*), coho salmon (CS, *Oncorhynchus kisutch*), cutthroat trout (CTT, *Oncorhynchus clarki*), dolly varden (DV, *Salvelinus malma*), masu salmon (MS, *Oncorhynchus masou*), rainbow trout (RT, *Oncorhynchus mykiss*), and white-spotted charr (WSC, *Salvelinus leucomaenis*). The code refers to the type of analysis for which data from each study were used: a = abundance, g = growth, f = foraging, h = habitat, i = interaction (aggression, dominance), s = survival.

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* The results were published after January 2008 (see Korsu et al. 2009, 2010).
we included also two papers (Cunjak and Green 1984, Hasegawa et al. 2004) that reported the achieved dominance status in two-fish trials (as a proportion of dominant to subordinate individuals). To measure the effects on native species’ abundances, we used values from manipulative (removal) experiments, natural ‘experiments’ (allopatric vs. sympatric conditions in the field), as well as documented invasions (before-after data). In some cases, true allopatry was hard to define because of, for example, incomplete removal of the alien species (e.g. Peterson et al. 2004). We, therefore, used a 10% density threshold to categorize a site as allopatric or sympatric. For studies reporting abundance responses by the native fish, we also tested for the impact of introducing multiple alien species compared with single-species introductions. Because introduced species often rearrange the community rather than simply enter an empty slot (Herbold and Moyle 1986), we hypothesized that the magnitude of the impact should be greater when several species were introduced. This hypothesis is supported by recent theoretical evidence showing that strong biotic resistance only occurs when the invasion process is restricted to a single species, whereas the presence of multiple invaders tends to weaken the resistance (Hewitt and Huxell 2002).

Next, we compared the species-specific impacts of three salmonid species: brown trout, rainbow trout, and brook trout. We chose these species because the two first-mentioned are included in the list of 100 of the world’s worst invasive alien species (Lowe et al. 2000). Brook trout, although extensively transferred from its original range in eastern North America to other parts of the continent, as well as to other continents, is often referred to as a relatively harmless intruder with little impact on native species (Vooren 1972, Blanchet et al. 2007a, Hesthagen and Sandlund 2007). However, an increasing number of studies indicate harmfulness of this species for recipient systems (Dunham et al. 2002, Spens et al. 2007, Korsu et al. 2007). For these three species, we calculated effect sizes (see below) by including all response variables in a single categorical meta-analysis to demonstrate the general impact of these species on native salmonids.

We calculated effect sizes for each study as the logarithmic response ratio, ln$R$, where $R$ refers to values in sympathy (treatment) divided by those in allopatry (control) (see Rosenberg et al. 1997). Thus, negative values of ln$R$ mean that, for the native species, the value of a response variable was lower in sympatric than allopatric situations, indicating a negative impact of the alien species on the native one. However, as there was generally no means of deciding a priori whether a certain habitat shift was harmful to a native species, we considered all habitat shifts caused by the invader harmful (e.g. to either shallower or deeper stream positions); thus, habitat use is presented as negative (or zero) ln$R$ values only. For aggression, we calculated ln$R$ only for sympatric trials, with negative ln$R$ indicating that the alien species dominated and/or expressed more aggression towards the native species. For all effect size calculations, we used study means weighted by the number of replicates (Rosenberg et al. 2000). This was done because, in many cases, treatments were unreplicated, or the study was pseudoreplicated (for example, multiple sampling sites in one stream), thus not allowing us to compute study-specific standard deviations. We calculated 95% bias-corrected bootstrap confidence intervals for ln$R$ (4999 permutations). All calculations were made using the MetaWin 2.0 software (Rosenberg et al. 2000). This procedure partitions the total heterogeneity for a particular comparison ($Q_w$) into within-group ($Q_{w'}$) and between-group ($Q_b$) components. Means were considered to be significantly different from zero if bootstrap confidence intervals did not overlap zero.

We further examined whether the magnitude of the alien impact depended on the study type. For this purpose, we divided the studies based on whether they were conducted in (i) laboratory channels, (ii) fish enclosures in natural streams or semi-natural outdoor channels, or (iii) natural streams (both broad-scale removal experiments and natural ‘experiments’ included). We hypothesized that studies using restricted spatial scales could intensify interspecific interactions, reducing the native species’ performance and potentially resulting in stronger effect sizes. However, as many studies have shown that the growth of a native salmonid may be either suppressed or enhanced by the presence of an alien fish (e.g.
Volpe et al. 2001, Blann and Healey 2006, Blanchet et al. 2007b), we analysed growth separately from other response variables (survival, foraging, and habitat use combined).

Results

Studies of salmonid invasions in streams show a strong geographical bias: a great majority of studies come from North America (n = 49), while only a few studies have been conducted in Europe (n = 4) or Japan (n = 5) (Table 1). The harmful impact of alien salmonids on the native ones was most clearly demonstrated by the negative effect sizes on the foraging rate, abundance and survival, while no effects were detected for aggression or growth (Fig. 1). Fish habitat use, particularly use of cover and water depth, was also modified by the invader (Fig. 2).

Brown trout was by far the ‘worst’ alien salmonid (i.e. had the strongest impact on native fish), while rainbow trout and brook trout had similar and only weakly negative impacts on native salmonids (Q_B = 27.82, p < 0.0001) (Fig. 3). Furthermore, the effect on native fish abundance was most pronounced when more than one alien fish were present: with one alien, lnR was −0.40 (bootstrap confidence intervals: −1.06 to 0.06, n = 14), whereas it was −1.15 (−1.75 to −0.95, n = 8) in systems with at least two alien salmonids (Q_B = 12.24, p < 0.001).

The magnitude of the impact was related to study type, with much stronger impact in spatially restricted laboratory channels as compared with that in more natural settings (survival, foraging, and habitat use combined: Q_B = 13.74, p < 0.001, Fig. 4a; growth: Q_B = 7.90, p = 0.019, Fig. 4b). The growth response was slightly, though non-significantly positive (CI overlapped zero), but only in studies conducted in laboratory channels (Fig. 4b). For other variables, the impact was negative, regardless of the methodology and the study scale (Fig. 4a).

Discussion

Our results showed that introduced stream salmonids, especially brown trout, have diverse negative effects on native salmonids. Especially habitat use, foraging rate, abundance, and survival were modified by the aliens. Moreover,
populations of the native species were severely reduced in streams supporting more than one introduced species. The magnitude of the impact was also affected by the methods used, with laboratory studies reporting the strongest impacts.

Our meta-analysis comprised studies from North America, Europe and Japan, with a great majority being conducted in North America where salmonids have been extensively transferred across the continent. Our data do not allow a rigorous assessment of pattern similarity between continents, but the adverse impacts of alien salmonids are clearly not unique to North America: similar effects have been reported in South America (Rodríguez 2001), Japan (e.g. Taniguchi et al. 2002) and Europe (Korsu et al. 2007), reinforcing the generality of our findings. Furthermore, the impacts of introduced salmonids may even be stronger if the recipient habitat does not contain any closely related native fish (i.e. native species are naïve to the introduced species; see Cox and Lima 2006). For example, in New Zealand, the introduced brown trout have caused extensive population fragmentation and endangerment of native galaxids (Townsend and Crowl 1991), as well as strong cascading impacts on stream food webs (Nyström et al. 2003).

According to the enemy release hypothesis, alien species benefit from having left their old enemies (predators, competitors, and parasites) behind, while native species continue to struggle against their co-evolved, natural enemies (Sax and Brown 2000, Shea and Chesson 2002). Our results lend indirect support to this hypothesis, because the same species were often reciprocally aliens and natives, depending on the direction of introductions and the recipient salmonid guild. For example, brook trout is native in eastern North America where its populations are reduced by both rainbow and brown trout (Krueger and May 1991, Fausch 2008). However, in the native ranges of these two invaders, the introduced brook trout meet only limited biotic resistance, allowing their establishment and spread, with sometimes severe impacts on native trout (Benjamin et al. 2007, Korsu et al. 2007, Fausch 2008).

The negative effects of introduced fish on native species’ abundances were most pronounced in streams with more than one introduced species. This finding supports niche-based explanations of invasion success: the more alien species there are, the less empty niche space is available, forcing the native species to adjust to biologically modified environments with multiple new competitors (see Davis 2003). It is also possible that an increased number of introduced species may create positive feedback cycles that cause the effects of invaders to rapidly accumulate over time, a phenomenon called ‘invasion meltdown’ (Simberloff 2006). Interestingly, studies examining the impact of multiple alien species are rare, particularly if compared to the large body of literature addressing the role of species richness in preventing invasions (e.g. Shea and Chesson 2002, Hierro et al. 2004, Levine et al. 2004).

The magnitude of the impact also depends on the identity of the species introduced, with brown trout being the worst invader of the three species examined. Interestingly, rainbow trout and brook
trout appeared to be equally bad, although only the former one is included in the list of 100 of the world’s worst invasive alien species (Lowe et al. 2000), while the latter species is often considered a harmless invader (Vooran 1972, Blanchet et al. 2007a, Hesthagen and Sandlund 2007). It thus appears that interactions among native and alien salmonids are highly context-dependent, varying in relation to case-specific factors such as characteristics of the species involved and the recipient environment (Fausch 2008, Korsu et al. 2008, Ricciardi and Kipp 2008). Furthermore, methodological issues are also involved: impacts appeared much stronger in laboratory settings than in stream enclosures or reach-scale observational studies. While this may hint to a laboratory artifact, it might also reflect a scaling problem, with the strongest effects being observed in spatially restricted laboratory streams. The impact of the alien species at small spatial scales is not necessarily negative, however: in fact, the growth of the native species in laboratory tanks was on average higher in the presence than absence of an invader. While this finding may also be a scaling artifact, it has indeed been suggested that growth facilitation among two fish species, one native, the other one introduced, might in fact take place through behavioural stimulation (Blann and Healey 2006). A whole suite of methodological approaches from laboratory and field experiments to observational studies at multiple spatial scales are needed to resolve mechanisms of alien species impact on native salmonids (see also Dunham et al. 2002).

The role of aggressive behaviour to salmonid invasion success is often postulated, because stream salmonids typically use agonistic acts to establish social hierarchies and maintain energetically optimal feeding positions (Fausch 1984, DeWald and Wilzbach 1992, Wang and White 1994). Our results, however, gave no support for aggression as the driving force for the superiority of introduced salmonids. Indeed, Korsu et al. (2007) showed that brook trout, a species regarded as relatively non-aggressive (DeWald and Wilzbach 1992), has invaded across the native range of the more aggressive brown trout in North European streams. Thus, it is likely that other factors, operating beyond direct interference, regulate salmonid invasions in streams.

It is also possible that, if competition is important, it is so only during certain periods of time (e.g., immediately after hatching; Rose 1986) and in relatively homogenous, non-fluctuating environments where the invaders may establish through a ‘hostile takeover’ (sensu Melbourne et al. 2007, Korsu et al. 2010). As an interesting parallel, Sax et al. (2007) suggested that research on biotic resistance should change focus from competition-based explanations to more comprehensive consideration of other biotic interactions such as predation and pathogens. Being notoriously variable and disturbance-prone environments (e.g. Lake 2000), streams can be expected to produce constantly new niche opportunities for exotic species, with little need to invoke competition-related explanations.

Despite considerable context-dependency, our analyses do provide some evidence for general patterns in salmonid invasions. Adverse effects were detected for both individual- and population-level variables, potentially driving native fish to the brink of extinction. An important implication from our study is that introductions of alien salmonids beyond their natural ranges almost certainly incur a high risk of negative impacts on native biota. Therefore, if no prior information on the impacts of alien salmonids is available, it is preferable to avoid introductions altogether rather than being forced to costly and unreliable eradication measures after the harm has already been done. This is even more so because species considered harmless to native fish in some areas (e.g. brook trout in southern Europe; Blanchet et al. 2007a) may cause serious damage in other parts of their introduced range (e.g. brook trout in northern Europe, Korsu et al. 2007, Spens et al. 2007).

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