

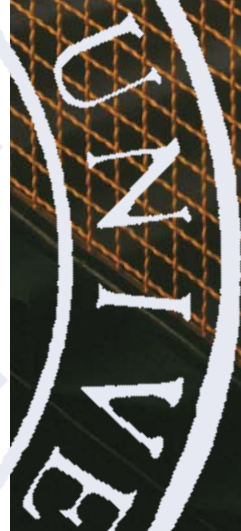
Kai Korsu

ECOLOGY AND IMPACTS
OF NONNATIVE SALMONIDS
WITH SPECIAL REFERENCE
TO BROOK TROUT
(*SALVELINUS FONTINALIS*
MITCHILL) IN NORTH
EUROPE

FACULTY OF SCIENCE,
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KAINUU FISHERIES RESEARCH

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KAI KORSU

**ECOLOGY AND IMPACTS OF
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MITCHILL) IN NORTH EUROPE**

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Abstract

My main objectives in this thesis were to explore general patterns and mechanisms driving salmonid invasions globally and, more specifically, to examine the invasion dynamics and impacts of the North American brook trout in North European stream systems.

Non-native salmonids have often spread extensively and caused many harmful impacts on their native counterparts. Among the three globally introduced salmonids, the European brown trout appeared as the 'worst' alien species (strongest impact on native fish), followed by the North American rainbow trout and brook trout.

Brook trout, which is widely established in European streams, was found to be a non-aggressive species. Moreover, the growth of brown trout was unaffected by brook trout, indicating negligible interspecific interactions between the two species. Habitat niche segregation between brook trout and brown trout was evident, with brook trout occupying mainly low-velocity pool habitats, whereas brown trout resided in fast-flowing riffles. At the river-wide scale, brook trout occurred mainly in small, slightly acid headwater streams, whereas brown trout was found primarily in larger downstream river sections. Evidently, North European streams with a very low number of native fish species offer underutilized niche space for tolerant headwater specialists such as brook trout.

However, the habitat niche filled by brook trout was not completely vacant, as brown trout co-occurred with brook trout in numerous small and mid-sized (3–16 m wide) streams. In these streams, brown trout reproduction was negligible presumably related to the presence of brook trout. Brook trout had also increased in density relative to brown trout during the 10-yr study period (1994 vs. 2004). Moreover, the growth rate and population densities of brook trout were high and the species had spread extensively towards the upmost headwater streams during the 10-yr study period. Thus, harmful effects on the native brown trout by brook trout are likely to occur in the core habitat of the invader, i.e. headwater streams, leaving populations of the native species unaffected elsewhere. Due to the high conservation value of the potentially impacted populations of brown trout, I strongly caution against further stocking of brook trout in European watersheds.

Keywords: biological invasions, brook trout, brown trout, growth, habitat use, interspecific competition, meta-analysis, multi-scale, niche segregation, salmonids, species replacement, streams

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List of original papers

This thesis is based on the following original papers, which are referred to in the text by their Roman numerals:

- I Korsu K, Huusko A & Muotka T (2008) Ecology of alien species with special reference to stream salmonids. *Boreal Environment Research* 13 (Supplement A): 43–52.
- II Korsu K, Huusko A & Muotka T (2008) Impacts of invasive salmonids on native fish: using meta-analysis to summarize four decades of research. Manuscript.
- III Korsu K, Huusko A & Muotka T (2007) Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. *Proceedings of the National Academy of Sciences USA* 104: 9725–9729.
- IV Korsu K, Huusko A & Muotka T (2008) Invasion of North European streams by brook trout: hostile takeover or pre-adapted habitat niche segregation? Manuscript.
- V Korsu K, Huusko A & Muotka T (2008) Does the introduced brook trout affect the growth of brown trout in North European streams? Combining evidence from artificial-stream experiments and field surveys. Manuscript.

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1 Introduction

Invasions by non-native organisms are recognized as a major threat to global biodiversity, leading to species extinctions and worldwide homogenization of the biota (e.g. Rahel 2000, Olden 2006). Invaders can also alter fundamental ecological properties of the host ecosystems, such as species dominance, nutrient cycling, and productivity (Simon and Townsend 2003). For the next few decades, management and control of invasive species is indeed one of the biggest challenges conservation biologists will face (Allendorf & Lundquist 2003).

For tens of millions of years, species incapable of long-range dispersal have diverged evolutionarily behind geographical barriers, coming together only through, for example, continental movements. Such barriers no longer exist, because human-aided dispersal is overcoming the effects of geographical isolation. Ancient human migrations and trade led to an early spread of some domesticated species. Growth of global commerce has provided scope for a corresponding increase in biotic invasions which is now about 50 000 times higher (Crooks 2005, see also Ricciardi 2007) than it was without human-aided movement of species.

The establishment success of non-native species in recipient ecosystems has been relatively high, as 10 - 50 % of species entered in recipient ecosystems have subsequently established themselves (Jeschke & Strayer 2005, Williamson 2006). Such a high invasion success creates a paradox for scientists studying invasions: if natural selection operates to adapt species to their native environments, then why are non-native species able to establish and even exclude some of the native species, presumably well-adapted to local environmental conditions (Sax & Brown 2000, Fausch 2008)? A lot of work has been done to disentangle the mechanisms underlying successful invasions, but no single-factor explanations have been found (Lodge 1993, Hierro *et al.* 2004, Moyle & Marchetti 2006). The mechanisms explaining invasions include: (1) release from natural enemies, (2) rapid genetic changes during invasion, (3) empty niches in the recipient system, (4) novel attributes or weapons possessed by the invader, (5) environmental disturbance promote invasion, (6) diverse systems keep invaders out, and (7) high propagule pressure (i.e. number of individuals introduced and number of introduction events). It has also been suggested that some trait characteristics facilitate invasions: for example, species with r-selective life history are often efficient invaders (Lodge 1993, Ruesink 2005). Further, the invasional meltdown

hypothesis suggests that the presence of one invader facilitates subsequent invasions (Simberloff 2006).

Stream-dwelling salmonids have been successfully established throughout the world (Rahel 2007). These commercially valuable, originally holartic, game species now occur in all continents except Antarctic. Concerns have been raised about the negative effects of introduced salmonids in many areas as they have affected not only native fish species but also whole stream ecosystems (Krueger & May 1991, Dunham *et al.* 2002, Simon & Townsend 2003). It is therefore not surprising that two salmonids (brown trout and rainbow trout *Oncorhynchus mykiss* Walbaum) are among the eight fish species included in the list of 100 of the world's worst invasive species (Lowe *et al.* 2000). Fisheries managers around the world have launched extensive management programs to control salmonid invasions and to eradicate already established populations of non-native salmonids, with the aim of conserving native fish populations (Novinger & Rahel 2003, Jackson *et al.* 2004, Finlayson *et al.* 2005).

What explains the high invasion success of salmonids and various adverse effects these species have caused in recipient ecosystems? As in the case of general invasion ecology (see above), no single-factor explanations have been found (Dunham *et al.* 2002, Fausch 2008). Probably the most often cited explanations for salmonid invasions deal with (i) open niche space for the non-native species within the mainstream-headwater gradient of the recipient stream system (e.g. Rahel & Nibberlik 1999) and (ii) interspecific aggressive behaviour through which non-native salmonids displace the native ones (e.g. DeWald & Wilzbach 1992). Underlining these two factors is logical because stream salmonids are territorial drift feeders, defending energetically optimal feeding positions through agonistic acts (Fausch 1984, Nakano 1995), yet they also show niche separation, which often results in a distinct zonation pattern along the mainstream-headwater gradient (Bozek & Hubert 1992, Flebbe 1994, Rahel & Nibberlink 1999). Thus, salmonid guilds are structured by both large-scale and small-scale processes that eventually shape the zonation pattern through the combined effect of species-specific adaptations to different niches and environmentally-driven ecological performances (DeStaso & Rahel 1994, Taniguchi & Nakano 2000, De la Hoz Franco & Budy 2005). There have also been attempts to explain invasions through biological characteristics of successfully invaded salmonid species but this approach suffers from largely anecdotal observations and *a posteriori* argumentation making this reasoning highly problematic (Fausch 2008). In order to be established, biological traits of

the invader must suit the specific conditions of the recipient environment as a key-to-lock mechanism (low environmental and biotic resistance, see Moyle & Light 1996), making outcomes of invasions highly context-dependent (Lodge 1993, Heger & Trepl 2003). Moreover, propagule pressure can determine the high establishment success of salmonids – species that have been traditionally stocked in extremely high numbers in order to meet the commercial sport fishing requirements (Colautti 2005).

In this thesis, my main objectives were, first, to explore general patterns and mechanisms driving salmonid invasions globally (I) and, more specifically, to quantify impacts of non-native salmonids on native salmonids through a meta-analysis (II). Secondly, I used a temporally replicated data set to examine the dispersal dynamics and impacts of introduced brook trout in a large Finnish stream system previously dominated by the native brown trout (III). Brook trout is a North American salmonid fish that has been introduced in several streams and lakes across Europe (Holčík 1991). Brook trout typically dwell in small streams (Rahel & Nibberlink 1999), thus its habitat niche partially overlaps with that of the native brown trout which occupies a large variety of stream habitats (Elliott 1994). Accordingly, the empty niche hypothesis (see above) was considered in paper III. Furthermore, the hypothesis was more specifically assessed in the next two papers (IV and V), where I used an approach combining experimental and observational studies conducted at several spatial scales from 1-m long experimental channels to entire drainage systems. The main questions in these two papers were: (i) do brook trout and brown trout utilize similar habitat niches, and if not, is the segregation pre-adaptive or interactive (IV), and (ii) do brook trout have an effect on the growth of brown trout, indicating competitive interactions (V)? A multi-scale approach was used in papers IV and V because results gained from small-scale studies rarely extrapolate to complex field situations (Underwood *et al.* 2005). Furthermore, the question of whether the study scale and methods affect the results was addressed with a meta-analysis on studies examining the impacts of salmonid invasions (II).

2 Material and methods

2.1 Literature survey and meta-analysis (I, II)

I used both narrative (I) and meta-analytical (II) approaches to summarize the available literature on the impacts of non-native stream salmonids on their native counterparts. Using meta-analysis, I present responses from individual- to population-level studies, comparing responses of native species in allopatry (control) to those in sympatry (treatment) with introduced species. I made a thorough literature search on studies published between 1970 and January 2008 using ASFA (Aquatic Sciences and Fisheries Abstracts) and Google Scholar™, supplemented with my own reference collections. I also added my own unpublished studies to this data set which thus comprised 58 studies. I divided the studies in six groups based on the response variables measured: aggression, habitat use, foraging, growth, survival, and abundance. I also examined whether the three extensively introduced salmonids, brown trout, brook trout and rainbow trout, differed in their impacts on native salmonids. Finally, I explored whether the responses of native species to invader presence depended on study methods. For this purpose, I separated studies conducted in (i) laboratory channels, (ii) fish enclosures in natural streams or artificial, natural-like outdoor streams, and (iii) natural streams.

2.2 Study areas and species (III, IV, V)

Extensive field surveys were conducted in two drainage systems (River Iijoki 65°N, 28°E and River Kemijoki 67°N, 28°E, Fig. 1) in northern Finland. In total, 142 stream sites, comprising variable stream habitats from 100-m wide channels to heavily shaded headwater streams, were sampled.

Brook trout were introduced in multiple events in both systems mainly in the 1970s and 1980s. Up till now, brook trout have established naturally reproducing populations in both rivers, and its present distribution covers large parts of both drainage systems. Consequently, the present distribution of brook trout overlaps with that of brown trout, but allopatric sites of each species are also frequent.

Brook trout is the only native stream-dwelling trout in eastern North America. Brook trout dwell mainly in small headwaters but also occur in lakes and have sea-run (anadromous) populations in coastal rivers (Kerr & Grant 1999). Brook

trout spawns on gravel substrate and loose bottom materials in both lakes and streams in the fall (September-October). Spawning sites are typically closely associated with upwellings of groundwater, which provide favorable temperature and dissolved oxygen conditions for egg development during winter (Cucherousset *et al.* 2008). In spring, free-swimming fry emerge and seek shallow areas along shorelines and stream margins. Adult brook trout prefers cold, spring-fed waters, where overhead cover, slow-velocity pools, and invertebrate prey are available. Brook trout seldom lives longer than five years with sexual maturity usually reached by age two or three. (Kerr & Grant 1999.)

Brown trout is native to streams of Europe and western Asia. Brown trout occurs in variable habitats from small headwaters to large lowland rivers, and has sea-run (anadromous), lake-run, as well as stream-resident populations (Elliott 1994, Olsson *et al.* 2006). Brown trout is an autumn-spawner, having largely similar spawning habitat requirements as brook trout. However, brown trout is less discriminate in its choice of sites near groundwater upwellings and also spawns in higher flows and on larger gravel substrate than brook trout (Kerr & Grant 1999, Cucherousset 2008). These habitat features also characterize the general habitat use of these species, with brown trout utilizing mainly fast-flowing riffles and brook trout mainly pools. Brown trout generally lives longer and achieve larger adult size than brook trout. Large brown trout (35-40 cm) tend to shift their diet from insects to fish. (Kerr & Grant 1999.)

Other species present in the study systems were sculpins (*Cottus gobio* L. and *C. poecilopus* Heckel), European minnow (*Phoxinus phoxinus* L.), brook lamprey (*Lampetra planeri* Bloch), burbot (*Lota lota* L.), nine-spined stickleback (*Pungitius pungitius* L.), and European grayling (*Thymallus thymallus* L.). Fish species richness was very low: on average three species (including brown trout and brook trout) were collected per sampling site.

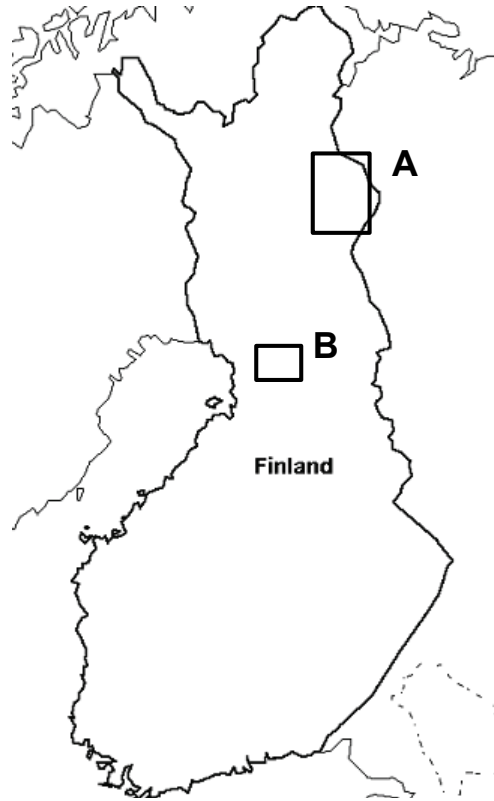


Fig. 1. Locations of the study areas in the two drainage systems: River Kemijoki (A) and River Iijoki (B).

2.3 Field procedures (III, IV, V)

Field surveys were conducted in 142 sites across the two drainage systems between 1994 and 2005 during the late-summer low-flow conditions. Fish were sampled by electroshocking: sampling started from the downstream end of each site, and it was done by two persons, one operating the backpack shocker, the other using a dip net to catch stunned fish. All fish captured were measured and then returned to the stream. Fish densities were estimated by the removal method (Bohlin *et al.* 1989, Carle & Strub 1978), and fish age-classes were determined based on scale analysis and length-frequency histograms. Several habitat variables were measured at each site. Measurements were made along randomly placed cross-sectional transects covering the whole study section (III, IV). The

number of habitat measurements varied between 18 and 25, depending on stream width. Measured habitat variables were: (1) the percent cover of instream vegetation (mainly bryophytes), (2) canopy shading (% cover), (3) dominant substrate size (modified Wentworth scale), (4) current velocity (at 0.6 x depth), (5) water depth, and (6) stream width. Also pH and conductivity ($\mu\text{S cm}^{-1}$) were measured at each site.

In the River Kemijoki drainage system, 69 stream sites were sampled both in 1994 and 2004, to examine whether brook trout had spread during the intervening years and whether there were any impacts on the native fish associated with the presence of brook trout (III). In the River Iijoki drainage system, a subset of streams were sampled five times during summer 2005 to monitor fish growth in both allopatric ($N = 3$) and sympatric ($N = 3$) sites (V).

2.4 Experimental procedures (IV, V)

The experiments were conducted, and experimental fishes reared, at Kainuu Fisheries Research (Finnish Game and Fisheries Research Institute), Finland (64°N , 27°E). In early summer (May-June) of 2005 and 2006, I performed experiments in (1) indoor flumes, (2) indoor aquaria, and (3) outdoor semi-natural streams. In each of these settings, I had four replicated treatments randomized among the experimental units: (1) brown trout at low density (Brw), (2) brown trout at high density (Brw+Brw), (3) brown trout + brook trout, high density (Brw+Brk), and (4) brook trout at low density (Brk). I performed the Brw+Brw treatment to control for the effects of increased fish density in the sympatric treatment (see Weber & Fausch 2003). Comparison of the Brw vs. Brk treatments allowed me to test for differences in response variables for the two species in isolation. Fish densities reflected those observed in natural streams of River Kemijoki and River Iijoki drainage systems. Water temperatures during the experiments were between 9 and 20°C.

In the indoor flume experiments, I used four experimental arenas of 1 x 0.25 m. To mimic a riffle habitat with variable current velocities and abundant low-velocity microhabitats, I placed a gravel (diameter 1-3 cm) bed and a velocity shelter (a 5 x 10 cm “pocket” in the flume wall) in the upstream portion of each arena (‘riffle’). No structures were installed in the downstream portions which had deeper water with less turbulent flow (‘pools’). In the indoor aquaria experiments, I used glass aquaria (50 x 25 x 30 cm) that had no added habitat structure. I used age-0 fish in all indoor experiments. Fish were allowed to

acclimate in the experimental arenas for 20 h before the start of each trial. After the acclimation period, I started to film fish behavior using video cameras. Video recording was automatic and there was no observer disturbance in the experimental facilities during the recordings or the acclimation period. Recordings were made between 10.00 and 12.00 hours, in 40-s intervals for each arena. I analyzed 30 such intervals, for a total of 20 min per arena, recording inter- and intraspecific agonistic behaviors and fish habitat use.

In the outdoor semi-natural streams, I conducted habitat selection and growth experiments. The six streams are 26-m long and 1.5-m wide, made of concrete, but stream bed consists of natural gravel and cobbles supporting benthic invertebrate communities. Moreover, to better mimic the conditions of headwater streams with dense riparian canopies, the streams were covered with camouflage nets (mesh size 4 cm, mixed green/brown coloration). Each of the six streams was divided in three sections (by wire mesh) that contained comparable upstream riffles (high velocity, large substrate) and downstream pools (low velocity, small substrate). Hence, there were 18 similar sections, where I performed the four treatments. Before fish were released to the sections, they were anaesthetized (MS-222) and their body cavities were injected with 23 mm PIT-tags (Passive Integrated Transponder) to obtain individual-level data on fish habitat use and growth. I used age-1 brook trout (mean weight 66.9 g, length 18 cm) and age-2 brown trout (mean weight 51.4 g, length 17 cm) in these experiments. I selected these age-classes to control for the unnatural between-species size difference that appeared in rearing conditions (for comparison, see V). During the study period, the fish were located four times by slowly moving a customized portable PIT-antenna about 20 cm above the water surface. A signal from each fish was obtained in all study sections during the experiment, suggesting that the PIT technique was successful (see also Linnansaari *et al.* 2007). At the end of the 36-day trial (July 4), the fish were collected by electroshocking, measured (weigh and length) and their individual PIT-tag codes were recorded. Finally, their stomachs were preserved in 70 % ethanol. In the laboratory, stomach contents were dried (24 h at 60°C) to determine dry weights of consumed prey.

2.5 Statistical analysis

In paper II, I calculated effect size for each study as the logarithmic response ratio, $\ln R$, where R refers to values of a response variable in sympatry (treatment) divided by those in allopatry (control) (see Rosenberg *et al.* 2000). 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 non-native species on the native one. However, as there was generally no means of deciding a priori whether a certain habitat shift was harmful for a native species, I considered harmful all habitat shifts caused by the presence of the invader (e.g. to either shallower or deeper stream positions); thus habitat use is presented as negative (or zero) $\ln R$ values only. For aggression, I calculated $\ln R$ only for sympatric trials, with negative $\ln R$ indicating that the non-native species expressed more aggression towards the native species.

For all effect size calculations, I used study means weighted by the number of study-specific replicates (Rosenberg *et al.* 2000). I also calculated bias-corrected bootstrap confidence intervals for $\ln R$ (4999 permutations). I made all calculations with MetaWin 2.0 software (Rosenberg *et al.* 2000). This procedure partitions the total heterogeneity for a particular comparison (Q_T) 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 (e.g. Worm *et al.* 2006).

In paper III, I compared trout densities between time periods and site categories (sympatric, allopatric, invaded by 2004) by two-way repeated measures ANOVA. Further, I used paired t-test to test for brown trout/brook trout density ratio changes between time periods in the sympatric sites. To examine the effect of brook trout on the reproduction of brown trout, I calculated the number of sites where age-0 brown trout were found, separately for small (< 7 m) and large (> 7 m) streams, in each of three site categories: (i) sites where brook trout were present in both years, (ii) invaded sites (brook trout present in 2004 but not 1994), and (iii) allopatric brown trout sites (brook trout absent in both years). To examine fish-habitat relations in papers III and IV, I used Principal Component Analysis (PCA). I examined if site categories, represented by site scores in PCA, differed in stream habitat structure with one-way ANOVA, followed by Tukey's pairwise comparisons (III).

In the experimental part of the paper IV, I used one-way ANOVA to test for differences between treatments in the total number of agonistic acts in the indoor experiments. In the Brw+Brk treatment, I also used one-way ANOVA to test for differences in the proportions of four interaction types: (1) brown trout intraspecific; (2) interspecific, initiated by brown trout; (3) interspecific, initiated by brook trout; and (4) brook trout intraspecific. I also used one-way ANOVA to examine the effect of brook trout on the habitat use of brown trout and t-test to

compare the habitat use of the two species in isolation. In the experimental part of paper V, I compared the specific growth rates and relative dry weights of stomach contents (RDW) between the treatments by one-way ANOVA and t-test. In these analyses, I used section-specific averages instead of values for individual fish to avoid pseudoreplication.

To examine the effect of brook trout on the growth of brown trout in field conditions (paper V), I compared brown trout mass (g) in allopatric vs. sympatric streams by t-tests and ANCOVA with trout density as a covariate. As the temperature regime of the streams varied considerably, I also estimated the maximum achievable weights of brown trout in the six study streams by using the model of Elliott *et al.* (1995). Thus, I compared the modeled maximum weights to those observed in the field.

3 Results and discussion

3.1 Explaining invasion success of non-native salmonids and determining their impacts on recipient stream systems (I, II)

In paper I, we emphasize that the high invasion success of salmonids partly results from the extremely high propagule pressure. Interspecific interactions may also play a role, because the close ecological similarity of salmonids potentially results in niche overlap and interspecific aggression. Often newly invaded species take advantage of their species-specific core habitats, forcing other fish to spatial refugia. This may result in the disruption of the original distribution patterns of species along the headwater-to-mainstream continuum. Moreover, non-native salmonids may have wide-reaching impacts on the trophic organization of stream communities and even on terrestrial organisms such as insects, spiders, amphibians, reptiles, birds and mammals.

In the succeeding paper (II), we show quantitatively (through meta-analysis) that non-native stream salmonids have diverse negative effects on native salmonids. The negative impact was highest for foraging rate, abundance, and survival. Native species were also forced to alter their habitat use in the presence of non-native species. The magnitude of the impact depended on the identity of the species introduced, with brown trout being the worst invader (strongest impact on native fish) of the three species examined. Interestingly, rainbow trout and brook trout appeared equally bad, although only the former is included in the list of 100 of the world's worst invasive alien species (Lowe *et al.* 2000).

The role of aggressive behaviour in explaining invasion success of non-native salmonids was not supported by the data. We therefore suggest that successful invasions are more likely driven by large-scale phenomena operating beyond direct individual interference (e.g. evolutionary history, adaptations, niches) (see also Fausch 2008). Our results indirectly supported niche-related explanations as we found that the negative effect was most pronounced in river systems that have received more than one non-native species. Apparently, the more non-native species present, the lower the availability of niche space and resources, forcing the native species to adjust to a biologically modified environment with multiple new competitors. It is also possible that increasing the numbers of introduced species can create positive feedback cycles that cause invaders and their effects to

rapidly accumulate over time, a phenomenon termed ‘invasional meltdown’ (Simberloff 2006).

Our results lend indirect support for the enemy release hypothesis, whereby non-native species are freed from their native predators and pathogens (Sax & Brown 2000). Accordingly, we found that the most successful invaders 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 & May 1991, Fausch 2008). However, in the native ranges of rainbow and brown trout, the introduced brook trout meets only limited biotic resistance, allowing its establishment, and sometimes severe impacts on native trout (III, Benjamin *et al.* 2007, Spens *et al.* 2007, Fausch 2008, Öhlund *et al.* 2008).

Finally, we found that the magnitude of the impact was related to study methods, with much stronger impacts in spatially restricted laboratory channels than in more natural settings. While this may hint at a laboratory artifact, it might also reflect a scaling problem. Clearly, a whole suite of methodological approaches from laboratory and field experiments to observational studies at multiple spatial scales are needed to resolve the mechanisms of alien species’ impact on native salmonids (Dunham *et al.* 2002, see also Werner 1998, V).

3.2 The spread of the non-native brook trout and replacement of the native brown trout (III)

During the 10-yr study period brook trout had spread 20 km towards the headwaters of River Kemijoki. The density of brook trout was very high in small and slightly acid streams (c. 3 m in width), whereas in larger streams the invader was typically absent or occurred in low numbers only. Accordingly, the effect of brook trout on brown trout was habitat-specific: brook trout excluded the native species only in small tributary streams where the reproduction of brown trout was severely reduced (mean density of brown trout 0.06 ind m⁻²). In larger streams, brown trout was largely unaffected by brook trout.

These results were rather unexpected, because in eastern North America, the European brown trout generally dominates over, and eventually replaces, the native brook trout (Waters 1999). Brown trout is also a dominant competitor in New Zealand and Japanese streams, having far-reaching effects on lotic food webs (Simon & Townsend 2003, Morita *et al.* 2004), and it has been listed as one of the 100 worst alien species in the world (Lowe *et al.* 2000). Thus, based on the

available knowledge, one might predict that brook trout should be unable to establish populations in our study streams because the competitively dominant native species, brown trout, is present. Indeed, many fish biologists and fisheries managers have assumed that brook trout does not pose a serious threat to brown trout or other native fish in European streams (Vooren 1972, Blanchet *et al.* 2007).

How can these contradicting views be explained? Our data were extensive and temporally replicated, allowing us to compare the effects of brook trout in different habitats, and it turned out that the invader was able to replace brown trout in the smallest streams only. It should also be noted that in North America, where the introduced brown trout have spread extensively, small headwater streams often serve as a refuge for the native brook trout (Rahel & Nibberlink 1999). Thus it appears that being an acid-tolerant headwater specialist (Baldigo & Lawrence 2000, Pirhalla 2004), brook trout ultimately settle in narrow headwater streams and tributaries, whereas brown trout utilize these habitats only marginally, being prevalent mainly in larger, more benign downstream sites. Accordingly, the pattern of reciprocal replacement is habitat-specific, with the exclusion of native species occurring only in their secondary habitat, leaving populations in core habitats unaffected.

Our data demonstrate that a subordinate native species can become a harmful invader when transferred to systems outside its native range. These data also show that the outcome of biotic interactions can be highly context-dependent, and when trying to understand the mechanisms underlying a successful invasion, or to identify potential invaders a priori, one should have ample information about the invaded habitat, recipient biota, and niche characteristics of the introduced species (see also Bøhn & Amundsen 2001). Importantly, this result implies that if the niche characteristics of an introduced organism are well-known, its invasion potential in the introduced range can be predicted and management actions targeted accordingly.

3.3 The relative roles of interspecific interference and pre-adaptive niche segregation in explaining the invasion success of brook trout (IV)

Our results demonstrate habitat segregation between the invading brook trout and native brown trout in laboratory and mesocosm experiments. This spatial segregation was both vertical, with brook trout using the upper parts of the water

column, and horizontal, with brook trout occupying mainly low-velocity pool or run habitats while brown trout tended to reside in riffles. Furthermore, the same pattern of spatial segregation appeared across a wide array of scales, ranging from 1-m long experimental flumes to entire drainage systems. In the field, however, the between-species pool/riffle segregation pattern was less distinct, although still apparent in both drainage systems where the distributions of the two species overlapped extensively. The fact that the experimental results did not fully extrapolate to natural situations was probably due to numerous environmental factors (e.g., stream width), partly masking the between-species habitat differences observed in the simplified experimental settings. Due to habitat segregation, direct competitive encounters and aggressive acts between the species are largely avoided, allowing the inclusion of novel species with limited interspecific interference.

Habitat differentiation among the species reflected their differential habitat requirements, stressing the importance of comparing species' niches in their native and introduced ranges to better understand and predict their establishment and spread in novel environments. Our results support the hypotheses that a match between species niche requirements in its native range and habitat availability in the new environment may provide the basis for understanding invasion success (the "key-lock" principle of Heger & Trepl 2003). There are also other examples of this phenomenon: for example, an invasive tree species with roots that do not penetrate deep into the soil avoid root competition with native deep-rooted trees. Thus, the non-native tree has located an empty niche with no need for direct interspecific interference (Heger & Trepl 2003, see also Krassoi *et al.* 2008). Interestingly, we demonstrated a closely matching pattern between the two salmonid fishes, as brook trout inhabited a marginally inhabited slot (species-poor headwater stream pools), without major agonistic interactions with the native brown trout. Indeed, it may well be that such pre-adaptive niche differentiation may help explain the invasion success of non-native organisms more generally, far beyond the special case of stream salmonids reported here (see e.g. Ricciardi & Atkinson 2004, Strauss *et al.* 2006, Olden *et al.* 2006).

3.4 The effect of the non-native brook trout on the growth of the native brown trout (V)

In this paper, we studied whether brook trout suppress the growth of the native brown trout at early juvenile stages, thereby having potentially severe population

level effects on brown trout. As also in paper IV, we combined evidence from a small-scale experiment and broad-scale field surveys. The main result was that brook trout did not suppress the growth of brown trout, not in the experimental streams nor in the field. These results strongly indicate that the two species are not involved in major interspecific interactions with each other. Interestingly, however, the growth and stomach fullness of brook trout was reduced in the sympatric compared to the allopatric treatment, suggesting that, when forced together, the invader was the inferior competitor of the two species. In natural streams, however, the lack of spatial constraints allowed brook trout to achieve a high growth rate (compared to brown trout) even in the presence of the native competitor. This mismatch between experimental and observational results highlights the importance of performing studies at several scales using multiple methods in order to understand ecological phenomena. Further, the mismatch cautions against uncritical acceptance of findings from small-scale experiments, because they can rarely be extrapolated to more complex field situations (Werner 1998, Underwood *et al.* 2005, see also II). Indeed, artifacts from small-scale experiments may have wide-ranging consequences: for example, based on our experimental results, brook trout might be considered as a harmless invader in streams dominated by brown trout, whereas recent findings have shown that brook trout is in fact currently replacing the native brown trout in several North European watersheds (III, Spens *et al.* 2007). These results reinforce the idea that brook trout take advantage of underutilized niche space without major competitive interactions with brown trout (III, IV), resulting in a high growth rate and establishment of dense populations of the invader in North European streams.

4 Conclusions

An ability to understand and predict biological invasions is elemental for controlling the detrimental effects of introduced organisms on native biota. My results underline the importance of knowing species' niche characteristics to explain biological invasions. It appeared that interspecific aggression among brook trout and brown trout in their first summer were negligible, yet there was niche segregation between the species: brook trout occupied mainly pool habitats in small and acid streams while brown trout tended to reside in larger, fast-flowing riffles. Moreover, I found that brook trout did not suppress the growth of brown trout, a result further underlining that direct interspecific interactions among the species were weak. Given that brook trout has been highly successful in establishing populations in northern Europe (III, Spens *et al.* 2007, Öhlund *et al.* 2008), it seems obvious that the establishment has been facilitated by the presence of marginally utilized niche space (headwater streams and lakes). Brook trout appeared also as an efficient disperser locating unoccupied habitats in headwaters where they had high population densities, indicating high suitability of these habitats for the invader. The low fish species richness in the study streams, and North European streams in general (Matthews 1998), may facilitate the further spread of the invader without intense biotic interactions (i.e. biotic resistance) with the native fish. Moreover, brook trout is known as a successful invader in regions where the natural flow regime resembles that in its ancestral native range (spring flood – winter low flows) (Fausch 2008), much as in the streams studied here. Thus, brook trout are 'preadapted by chance' (sensu Fausch 2008) to the environmental conditions of North European headwater streams, where they also meet low biotic resistance and unexploited niche opportunities. Therefore, it is likely that if propagule pressure is high enough (see Lockwood *et al.* 2005), as it certainly has been in my study streams (up to 1.5 million individuals introduced, mainly during 1970-1980), brook trout will continue to invade river systems even in the remote, near-pristine regions of northern Europe.

The habitat niche segregation pattern was weaker in the field than in simplified laboratory and mesocosm experiments. The species co-occurred in a large number of field sites with intermediate habitat characteristics (IV). In the zone of overlapping distributions an interesting pattern arose: brown trout was partially replaced during the 10-yr study period and its reproduction was reduced to negligible levels (III). These phenomena took place only in small streams (less than 7 m wide) that serve as a core habitat for brook trout adapted to the harsh

and variable headwater environments (Rahel & Nibberlink 1999, Baldigo & Lawrence 2000, Pirhalla 2004). I suggest that these adaptations facilitated the high ecological performance (high densities and growth rate) of brook trout, which eventually resulted in the replacement of brown trout in small streams. Similar results have been gained in Sweden, where brook trout had severe effects on the growth, maturation and mortality rates of the native brown trout that suffers from local extinctions due to brook trout invasion (Spens *et al.* 2007, Öhlund *et al.* 2008). It should be noticed, however, that brook trout may be only an indirect cause of this replacement process: stochastic effects (e.g. droughts, harsh winters) may repeatedly displace brown trout from headwaters, ensuring brook trout a permanent demographic advantage which could inhibit brown trout recolonization (Spens *et al.* 2007). Moreover, there are observations that spawning interactions (redd superimposition, hybridization) may also play a role in the replacement process between brook trout and brown trout both in North America (Grant *et al.* 2002) and Europe (Cucherousset *et al.* 2008).

The finding that brook trout grew faster than brown trout is interesting because the introduced brown trout has frequently been considered as the faster-growing species of the two in North America (Zorn & Nuhfer 2007, Carlson *et al.* 2007). Given that the growth patterns observed parallel the invasion success of each species in the two continents (Waters 1999, Spens *et al.* 2007, III), it thus seems possible that introduced species, by leaving their native enemies (predators, competitors, and parasites) behind, may generally increase their ecological performance as suggested by the enemy release hypothesis (Sax & Brown 2000, Shea & Chesson 2002, Torchin *et al.* 2003, see also II). Therefore, release from natural enemies may have facilitated and may further facilitate the invasion of European streams by brook trout.

Although the small headwater streams, where the distributions of the two species overlap, are marginal habitat for the native brown trout that dwell mainly in larger streams, it does not necessarily mean that headwaters are unimportant for the species. Firstly, genetic stocks of brown trout are considered threatened in many parts of Europe (Rassi *et al.* 2001, Almodóvar & Nicole 2004) and the few naturally reproducing populations that still remain in headwater streams have high adaptive and evolutionary significance. This is particularly so because populations in mainstream channels have been negatively affected by hydropower stations, overfishing, and extensive aquaculture releases (Northcote 1997). Secondly, headwaters can be crucial habitats not only for resident brown trout but also for the migratory brown trout inhabiting small streams temporarily for

spawning, as nursery habitats, or as thermal refuges (Meyer *et al.* 2007). Ironically, headwaters are the very environment where brook trout have established dense populations and threaten the native brown trout. To conclude, exclusion of brown trout in headwaters, but coexistence at the watershed-scale, is the likely outcome of this invasion process currently underway in numerous European river systems, strongly cautioning against any further stocking of brook trout. Moreover, it has been repeatedly observed across the world that introduced salmonids generally have detrimental impacts on native fish and even ecosystems (I, II), highlighting the need to cease these introductions, instead of being forced to costly and unreliable eradication measures after the harm has already been done.

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