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ORIGINAL PAPER

Invasion of north European streams by brook trout: hostile takeover or pre-adapted habitat niche segregation?

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Abstract We combine evidence from small-scale experiments with a large-scale field survey to clarify the roles of biotic resistance and pre-adapted habitat niche segregation to the invasion success of the North American brook trout (*Salvelinus fontinalis*) in North European streams previously dominated by brown trout (*Salmo trutta*). Interspecific aggressions among the two species were negligible, yet there was distinct habitat niche segregation between them: brook trout occupied mainly pool habitats while brown trout tended to reside in fast-flowing riffles. Habitat niche segregation among brook trout and brown trout prevailed across a wide array of scales from experimental flumes to entire drainage systems, although the segregation pattern was weaker in the field. Habitat differentiation among the two species reflected their differential habitat requirements, suggesting that a match between a species' niche requirements in its native range and habitat availability in the new environment is a prerequisite for understanding invasion success.

Keywords Habitat selection · Interspecific competition · Multi-scale approach · Niche differentiation · Nonnative salmonids · Trout

Introduction

When released in a novel environment, alien species meet biotic resistance by the native community, potentially hindering their establishment (Moyle and Light 1996). This is especially true if the host community contains species that resemble the newcomer ecologically, yet lack a shared history of niche differentiation with it. In order to establish in such a community, alien species should be competitively superior, resulting in 'hostile takeover' (sensu Melbourne et al. 2007). Alternatively, if there are considerable interspecific niche differences (pre-adaptations, see Connell 1980) among the invader and the native species, the invader may benefit from the presence of unexploited niches in its new environment. Hence, a close match between the niche requirements (e.g. food or habitat) of the invader and the presence of underutilized niche opportunities (sensu Shea and Chesson 2002) in the recipient ecosystem should enhance the probability of invader establishment (Ricciardi and Atkinson 2004; Strauss et al. 2006; Olden et al. 2006).

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Strong competitive ability is often regarded as a prerequisite for successful invasion (Sakai et al. 2001), yet the importance of competition is based largely on anecdotal information and correlative measures instead of experimental manipulation and direct observations of animal behavior (Holway and Suarez 1999; Peterson and Fausch 2003). However, results from manipulative experiments should also be interpreted cautiously, because they cannot be readily extrapolated to natural conditions if they have been conducted at restricted spatial scales that force individuals to compete in unrealistically high densities for unnaturally low resources. Therefore, to clarify the mechanisms that facilitate invasions, one should combine evidence from carefully planned manipulative experiments, often confined to small spatial and temporal scales, with large-scale correlative field surveys (Werner 1998). Such an innovative use of multiple methodological approaches has been rare in studies of salmonid invasions, a recent exception being the study by Blanchet et al. (2007a) who combined laboratory and semi-natural stream experiments to show that an alien intruder (rainbow trout, *Oncorhynchus mykiss* Waldbaum) disrupted the dominance hierarchy of a native species (Atlantic salmon, *Salmo salar* L.), but only if analyzed at the individual level. This negative impact of the exotic species was strong enough to potentially alter individual fitness and patterns of selection in native fish populations.

Due to their commercial value, stream salmonids are among the most extensively introduced species in the world (Rahel 2007). Salmonids are ideal organisms for assessing the relative roles of competitive interactions and pre-adapted niche segregation to invasion success. This is because stream salmonids are territorial drift-feeders, defending energetically optimal feeding positions (Fausch 1984; Nakano 1995). They also show habitat niche separation, often resulting in a distinct zonation pattern along the mainstream-headwater gradient (e.g. Flebbe 1994; Rahel and Nibbelink 1999; Korsu et al. 2007). Thus, distribution patterns of salmonids are regulated by processes effective at multiple spatial scales, eventually shaping the zonation pattern through the combined effect of species-specific niche adaptations and environmentally driven ecological performances (De Staso and Rahel 1994; Taniguchi and Nakano 2000; De la Hoz Franco and Budy 2005). Nevertheless, the relative roles of competitive interactions and adaptive habitat segregation to salmonid invasions remain unclear in most cases, making invasions look idiosyncratic and largely unpredictable (Korsu et al. 2008; Fausch 2008).

The European brown trout (*Salmo trutta* L.), although often considered as a dominant, aggressive competitor (DeWald and Wilzbach 1992; Blanchet et al. 2007b), occur sympatrically with the introduced brook trout (*Salvelinus fontinalis* Mitchill) in many European streams (Holčik 1991). Brown trout have been introduced to North America for more than 100 years, spreading extensively across the native range of brook trout. In many cases, pressure from the alien intruder has forced brook trout into spatial refugia in the upmost headwaters (Krueger and May 1991; Rahel and Nibbelink 1999). In Europe, by contrast, brook trout, that have been introduced from 1869 onwards (Holčik 1991), have established and spread within the native range of brown trout, whose some populations are now seriously threatened by the invader (Korsu et al. 2007; Spens et al. 2007; Cucherousset et al. 2008; but see Blanchet et al. 2007b). Cucherousset et al. (2007) showed recently that the presence of brook trout potentially causes brown trout to shift their diet toward terrestrial invertebrates. Thus, the invader may induce a niche shift in the native species, but little is known about the effects of direct interactions with brook trout on the habitat niche of brown trout in Europe. To clarify the relative roles of pre-adapted habitat niche segregation and biotic resistance through interspecific competition with brown trout in the invasion of brook trout in North European lowland streams, we performed a multi-scale study, ranging from behavioral observations and small-scale competition experiments to broad-scale field surveys. By using a substitutive experimental design (Fausch 1998) we were able to separate the effects of intra- vs. interspecific competition on aggressions and habitat use of the focal species. We then related these findings to the large-scale distribution patterns of the two trout species in two drainage systems in northern Finland.

Materials and methods

Experimental studies

The experiments were conducted, and experimental fishes reared, at Kainuu Fisheries Research (Finnish

Table 1 Key information on the four treatments of the three experiments

Experiment type	Flumes				Aquaria				Semi-natural streams			
Month of experiment	July				July				May–June			
Duration	2 h				2 h				15 days			
Mean water temperature (°C)	19.5				16.5				12.5			
Age of Brw	0				0				2			
Age of Brk	0				0				1			
Observation type	Video				Video				PIT			
Treatment	Brw	Brw + Brw	Brw + Brk	Brk	Brw	Brw + Brw	Brw + Brk	Brk	Brw	Brw + Brw	Brw + Brk	Brk
No. of replicates	5	5	9	4	6	6	11	6	5	5	5	3
No. of fish	3	6	6	3	2	4	4	2	5	10	10	5
Experimental arena (m^2)	0.25	0.25	0.25	0.25	0.125	0.125	0.125	0.125	13	13	13	13
Fish density (ind. m^{-2})	12	24	24	12	16	32	32	16	0.38	0.77	0.77	0.38

Brw brown trout, *Brk* brook trout

Game and Fisheries Research Institute), Finland (64°30′N, 27°10′E). We performed separate experiments in (1) indoor flumes, (2) indoor aquaria, and (3) outdoor semi-natural streams (Table 1). In each of these settings, we used hatchery fish and had four treatments: (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*). We performed the *Brw* + *Brw* treatment to control for the effects of increased fish density in the sympatric treatment. In particular, if brook trout dominated brown trout (i.e., interspecific competition was stronger than intraspecific competition), then the change in habitat use or aggressive behavior by brown trout from allopatric (*Brw*) to sympatric (*Brw* + *Brk*) treatments should be greater than from *Brw* to *Brw* + *Brw*. Comparison of the *Brw* vs. *Brk* treatments allowed us to test for differences in habitat niches of the two species in allopatry. Note that the substitutive design in our experiment was only partial, because a high-density treatment for brook trout was not included. This was partly because of logistical constraints (restricted number of experimental sections available), but also because brown trout was clearly the target species of our experiments, and intraspecific density effects of brook trout were of secondary importance.

We mainly focused on fish habitat use at the mesohabitat (pool/riffle) scale (see Hawkins et al. 1993; Morita et al. 2004), but in the behavioral laboratory trials (2), we also measured the vertical position of the species. Fish densities used in the experiments were generally within the range observed in natural streams in northern Finland. Densities in the aquarium experiments were relatively high (up to 32 fish m^{-2}; see Table 1), but even these are not completely unnatural for age-0 fish in favorable microhabitats in the field. Corresponding, or nearly so, densities have been reported for both brown trout and other salmonids in other subarctic streams (Muotka et al. 1998; Niemelä et al. 1999) and elsewhere (e.g. Grant and Kramer 1990). There was also a size difference among the two species in our experiments, brook trout being larger, but this reflected the situation in natural streams in our study area (Korsu et al. 2009) and elsewhere in northern Europe (Öhlund et al. 2008).

Indoor experiments

In running-water experiments, we used four indoor flumes with experimental arenas of 1 × 0.25 m (see Vehanen 2006). Fish emigration from the arenas was prevented by a wire mesh (mesh size 5 mm). To mimic a riffle habitat with variable current velocities and abundant low-velocity microhabitats, we placed a gravel (diameter 1–3 cm) bed and a velocity shelter (a 5 × 10 cm 'pocket' in the flume wall) in the upstream portion of the arena (hereafter called 'riffle'). No structures were installed in the downstream portions which had less turbulent flow ('run'). We could not use greater habitat complexity in these experiments because this would have created high water turbulence, thus obstructing visual observations of fish behavior. Mean water velocity was similar (0.16 m s^{-1}) among the sections, but it was more variable in the riffles than in the runs (CV: 0.70 vs. 0.42, respectively, $t_6 = 8.15$, $P < 0.001$). Maximum water velocity in the riffles was 0.25 m s^{-1}, whereas it was 0.20 m s^{-1} in the runs. Water depth varied little, being 4.5–5.0 cm in the runs and 3.5–4.5 cm in the riffles. More information about the experimental system is available in Vehanen (2006).

Standing-water experiments were conducted in glass aquaria (50 × 25 × 30 cm) with no added structure. These experiments were conducted to mimic drought periods during which fish in small streams are trapped in isolated still-water pools where their density is typically high (see Grant and Kramer 1990), a situation potentially intensifying competitive interactions (Magoulick and Kobza 2003).

We randomized the four treatments among the experimental units in both experiments. The experiments were conducted between 4th and 10th July 2005 (Table 1). Fishes for each trial were randomly selected from rearing tanks and transported immediately to experimental units. We used age-0 fish in these experiments because competitive interactions are known to be intense at this stage (e.g., Rose 1986; Peterson et al. 2004). Reared brook trout grew faster than brown trout, resulting in a length difference of 10 mm (brown trout 44 ± 3 mm vs. brook trout 54 ± 2 mm; mean ± 1 SD) at the start of the experiments. Fish were allowed to acclimate in the experimental arenas for 20 h before the start of the trials. Fish were not fed during the experiments.

After the acclimation period, we started to film fish behavior using video cameras placed one meter above each flume. Fish behavior in the aquaria was videotaped from the side. 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 h, in 40-s intervals for each arena. We analyzed 30 such intervals, for a total of 20 min per arena, recording inter- and intraspecific aggressions (chases, displaces, and bites combined) and fish habitat use. Habitat use was recorded by marking fish locations on a map of the arena in the beginning of each 40-s observation period. For the flume experiments, we calculated the mean frequency of fish in the two habitat types (run vs. riffle), and for the aquarium experiments, we recorded the vertical positions of fish in the water column.

We used one-way ANOVA to test for differences between treatments in the total number of agonistic acts. In the *Brw* + *Brk* treatment, we also used one-way ANOVA to test for differences in the proportions of the four types of aggressions (arcsin-transformed): (1) brown trout intraspecific; (2) interspecific, initiated by brown trout; (3) interspecific, initiated by brook trout; and (4) brook trout intraspecific. We used one-way ANOVA to examine the effect of brook trout on the habitat use (flume experiments: % of fish in runs, arcsin-transformed; aquarium experiments: vertical position of fish, cm from the bottom, log-transformed) of brown trout (by comparing *Brw*, *Brw* + *Brw* and *Brw* + *Brk*). Finally, *t*-test was used to compare the habitat use of the two species in the allopatric, low-density treatments.

Outdoor experiments

We conducted habitat selection experiments in six 26-m long and 1.5-m wide outdoor semi-natural stream channels (see Vehanen 2006). An upstream lake provided a continuous water supply for the channels. The channel walls were made of concrete, but the stream bed consisted of gravel and cobbles. 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). The nets were installed 15 cm above the water surface to achieve a high PIT-tag signal strength (see below). Light level in a nearby stream was similar to that measured under the camouflage nets (mean ± 1 SD: 8.9 ± 2.6 vs. 8.8 ± 3.7 klux, respectively; $n = 20$) in the experimental channels, suggesting that the nets mimicked natural stream canopy rather well. The channels supported benthic invertebrate communities closely similar to those in a nearby river in terms of both species composition and total density (Vehanen 2006). Therefore, we did not feed the fish during the experiments. We divided each of the six streams in three sections using wire mesh (mesh size 10 mm) which was cleared of organic matter each day of the trial to ensure normal water flow. Based on semiquantitative kick-net samples, the mean density of benthic invertebrates was 3,500 ind. m^{-2} (SD = 971.6) and it was unaffected by the position of a section within a stream (one-way ANOVA, $F_{2,15} = 0.25$, $P = 0.78$). Each section comprised an upstream riffle (water velocity 20–60 cm s^{-1}, depth 15–25 cm, mean substrate diameter 15 cm, mean invertebrate density 6,263 ind. m^{-2}) and a downstream pool section (velocity 0–20 cm s^{-1}, depth 25–35 cm, substrate size 4 cm, invertebrate density 745 ind. m^{-2}). Hence, we had 18 similar sections, where we performed the four treatments. Before fish were released to experimental arenas, we anaesthetized (MS-222) them and injected their body cavities with 23 mm PIT-tags (Passive Integrated Transponder) to obtain individual-level data on fish habitat use. To mimic the natural size difference in the field during the experiments, we used age-1 brook trout (mean length 18.1 cm, weight 66.9 g) and age-2 brown trout (mean length 16.6 cm, weight 51.4 g) in these trials. We could not use age-0 fish in these trials because (1) age-0 fish were too small for 23-mm PIT tagging, and (2) they would have escaped through the wire mesh separating different experimental sections, thus obscuring the initial treatments.

During the study period (29 May–13 June 2006), we located the fish four times by slowly moving a customized portable PIT-antennae (Texas Instruments TIRIS S-2000; Linnansaari et al. 2007) above the camouflage nets (about 20 cm above the water surface) in the upstream direction. When a fish was located, we marked its individual code on a map. We located the fish twice around midnight and twice at noon, but since there were no diel differences in habitat use (due probably to high ambient light throughout the day during the experiment), we combined data across the four sampling events. We obtained a signal from each fish in all study sections during the experiment, suggesting that the PIT technique was very efficient.

Prior to analysis, we checked for potential effects of the location of a section (upstream–downstream) on fish habitat use. No such effect was found (one-way ANOVA, $F_{2,15} = 0.56$, $P = 0.59$) and we therefore consider experimental sections independent. We used one-way ANOVA and *t*-test to examine for differences between treatments in fish position (riffles vs. pools), using distance (m) upstream from the pool outlet (log-transformed) as a proxy of fish position, with the first four meters referring to pools and four to eight meters to riffles.

Field surveys

To investigate whether results from small-scale experiments translate to more relevant natural scales, we conducted an extensive field survey in two lowland drainage systems (River Kemijoki, 67°N, 28°E, and River Iijoki, 65°N, 28°E) in northern Finland (Table 2). Brook trout were introduced in multiple events in both systems in the 1970s and 1980s (archives of the Finnish Game and Fisheries Research Institute), but introductions ceased in 1983 in River Kemijoki and 2000 in River Iijoki. Up till now, brook trout have established naturally reproducing populations in both rivers, and their present distribution thus overlaps extensively with that of brown trout, but allopatric sites are also frequent in both rivers. Species richness in our study streams was low: we collected on average three species (including both trout species) per sampling site. Other species present (usually in very low numbers) 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 (*Pungitus pungitus* L.) and European grayling (*Thymallus thymallus* L.).

Altogether 142 stream sites (elevation range: 150–300 m) within the two drainage systems (Table 2) were sampled using electrofishing (Bohlin et al. 1989). The distance between two consecutive sites within a stream varied from 300 m to several kilometers**.** Sampling started from the downstream end of a site, and it was performed by two persons, one operating the backpack electroshocker, the other using

Table 2 Mean values (range) of habitat variables in the two studied drainage systems in northern Finland. Number of sites sampled (*N*) for each site category is also given

	Drainage system	
	River Iijoki	River Kemijoki
Habitat variable		
Width (m)	6.8 (1–100)	9.7 (1–60)
pH	5.1 (4.1–7.1)	6.6 (4.9–7.2)
Velocity (m s^{-1})[a]	0.18 (0.04–0.48)	0.37 (0.07–0.68)
Depth (cm)	25 (10–57)	36 (11–66)
Substrate size[b]	4.7 (0.4–7.8)	4.2 (0.0–7.4)
Aquatic vegetation (% cover)	49 (1–88)	54 (1–100)
Site category		
Allopatric brook trout (*N*)	13	15
Sympatric (*N*)	15	45
Allopatric brown trout (*N*)	10	44
Area sampled (m^2)	200 (46–1,300)	224 (30–636)
Site lenght (m)	49 (12–112)	37 (12–74)

[a] At 0.6× depth

[b] *Modified Wenthworth scale*: (0) <0.07 mm, (1) 0.07–2 mm, (2) 2.1–8 mm, (3) 8.1–16 mm, (4) 16.1–32 mm, (5) 32.1–64 mm, (6) 64.1–128 mm, (7) 128.1–256 mm, (8) >256.1 mm

a dip net to catch stunned fish. One to three passes per site were made, but here we only use data from the first pass to standardize data among sites and drainage systems. In sites where several passes were made, catch probabilities (*P*) for brown trout and brook trout were 0.39–0.60 and 0.41–0.55, respectively. All fish captured were measured and then returned into the stream. Sampling was conducted during late summer low-flows between 2000 and 2005. Based on spot measurements, water temperature during the sampling varied between 5 and 15°C. The temperature difference between the largest (60 m wide) downstream river sections and the smallest (1 m) tributary streams was on average less than 2°C. Using trout presence–absence information, we categorized sampling sites in three groups (brown trout only—*Brw*; sympatric sites—*Brw* + *Brk*; brook trout only—*Brk*). We measured several in-stream habitat variables (water velocity, depth, substrate size, aquatic vegetation, stream width; see Table 2) at each site along randomly placed cross-sectional transects covering the whole study section. The number of measurements along these transects varied between 18 and 25, depending on stream width and area sampled. We also measured water pH at each site using a portable recorder (WTW pH/cond 340i/set®). Principal Component Analysis (PCA) was used to reduce environmental variability into a few interpretable components with eigenvalues >1.0. The environmental variables measured (log- or arcsin-transformed if needed) were entered in this analysis to examine whether the site groupings (*Brw* vs. *Brw* + *Brk* vs. *Brk*) differed in the multivariate habitat space. However, as the water temperature data were based on spot measurements, we did not consider them reliable enough and they were therefore omitted from this analysis. We performed all statistical analyses with SPSS for Windows version 12.0.1® (SPSS Inc., Chicago, USA).

Results

Fish species combination affected the total number of aggressive acts both in the flume (one-way ANOVA, $F_{3,21} = 11.65$, $P < 0.001$) (Fig. 1a) and in the aquarium experiment ($F_{3,28} = 5.68$, $P = 0.004$) (Fig. 1b). For both experiments, the rate of aggressions was highest in the *Brw* + *Brw* treatment. The relative proportions of the four types of inter- and intraspecific aggression in the *Brw* + *Brk* treatments (brown trout intraspecific; interspecific initiated by brown trout; interspecific initiated by brook trout; brook trout intraspecific) did not differ either in the flume (one-way ANOVA on arcsin-transformed data, $F_{3,35} = 1.13$, $P = 0.20$) or the aquarium experiment ($F_{3,43} = 0.76$, $P = 0.52$) (Fig. 1c, d).

In the indoor flumes, the habitat use (% in run) of brown trout was similar in all treatments ($F_{2,16} = 0.92$, $P = 0.42$, Fig. 2). In the presence of brown trout, brook trout were almost completely restricted to runs, but when brown trout were absent, brook trout shifted slightly toward riffles (*Brk* vs. *Brw* + *Brk*; $t_{11} = -2.70$, $P = 0.02$). This shift, however, may have occurred because of the increased total fish density in the *Brw* + *Brk* compared to *Brk* treatment. In allopatric treatments (*Brw* vs. *Brk*), the habitat use of the two species differed distinctly (% in run, $t_7 = 2.63$, $P = 0.04$), with brook trout being more restricted to runs (Fig. 2). Microhabitat segregation was also obvious in the aquarium

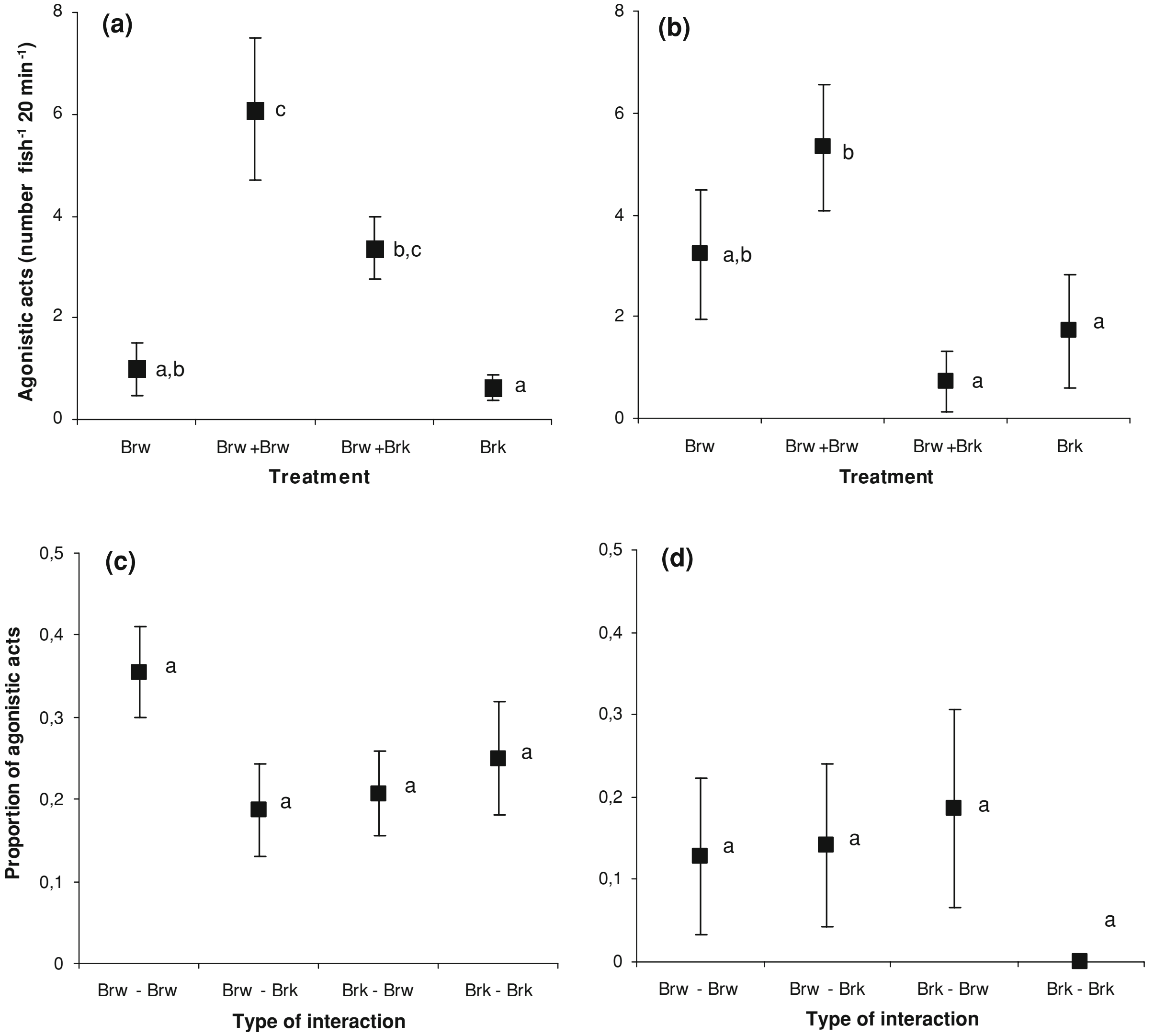

Fig. 1 Mean (±1 SE) number of total agonistic acts (acts/fish/20 min) for different treatments in the flume (**a**) and the aquarium experiment (**b**). Treatments with a *similar letter* do not differ significantly (Tukey's test, $P > 0.05$). Brw, brown trout; Brk, brook trout. Proportions of different interaction types in the sympatric treatment (Brw + Brk) in the flume (**c**) and the aquarium experiment (**d**). Brw-Brw, brown trout intraspecific; Brw-Brk, interspecific, initiated by brown trout; Bkr-Brw, interspecific, initiated by brook trout; Brk-Brk, brook trout intraspecific

experiment: brook trout used the upper parts of the water column, while brown trout remained closer to the bottom (*Brw* vs. *Brk*, $t_9 = -3.01$, $P = 0.01$, Fig. 3). However, treatment did not have any effect on the vertical position of either species (*Brw* vs. *Brw* + *Brw* vs. *Brw* + *Brk*; $F_{2,22} = 1.52$, $P = 0.24$; *Brk* vs. *Brw* + *Brk*; $t_{15} = 0.94$, $P = 0.36$).

The outdoor artificial stream experiments also illustrated clear habitat segregation between the species. Brook trout were found in pools, whereas brown trout occurred almost exclusively in riffles (*Brw* vs. *Brk*, $t_6 = 3.33$, $P = 0.02$; Fig. 4). Treatment had no effect on the habitat use of either species (brown trout: $F_{2,12} = 0.24$, $P = 0.79$; brook trout: $t_6 = -0.34$, $P = 0.74$).

In natural streams, allopatric brook trout sites were characterized by low current velocities and small substrates (i.e. pools), whereas the opposite was true

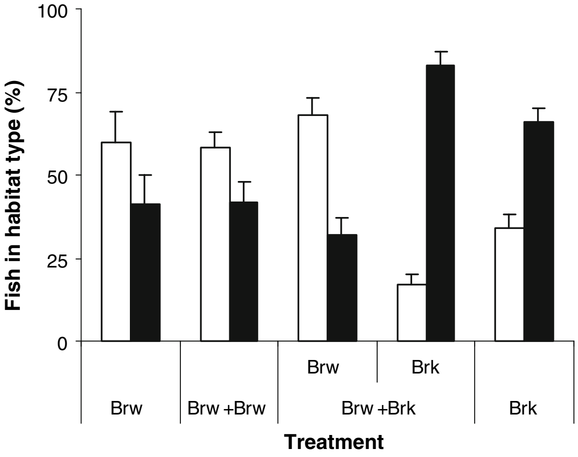

Fig. 2 Mean (±1 SE) percent of brown trout (Brw) and brook trout (Brk) in different habitat types, runs (*black bars*) and riffles (*open bars*), in the four treatments of the indoor flume experiments

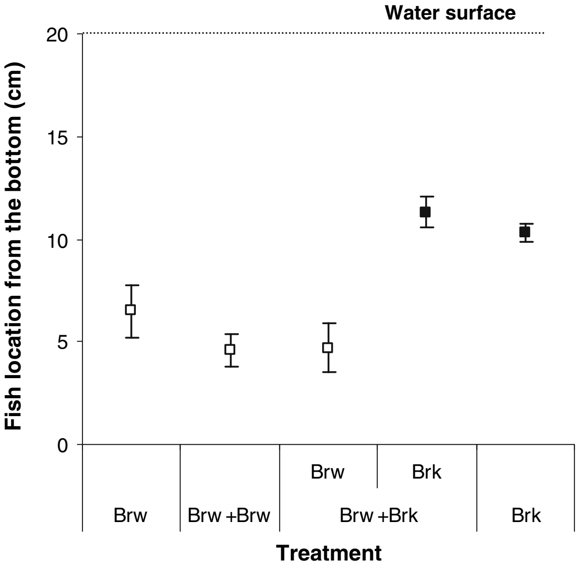

Fig. 3 Mean *vertical positions* (cm above bottom, mean ± 1 SE) of brown trout (Brw) and brook trout (Brk) in the four treatments of the aquarium experiments

for allopatric brown trout sites where current velocities were higher and substrates larger. However, the difference was rather small, being roughly 0.1 m s^{-1} for water velocity and a few centimeters for substrate size (Fig. 5a). PCA analysis showed largely similar results: within each drainage, allopatric brook trout sites were in narrower and more acid streams with lower current velocities, smaller substrates and deeper

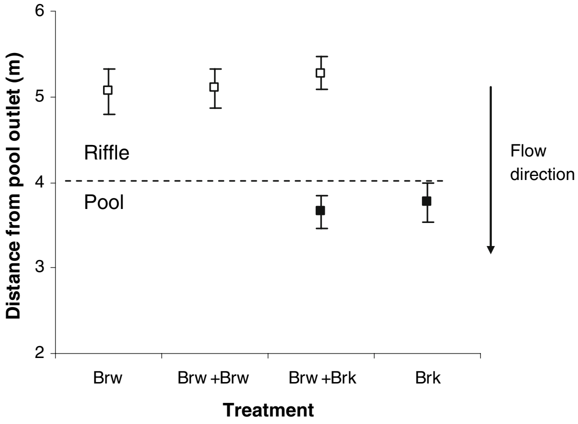

Fig. 4 Mean distance (m, ±1 SE) of brown trout (Brw, ☐) and brook trout (Brk, ■) upstream from the pool outlet in different treatments of the outdoor semi-natural stream experiments. 1–4 m refer to pools and 4–8 m to riffles

water, whereas allopatric brown trout sites were in wider, shallower, circumneutral streams with larger substrates. Sympatric sites tended to be intermediate in most characteristics (Fig. 5b).

Discussion

Our results demonstrate the existence of habitat segregation between the invading brook trout and native brown trout in laboratory and mesocosm experiments. This segregation appeared both vertically, with brook trout using upper parts of the water column, and horizontally, brook trout occupying mainly low-velocity pool or run habitats while brown trout tended to reside in riffles (see also Blanchet et al. 2007b). Furthermore, the same pattern of 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. The fact that the small-scale experimental results did not fully extrapolate to natural situations was due probably to the numerous environmental correlates in the field (e.g., stream width) partly masking the distinct between-species mesohabitat differences observed in the simplified experimental setting. Overall, however, our results suggest that pre-adaptations to species-specific fundamental habitat niches do play a role in the field where the habitat distributions of the two

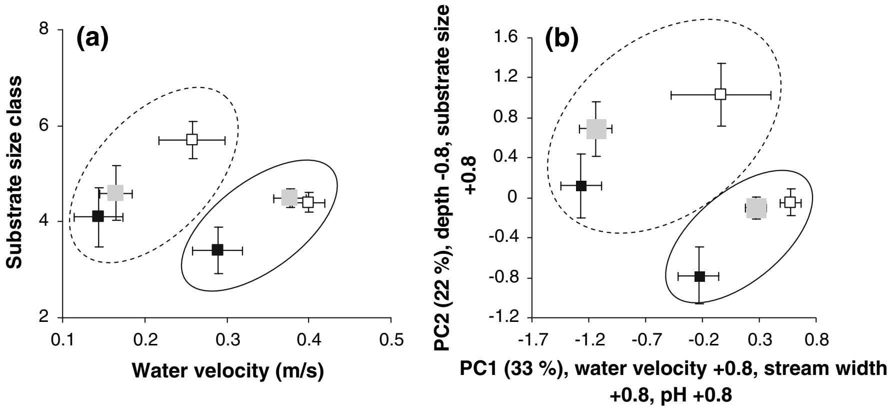

Fig. 5 Mean water velocities and substrate sizes (±1 SE) (**a**) and mean PCA scores (±1 SE) of the stream habitat data (**b**) in the three stream types studied. *Black squares* brook trout sites, *grey squares* sympatric sites, *open squares* brown trout sites. Study sites represent two drainage systems in northern Finland, River Iijoki (*dashed lines*) and River Kemijoki (*solid lines*). For substrate size categorization, see Table 2. Variation explained (%) by the two PCA axes and the highest loadings of the original habitat variables (see Table 2) are also given

species could be predicted based on their habitat use in small-scale experiments. Because of such habitat segregation, direct competitive encounters between the species are largely avoided, allowing a novel species packing with limited biotic resistance in our study systems. In the few occasions where the species showed interspecific aggressions, they were equally targeted toward both species. A largely similar explanation was proposed by Cunjak and Green (1984) to explain the stream-wide coexistence of the native brook trout and introduced rainbow trout in Newfoundland streams (see also Fausch 1988).

Although small-scale distributions of salmonid fishes are largely competition-driven (Fausch and White 1981; Cunjak and Green 1984; DeWald and Wilzbach 1992; Lohr and West 1992), we demonstrated the importance of pre-adapted niche segregation, with each species performing best in their species-specific environmental conditions (see also Taniguchi and Nakano 2000). Indeed, this may largely determine the distributions of riverine fishes along longitudinal gradients, where abiotic conditions change gradually. In our study systems, brook trout have become established in a habitat (headwater stream pools, see also Cunjak and Green 1984; Rahel and Nibbelink 1999) only marginally occupied by any native fish, usually brown trout that, however, mainly dwell in larger downstream sections (see Korsu et al. 2007). The segregation pattern in the field was, however, far from complete and the species co-occurred in a large number of sites in both river systems. Interestingly, environmental characteristics at sympatric sites were intermediate, possibly indicating that both species find suitable habitats in these mid-sized streams, allowing coexistence. Alternatively, this pattern of coexistence may not be stable, but rather represents a transient phase in the invasion process whereby the frontier of brook trout invasion is currently advancing towards the upmost headwater streams (Korsu et al. 2007).

In the experimental part of the study, the only indication of competition between the species was in the indoor flume experiments where a slight shift by brook trout toward riffles was observed in the absence of brown trout (*Brk* vs. *Brw* + *Brk*). Such flexible habitat niche adjustments are typical of stream salmonids (Hearn 1987), but the habitat shift observed in our study was rather weak. Moreover, as we performed no density control for brook trout, the shift might have occurred because of the increased total fish density in the *Brw* + *Brk* compared to *Brk* treatment.

The fish fauna of North European low-gradient streams is species-poor, offering niche opportunities for the establishment and spread of introduced species. Indeed, brook trout have already excluded brown trout in several North European headwater streams and lakes (see Korsu et al. 2007; Spens et al. 2007; Öhlund et al. 2008). Korsu et al. (2007) showed that the natural reproduction of brown trout (indicated by the presence of age-0 individuals) in the headwaters of a North Finnish river system ceased almost completely in the presence of brook trout, restricting brown trout to larger downstream sites less suitable for brook trout. At present, we do not know the mechanisms responsible of the replacement. Based on these results, however, aggressive behavior in the first summer of fry is a poor explanation because although fish density in the aquarium experiments was quite high, we did not detect any signs of intensified interspecific aggressions. Cucherousset et al. (2008) recently reported reproductive interactions and hybridization as mechanisms causing the negative population-level impact of brook trout on brow trout in southern Europe. Unfortunately, we have no corresponding data from our study systems. It is also possible that in some situations aggressions still may be important because the dominance relations between brook trout and brown trout can apparently change depending on study-specific conditions or source population of the fish (see Fausch and White 1981, 1986; DeWald and Wilzbach 1992; Blanchet et al. 2007b). For example, Fausch and White (1986) found brook trout to be the dominant species of the two in Great Lakes tributaries where both species were of similar size, whereas in our experiments brook trout, despite having a clear size advantage, did not dominate over brown trout. Finally, although brown trout in our study used almost exclusively riffles, there are other observations that brown trout may prefer pools over riffles (e.g. Fausch and White 1986; Greenberg et al. 2001). Habitat use of salmonid fishes is known to be flexible, changing daily and seasonally (e.g. Mäki-Petäys et al. 1997; Heggenes et al. 1999), and in relation to prey availability (Bridcut and Giller 1995). To this end, it is interesting to note that riffles in our artificial streams were far more productive than pools, and this may indeed be a partial explanation to brown trout's preference for this habitat type. The consistent use of riffles by brown trout may also be related to differential functional morphology of the two species, brown trout being more adept than brook trout at using pectoral fins to maintain position on the stream bed in fast flows (see Fausch 1984), thereby allowing them to use riffles.

Fausch (2008) presented a novel hypothesis to explain 'the paradox of invasion' (sensu Sax and Brown 2000) whereby brook trout that displace the native cutthroat trout (*Oncorhynchus clarkii* Richardson) in the western USA are themselves displaced by rainbow trout in the southeastern USA. The adaptation of species to natural disturbance regimes in their native ranges is a key factor in Fausch's (2008) model. Thus, brook trout is an effective invader in regions with low environmental resistance, i.e. where the natural flow regime (spring flood—winter low flows) resembles that in their ancestral native range. The extensive establishment of brook trout across our study systems partly supports this hypothesis, because these little-impacted high-latitude streams are characterized by snowmelt-induced spring floods and low winter flows. Largely similar flow pattern is typical in the southern Rocky Mountains where brook trout has been an effective invader of streams previously dominated by cutthroat trout. Thus, brook trout may be 'preadapted by chance' (see Fausch 2008) to the environmental conditions of North European headwater streams, where they also meet low biotic resistance and unexploited habitat niche opportunities, particularly in the headwater reaches of rivers. For instance, Correa and Gross (2008) had a largely similar explanation for the widespread establishment of North American Chinook salmon (*Oncorhynchus tshawytscha* Walbaum) in South America. Therefore, it is likely that if propagule pressure is high enough (as it certainly has been in many parts of North Europe), brook trout will continue to invade river systems even in the remote, near-pristine regions of northern Europe, much to the detriment of the native salmonid, the European brown trout.

Our results suggest 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 and Trepl 2003; see also Peterson and Vieglais 2001). 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 invader has located an empty niche, with little need for interspecific interference (Heger and Trepl 2003). Interestingly, we demonstrated a corresponding pattern among salmonid fishes, as brook trout, a species often considered as a headwater specialist (e.g. Rich et al. 2003), invaded a partly uninhabited slot (headwater streams) without major agonistic interactions with the native brown trout. Indeed, such pre-adapted niche differentiation may help explain the invasion success of alien organisms also more generally (e.g. Ricciardi and Atkinson 2004; Strauss et al. 2006; Olden et al. 2006; Krassoi et al. 2008). It is, however, an enormous task to demonstrate and quantify the critical characteristics of the invader and of the system invaded to create a powerful model (Lodge 1993; Heger and Trepl 2003). In any case, understanding the key environmental filters that determine the distributions of invasive species, and the scales at which these filters operate (see Poff 1997), is a necessary step toward effective risk assessment in the management of invasive species.

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