

Competitive interactions between native and exotic salmonids: a combined field and laboratory demonstration

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Abstract – We studied the impact of two exotic salmonid species (brook trout, *Salvelinus fontinalis* and rainbow trout, *Oncorhynchus mykiss*) on native brown trout (*Salmo trutta fario*) habitat, growth and survival. Habitat selection and vertical distribution between young-of-the-year of the three species were examined in a stream aquarium under different sympatric and allopatric combinations. In addition, similar species combinations were introduced in a Pyrenean mountain stream (southwest France) in order to extend laboratory results to growth and apparent survival. Both laboratory and field results indicated that rainbow trout significantly affected native brown trout habitat selection and apparent survival. On the contrary, brown trout habitat, growth and apparent survival were hardly affected by brook trout. These results support the idea that rainbow trout negatively influence native brown trout, and that competition could influence the outcome of fish biological invasions in freshwater ecosystems.

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Key words: biotic interactions; invasion; European streams; habitat selection; niche overlap; niche width; growth; apparent survival

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Introduction

Biotic interactions such as competition, predation or parasitism are considered to be major processes structuring communities and influencing the dynamics of the biocenoses (Begon et al. 1996). Connell (1983) and Schoener (1983) showed that competition is a very common phenomenon that occurs in most animal communities, and that both intra- and interspecific competitions can be harmful in terms of individual fitness and therefore affect the dynamics of populations. Recent works have underlined the role of competitive interactions in the dynamics of freshwater communities (Flecker & Townsend 1994; Vorburger & Ribi 1999; Cross & Benke 2002). Concerning fish, this phenomenon could be triggered through the introduction of exotic fish species that may compete with the native fauna (Crowl et al. 1992; Simon & Townsend 2003). This aspect has been reviewed for introduced salmonids by Crowl et al. (1992) and Fausch (1998). They demonstrated that interspecific

competition often occurs between native and introduced species and constitutes a determinant process affecting the outcome of nonindigenous invasions. In European streams, fisheries management policies have generated massive and regular stocking of exotic species for recreational angling purposes, which have promoted the acclimation or persistence of introduced species that are unable to reproduce in Europe (Ruesink et al. 1995; Keith & Allardi 2001). Indeed, Holcik (1991) listed at least 134 exotic and/or translocated species within 29 European countries. However, the ecological impact of invasive fish species on the native fauna is still hypothetical as potential interactions between native and introduced species in Europe have been little investigated (Elvira 1995, 2001; Williamson 1999).

The European native fish fauna is characterised by a very low species richness compared with similar streams in North American temperate regions. Oberdorff et al. (1998) suggested that European fish communities are unsaturated, and that some niches

could remain vacant. In this context, it seems likely that some introduced species could become established in Europe without depriving the native fauna. Therefore, we first investigated the strength of competition between native and exotic fish and the mechanisms involved in these competitive interactions. Finally, we discuss the competition outcome on native fauna sustainability.

For this purpose, salmonids were used as biological model as (1) salmonid biology benefits from a huge scientific background concerning ontogeny, habitat use, growth and population dynamics (Gatz et al. 1987; DeWald & Wilzbach 1992), (2) exotic salmonids, mainly rainbow trout, *Oncorhynchus mykiss* (Walbaum 1792) and brook trout, *Salvelinus fontinalis* (Mitchill 1814), are commonly introduced in many European rivers and constitute widespread populations, which are known to reproduce in some places in Pyrenean or Alpine rivers (Keith & Allardi 2001; Uiblein et al. 2001), (3) both rainbow trout and brook trout are often sympatric with the native brown trout, *Salmo trutta fario* (L.) (Delacoste et al. 1997; Keith & Allardi 2001; Uiblein et al. 2001) and (4) salmonids inhabit streams where fish species richness is low with a community originally dominated by brown trout, which avoids biases because of complex multispecific interactions.

We focused on two pairs of sympatric salmonids: brown trout versus brook trout and brown trout versus rainbow trout. Although previous studies demonstrated that brown trout generally outcompete both brook trout and rainbow trout with respect to spatial and feeding resources (e.g., Fausch & White 1981; Gatz et al. 1987; Kocik & Taylor 1995), the importance of competition for rainbow trout invasion success remains controversial (Fausch et al. 2001). Moreover, these studies were conducted in North American streams, where the brown trout are an introduced species. These results may therefore not be representative of the European situation. In this work, we considered young-of-the-year (YOY) fish, as the juvenile period is a critical period in the fish life cycle, which greatly influences the entire population dynamics (Byström et al. 1998). In addition, we also quantified intraspecific competition between YOY brown trout individuals, which is a crucial aspect for quantifying the strength of interspecific interactions (Creese & Underwood 1982; Cross & Benke 2002). We combined a laboratory stream experiment and biomanipulation in a small French Pyrenean stream. We first measured species competitive ability in the laboratory stream by measuring habitat selection and vertical distribution under different species combinations. Then, the field experiment allowed these results to be extended to fish growth and survival in a natural stream.

Materials and methods

Biological material

Fish used for laboratory and field experiments were wild strain YOY fish produced by regional hatcheries aiming to mimic the natural situation, as fish stocking constitutes a common procedure in most European streams (Poteaux et al. 1998). The mean total body lengths for brown trout, rainbow trout and brook trout were, respectively, 38.1 (± 3.02), 37.1 (± 4.4) and 37.9 (± 3.9) mm for the laboratory experiments and 35.4 (± 5.3), 51.4 (± 5.9) and 31.9 (± 3.8) mm for the field experiment.

Laboratory experiments

Experiments were conducted in an artificial channel fitted with a recirculating water system. The channel measured 4 m long, 0.20 m wide and 0.25 m deep (see Blanchet 2003 for more details). It was made of clear Plexiglas to permit direct visual observation. Two fine mesh grills were placed at each extremity of the channel to prevent fish escape. Two riffle/pool successions were shaped using sand, gravel and small and large pebbles to reproduce the natural stream granulometry with both sandy flats and pebble shelters. The water in each pool was 10–20 cm deep with a velocity of 0–15 $\text{cm}\cdot\text{s}^{-1}$. The riffles were 0–10 cm deep with a velocity of 0–35 $\text{cm}\cdot\text{s}^{-1}$. The current velocity used was based on a preliminary study conducted to determine the preferential velocity range of YOY trout (Blanchet & Brosse unpublished data). All the experiments were conducted at a water temperature of 15 °C (± 1 °C) and with the natural photoperiod. The available habitat was quantified by dividing the channel surface into 10 cm × 10 cm cells. For each of the 80 resulting cells, three habitat variables were measured: water depth (to the nearest 0.5 cm); water velocity (to the nearest 0.5 $\text{cm}\cdot\text{s}^{-1}$) measured using a wading rod and an electronic flow meter; and the percentage of large pebbles was visually determined. Such variables are considered to be general integrative variables describing salmonid habitat (Bovee 1982; Gatz et al. 1987). Fish were fed *ad libitum* using commercial food (i.e., micropellets). Micropellets were dropped at dawn and dusk (i.e., at least 1 h before or after observation) at the upstream end of the channel to allow even the most subordinate fish to obtain food. Habitat selection was therefore driven by the search for optimal space selection, each individual seeking to minimise energy expenditure (Fausch 1984).

The experimental design used to describe fish habitat selection and biotic interactions was inspired by Underwood (1986) and Fausch (1998): six different

Table 1. Experimental design in the laboratory experiment (experiments L1–L6) and in the field study (experiments F1–F4, from downstream to upstream).

Experiment	Number of fish introduced			Total density (ind·m ⁻²)
	RWT	BKT	BNT	
L1	5	–	–	5
L2	–	5	–	5
L3	–	–	5	5
L4	5	–	5	10
L5	–	5	5	10
L6	–	–	10	10
F1	136	–	136	0.5
F2	–	131	131	0.5
F3	–	–	293	0.5
F4	–	–	108	0.25

RWT, rainbow trout; BKT, brook trout; BNT, brown trout.

fish combinations were tested to sort out the effects of intraspecific brown trout competition and interspecific competition with rainbow trout and brook trout (Table 1). The fish density was set to a low value (i.e., 5 ind·m⁻²) in experiments L1, L2 and L3. In experiments L4, L5 and L6, fish density was higher (10 ind·m⁻²) to determine the impact of interspecific (experiments L4 and L5) and intraspecific (experiment L6) competitions. Each manipulation was repeated twice. For each low-density experiment (L1, L2 and L3), observations began after 15 h acclimatisation time and lasted 1 day. For experiments L4, L5 and L6, 5 ind·m⁻² of brown trout was first introduced in the channel and the other individuals (i.e., exotic species or brown trout) were introduced after 15 h brown trout acclimatisation to reproduce natural prior residence (Hayes 1989; Volpe et al. 2001). Then, fish observations began 24 h after the last introduction to ensure acclimatisation of all the fish, and lasted 1 day. Such acclimatisation periods have been found sufficient to ensure that each fish has selected its habitat and exhibits natural behaviour (Blanchet 2003; Young 2004). Fish horizontal and vertical distributions were recorded each hour for 10 h in each experiment. Vertical distribution was measured in the pools where depth allows fish to actively select their position in the water column. Vertical position was divided into three categories: category 1, first mid of the water column (surface); category 2, second mid of the column

Competition between native and exotic salmonids

(bottom), excluding fish lying on the bottom and category 3, fish staying on the bottom without swimming activity or fish sheltering in the substratum.

Field experiment

The experiment was carried out on the River Luz (43°06'N–0°12'E, Pyrenees mountains, southwest France). This stream flows from 700 m.a.s.l. to the River Arros, 300 m below. The section selected for this study was located 460 m.a.s.l., mean discharge was 0.4 m³·s⁻¹ and the stream was about 5 m wide and 0.20 m deep. Brown trout was the dominant species, accompanied by three small-bodied species: European minnow (*Phoxinus phoxinus* L.), stone loach (*Barbatula barbatula* L.) and River Lamprey (*Lampetra planeri* L.). In a preliminary study, we found a very low density of YOY brown trout (less than 0.05 ind·m⁻²) (Blanchet 2003). This allowed us to entirely control the YOY salmonid restocking experiments performed during the study. To avoid biases because of environmental variability, we preferred to establish sampling reaches on the same stream section. We therefore selected four similar stream reaches, from both physical and biological characteristics: depth, width, velocity, abundance and size structure of potential predators, i.e., ≥1-year-old brown trout (Table 2). The use of stop or seine nets, to avoid fish dispersion from one reach to the others, was not possible because of the high current velocity. Nevertheless, reaches were about 100 m long, each separated by a high flow velocity section (i.e., current velocity >100 cm·s⁻¹) of at least 25 m long to avoid upstream 0+ salmonid migrations (Jorgensen & Berg 1991; Mitro & Zale 2000, 2002). Moreover, fish were released in the first 50 upstream metres of each 100 m stream reach to avoid downstream fish exchanges between reaches. Indeed, Jonsson et al. (1999) and Bohlin et al. (2002) showed that at least 80% of the juvenile brown trout do not disperse further than 20 m from the stocking point during the first 2 months after introduction. Four different salmonid combinations (experiments F1–F4, Table 1) were introduced in the four 50 m experimental reaches.

Fish stocking was performed in early April 2003 and the YOY salmonid densities introduced into the

Table 2. Biological and physical characteristics of the four stream reaches (F1–F4) selected for the field study (mean ± SD value).

	F1	F2	F3	F4
Density BNT ≥ 1 year old (ind·m ⁻²)	0.39	0.5	0.54	0.42
Size BNT ≥ 1 year old (mm)	154.4 ± 41.2	169.0 ± 35.4	167.2 ± 42.0	149.5 ± 28.8
Depth (cm)	15.7 ± 7.7	20.8 ± 9.5	21.9 ± 11.2	23.4 ± 9.5
Velocity (m·s ⁻¹)	0.38 ± 0.22	0.33 ± 0.25	0.33 ± 0.29	0.30 ± 0.24
Width (m)	5.6 ± 0.3	4.9 ± 0.4	5.9 ± 0.9	4.4 ± 0.2
Reach length (m)	97.5	104.9	98.8	98.1

BNT, brown trout.

stream were close to the maximum observed in Pyrenean streams (Liebig 1998; see Table 1). Fish were recaptured 50 days later within the entire 100 m reaches to maximise the recapture rate (Jonsson et al. 1999; Bohlin et al. 2002). We performed a single-pass removal electrofishing (Lobon-Cervia & Utrilla 1993; Kruse et al. 1998) using a 10 cm ring anode, which is efficient at capturing the entire range of YOY fish sizes (Copp 1989). Fish collected in each sample were counted and identified to species level. This sampling design allowed us to estimate the species growth rate for each reach and each species combination. Daily instantaneous growth rates (G_i) were calculated as follows

$$G_i = \frac{\ln(\text{TL}_{t_2}) - \ln(\text{TL}_{t_1})}{(t_2 - t_1)}$$

where TL_{t_1} is the mean total length at introduction, TL_{t_2} the individual total length 50 days later and $(t_2 - t_1)$ equals 50 days. Finally, the percentage recapture (i.e., apparent survival) was used to estimate the percentage of individuals settled in the reach after a 50-day period.

Data processing

Habitat data obtained in the laboratory were used to develop habitat indices for each environmental variable as a measurement of habitat use by the fish population versus habitat availability. Habitat indices were calculated after dividing each variable into several categories. Habitat indices, based on the method of Beecher et al. (1993), were calculated as a ratio of utilisation to availability for the different categories of each environmental variable. This ratio was then normalised to vary between -1 and +1. Positive values indicate a preference and negative values avoidance for a given variable. The following formula was used

$$M_i = \left[\frac{(n_i/n_t)/(p_i/p_t)}{[(n_i/n_t)(p_i/p_t)] \max} - 0.5 \right] \times 2$$

where M_i is the normalised habitat index for category i ; n_i the number of samples with fish in the considered category; n_t the total number of individuals; p_i the number of samples belonging to category i and p_t the total number of samples in the reach.

Habitat selection differences were assessed using niche width and niche overlap indices. For each habitat variable, the observed niche width was measured by the standard deviation (Magurran 1984) of 90 habitat selection measurements. We used a bootstrap randomisation procedure to test whether the observed values of niche width differed from those expected under the null hypothesis H_0 (i.e., the species is

indifferent to its environment). To do this, we calculated the simulated niche width based on 90 available habitat measurements. We evaluated the significance of the observed niche width by comparing it to the distribution of 1000 simulated values obtained under the null hypothesis (Manly 1994). If less than 5% of the permutation values were lower than the observed one, we concluded that there was habitat selection (i.e., species has narrower niche width than expected by chance).

Niche overlap between species combinations was calculated using the nonparametric index for continuous data (NO) developed by Mouillot et al. (2005). NO is based on kernel density functions and calculated with the following formula

$$\text{NO}_k(i, j) = \int \min[f_{ik}(x), f_{jk}(x)] dx$$

where f_{ik} and f_{jk} are the kernel density functions for species i and j and habitat variable k . NO varies from 0 when the two distributions are disjoint to 1 when they are perfectly similar.

In accordance with Mouillot et al. (2005), the synthetic niche width and niche overlap were calculated by averaging the values obtained for the three habitat variables. Finally, bootstrap randomisation procedures were used to test differences between species combinations (pairwise comparisons, Manly 1994).

Growth rate differences were tested using one-way analysis of variance (ANOVA) followed by a Tukey multiple comparison test (Zar 1999). Differences in vertical distributions between species were assessed using Pearson's chi-square test with Yates' continuity correction applied to frequency data. Finally, the results concerning recapture were compared using a chi-square test applied to frequency data. For both latter analyses, we adjusted the alpha level using Bonferroni correction to account for the effect of multiple comparisons.

The inferential statistics used in the field experiment did not allow to generalise our results to a wider population (lack of replication), but can be employed in the context of the present study to assess the reliability of the descriptive statistics (Hurlbert 1984; Oksanen 2001; Cottenie & De Meester 2003).

Results

Laboratory experiments

Habitat selection

In low-density conditions, the habitat of brown trout, rainbow trout and brook trout showed high similarities, with fish using deeper areas, low velocities and a mixed substratum with ca. 50% of pebbles

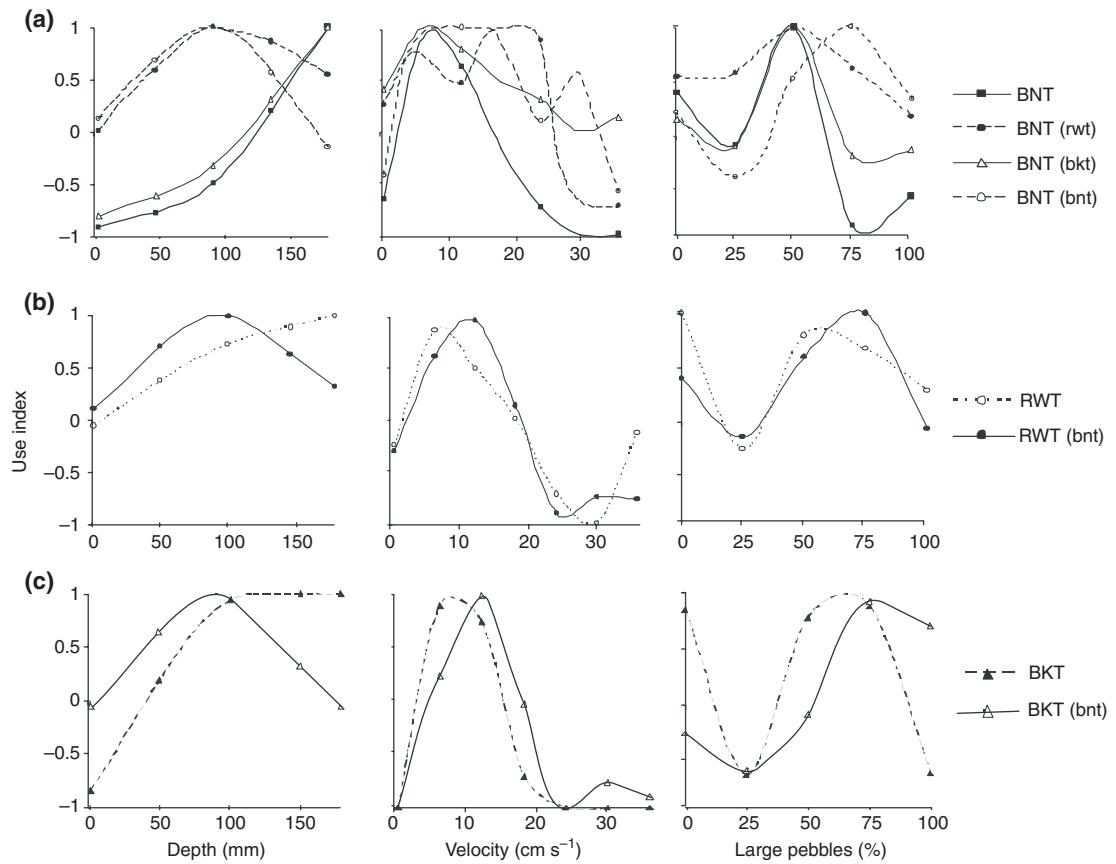


Fig. 1. Habitat indices in the laboratory experiments. (a) Brown trout (BNT). BNT was maintained in allopatric conditions under low (BNT, $4 \text{ ind} \cdot \text{m}^{-2}$) and high (BNT(bnt), $8 \text{ ind} \cdot \text{m}^{-2}$) densities, and in sympatric conditions with rainbow trout (RWT) and brook trout (BKT). (b) Rainbow trout (RWT). RWT was maintained in allopatric conditions and in sympatric conditions with BNT. (c) Brook trout (BKT). BKT was maintained in allopatric conditions and in sympatric conditions with BNT. The notation $X(y)$ means habitat selection of species X when maintained in sympatry with species y [e.g., BNT(rwt) means habitat selection of brown trout in presence of rainbow trout].

(Fig. 1). This was confirmed as niche overlap between brown trout and, respectively, rainbow trout and brook trout was relatively high and did not differ significantly ($P > 0.05$; Fig. 2). For the three fish species, niche width was significantly narrower than expected by chance for both velocity and depth (Table 3). Only rainbow trout did not significantly select large pebbles.

At high brown trout density, the habitat selection of this species was strongly affected, with large changes for the three variables (Fig. 1a), leading to a low niche overlap [see BNT-BNT(bnt); Fig. 2] and a significant expansion of the niche compared with the low brown trout density ($P < 0.001$; Fig. 3). This niche expansion mainly occurred over large pebbles (i.e., absence of habitat selection for this variable in high-density conditions, Table 3), whereas niche selection was significant for both velocity and depth variables.

Similar habitat changes occurred when brown trout were in sympatry with rainbow trout (Fig. 1a). In that case, brown trout habitat selection remained significant only for velocity (Table 3), and overlap between

brown trout at a low density and in sympatry with rainbow trout was significantly higher than overlap between brown trout at low and high density [see BNT-BNT(bnt) and BNT-BNT(rwt), $P < 0.05$; Fig. 2].

On the contrary, in sympatry with brook trout, habitat selection by brown trout was hardly affected (Fig. 1a) and the niche overlap between brown trout at low density and brook trout was relatively high when compared with others situations [see BNT-BNT(bkt) compared with BNT-BNT(bnt) and BNT-BNT(rwt), $P < 0.001$; Fig. 2]. Thus, brown trout niche expansion was lower than that when this species was at a high density, or maintained with rainbow trout ($P < 0.01$; Fig. 3).

Rainbow trout habitat selection was hardly affected by brown trout (Fig. 1), although rainbow trout did not select any more depth in this situation (Table 3). The niche overlap between rainbow trout alone and rainbow trout with brown trout was high (Fig. 2), and niche width was not affected [see RWT compared with RWT (bnt), $P > 0.05$; Fig. 3].

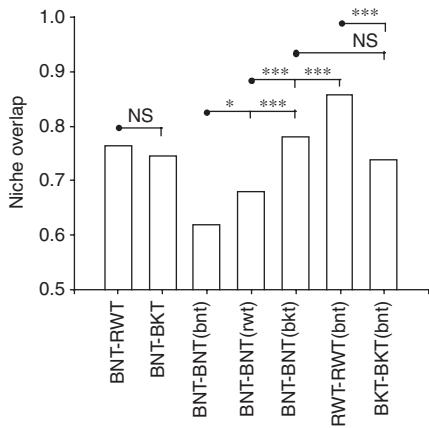


Fig. 2. Niche overlap between different species combinations for the three environmental variables. Brown trout: BNT; brook trout: BKT; rainbow trout: RWT. The notation $X(y)$ means habitat selection of species X when maintained in sympatry with species y . Differences between niche overlaps were only tested for comparisons relevant to this study. NS: not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$ and *** $P < 0.001$.

On the contrary, brook trout habitat selection differed in the presence of brown trout (Fig. 1), with a niche selection occurring only along the velocity gradient (Table 3). This was confirmed by a significant niche expansion [see BKT compared with BKT (bnt), $P < 0.001$; Fig. 3].

Vertical distribution

The water column utilisation differed significantly between species and treatments ($\chi^2 = 106.04$, d.f. = 14, $P < 0.001$). In low-density conditions, the distribution of brown trout significantly differed from the two other species ($\chi^2 = 44.66$, d.f. = 2, $P < 0.001$, for the comparison between brown trout and brook trout, and $\chi^2 = 37.28$, d.f. = 2, $P < 0.001$, for the comparison between brown trout and rainbow trout). The two exotic species occupied the entire water column (categories 1 and 2), whereas brown trout at low density occurred mainly in the lower half of the water column (Fig. 4). The nonswimming zone (category 3) was avoided by all three species.

At high brown trout density, surface layer use by this species significantly increased ($\chi^2 = 14.13$, d.f. = 2, $P < 0.001$) (Fig. 4a). On the contrary, neither rainbow trout nor brook trout affected brown trout vertical distribution (Fig. 4a, b) [see BNT compared with BNT (rwt), $\chi^2 = 4.418$, d.f. = 2, $P = 0.126$ and see BNT compared with BNT (bkt), $\chi^2 = 1.05$, d.f. = 2, $P = 0.591$].

Brown trout did not affect rainbow trout vertical distribution ($\chi^2 = 3.49$, d.f. = 2, $P = 0.174$; Fig. 4b) but significantly affect brook trout vertical distribution ($\chi^2 = 10.45$, d.f. = 2, $P = 0.006$), as the use of category 3 by brook trout significantly increased when brown trout was present (Fig. 4c).

Field experiments

Percentage recapture

The recapture rate differed significantly between species and treatments ($\chi^2 = 36.42$, d.f. = 5, $P < 0.001$) (Fig. 5). The apparent survival of brown trout was higher when maintained at low density and when maintained with brook trout ($\chi^2 = 1.87$, d.f. = 1, $P = 0.168$). On the contrary, it significantly decreased in the presence of rainbow trout or at high brown trout density ($\chi^2 = 11.90$, d.f. = 1, $P = 0.001$ and $\chi^2 = 21.64$, d.f. = 1, $P < 0.001$, respectively). The apparent survival of brown trout at high intraspecific density was similar to the interspecific situation with rainbow trout ($\chi^2 = 0.99$, d.f. = 1, $P = 0.317$). In sympatric situations, apparent survival of rainbow trout was similar to brown trout ($\chi^2 = 0.43$, d.f. = 1, $P = 0.511$), on the contrary, the recapture rate of brook trout was significantly lower than for brown trout ($\chi^2 = 10.43$, d.f. = 1, $P = 0.001$).

Growth

The individual daily growth rate of brown trout varied between 1.15% and 1.35% according to treatments, but no significant differences were found between the different combinations (ANOVA, $F_{3,134} = 2.187$, $P = 0.092$).

	Large pebbles		Velocity		Depth	
	Niche width	P-value	Niche width	P-value	Niche width	P-value
BNT	18.38	<0.001	4.13	<0.001	26.47	<0.001
RWT	24.53	0.136	7.6	0.002	43.8	0.002
BKT	22.52	0.018	4.17	<0.001	28.56	<0.001
BNT (bnt)	26.47	0.454	6.25	<0.001	42.09	<0.001
BNT (rwt)	23.03	0.062	6.54	<0.001	49.58	0.333
BNT (bkt)	24.8	0.172	5.81	<0.001	34.2	<0.001
RWT (bnt)	24.44	0.128	5.09	<0.001	48	0.133
BKT (bnt)	27.73	0.696	5.01	<0.001	47.85	0.108

RWT, rainbow trout; BKT, brook trout; BNT, brown trout.

Table 3. Niche width (measured as the standard deviation) along the three habitat variables for each species combination. Observed niche width with estimated probabilities for significance in habitat selection are indicated (see text for details). The notation $X(y)$ means niche width of species X when maintained in sympatry with species y .

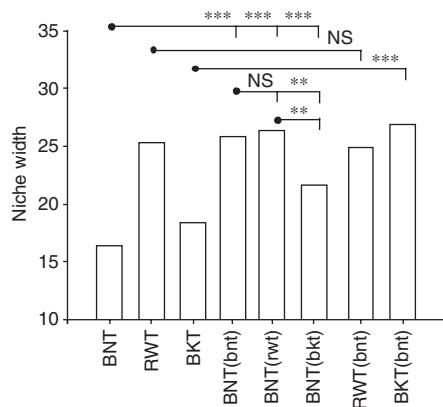


Fig. 3. Niche width of brown trout (BNT), brook trout (BKT) and rainbow trout (RWT) maintained in different sympatric and allopatric combinations. The notation $X(y)$ means habitat selection of species X when maintained in sympatry with species y . Differences between niche width were only tested for comparisons relevant to this study. NS: not significant ($P > 0.05$); $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

Discussion

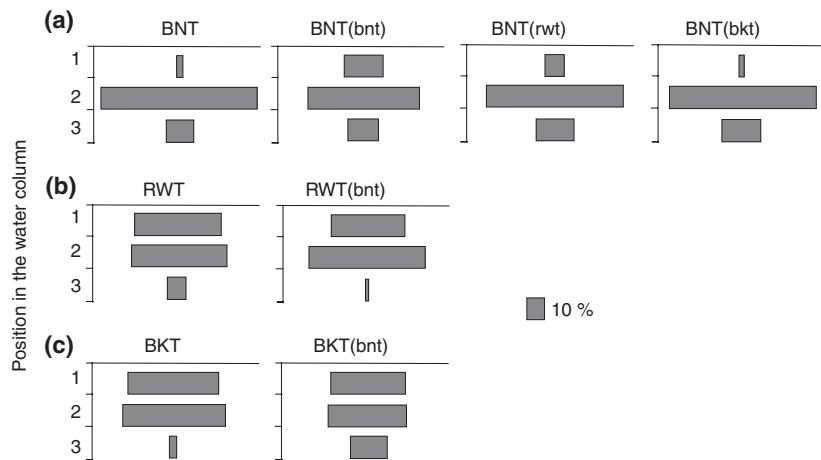
Many previous studies on competition have been criticised for their failure to consider simultaneously both intra- and interspecific competitions, as well as a tendency to overextrapolate laboratory results (Cross & Benke 2002). These two points were considered in the present study, and the laboratory results were consistent with the field study. Although it was not possible to replicate the field experiment, we applied severe corrections to the inferential statistics and combined field and laboratory results to provide a relevant description of what occurred in our system. According to Begon et al. (1996), the mechanisms involved in competitive interactions and the method of measuring interaction strengths are difficult to establish. Bohlin et al. (2002) and Cross & Benke (2002) found that secondary production (i.e., growth rate) is

an efficient way to identify and quantify interaction strength compared with apparent survival. On the contrary, apparent survival was considered to be a relevant measurement of interaction strength by Elliott (1994) and Keeley (2001). In the present work, only apparent survival (i.e., recapture rate) of brown trout differed significantly between treatments whereas growth rate was consistent. It seems likely that brown trout individuals displaced to unfavourable habitats had a higher probability of disappearing via drift and/or predation by adult brown trout. Therefore, these fish did not contribute to the decrease in growth rate expected under competitive pressure (Jenkins et al. 1999; Bohlin et al. 2002). We hypothesised that individuals still present after the 50-day study period had found a suitable habitat and exhibited no or little growth rate reduction. In the field experiment, secondary production could therefore constitute a biased estimator of competition strength, as it can only be calculated on the remaining individuals.

Brown trout versus rainbow trout

Brown trout habitat in the presence of rainbow trout was significantly affected, leading to the expansion of brown trout niche width. These results are supported by the field experiments showing a lower percentage recapture of brown trout in the presence of rainbow trout. We can therefore assume that rainbow trout has a negative impact on brown trout. These results differ from previous knowledge on YOY brown trout–rainbow trout biotic interactions, where brown trout usually outcompete with rainbow trout. For example, Gatz et al. (1987) and Baran et al. (1995) showed a strong asymmetrical competition in favour of brown trout that influenced rainbow trout habitat selection. Furthermore, Kocik & Taylor (1995) demonstrated that growth and mortality rates of brown trout were unaffected by the presence of rainbow trout.

Fig. 4. Vertical distribution of the three species in the laboratory experiments, under different sympatric and allopatric combinations. (a) Brown trout (BNT), (b) Rainbow trout (RWT) and (c) Brook trout (BKT). The notation $X(y)$ means vertical distribution of species X when maintained in sympatry with species y . The width of each bar corresponds to the percentage of individuals located in the considered stratum. (1) First mid of the water column (surface); (2) second mid of the column (bottom), excluding fish lying on the bottom and (3) fish staying on the bottom without swimming activity or fish sheltering in the substratum.



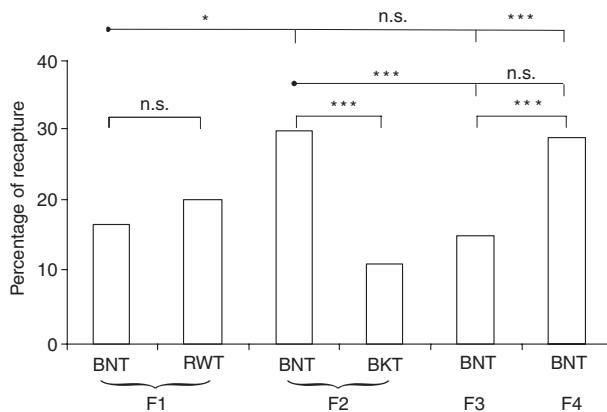


Fig. 5. Percentage of recapture of the three species under different combinations in the field study. BNT: brown trout, RWT: rainbow trout, BKT: brook trout. Reaches are identified by F1–F4 (see Table 1). Differences among and between reaches (only for brown trout) were tested using the chi-square test. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS: not significant, $P > 0.05$.

However, the discrepancy between studies may be explained by changes in the specific competitive ability of species with size, age and environmental conditions (Fausch & White 1986; Hayes 1989). We also noticed that in the field experiment, the rainbow trout were significantly larger than the brown trout individuals, and larger fish usually dominate smaller ones (Schoener 1983; Fausch & White 1986). Nevertheless, these size differences account for the situation found in both Europe and North America, where rainbow trout grows faster than brown trout (Kocik & Taylor 1995; Delacoste et al. 1997). Hence, our results suggest that the higher competitive ability of rainbow trout, because of species characteristics and body size advantage, negatively affected the native brown trout.

Brown trout versus brook trout

The habitat selection and vertical distribution of both species partly differed, although some spatial overlap was detected. The laboratory results do not support the findings of Nyman (1970), Fausch & White (1981) and DeWald & Wilzbach (1992) who identified a large habitat shift of brook trout in the presence of brown trout, attributed to the competitive dominance of brown trout. However, our study revealed that in the presence of brown trout, brook trout spent more time in a nonswimming position, hidden on the bottom, which is considered to be an unfavourable feeding position (Fausch & White 1981; DeWald & Wilzbach 1992). This shift can be attributed to brown trout aggression, which is significantly higher than that of brook trout (Nyman 1970; Blanchet & Brosse unpublished data). These results are supported by a

low recapture rate of brook trout in the natural stream, as already observed in North American streams by Nyman (1970) and Fausch & White (1981). An asymmetric competition (*sensu* Lawton & Hassell 1981) therefore occurred between brook trout and brown trout. Such competition slightly affected brown trout habitat but did not reduce its growth or apparent survival in the field, testifying to the strong dominance of brown trout. Although the competition strength may be shaped by environmental factors (Taniguchi & Nakano 2000; Fausch et al. 2001), we hypothesise that, on a longer time scale, brown trout may competitively exclude the remaining brook trout, or at least drastically reduce brook trout abundance, as frequently observed in North American and European streams (Fausch & White 1981; Delacoste et al. 1997).

Intraspecific competition

Although most studies about interspecific competition do not take into account the relative strengths of interspecific versus intraspecific competition, the importance of such comparisons has been underlined (e.g., Connell 1983; Cross & Benke 2002). In both experimental and natural situations, intraspecific competition between brown trout individuals was always greater or at least similar to interspecific competition between the brown trout and the two exotic species. Intraspecific interactions showed a significantly stronger impact on habitat than interspecific interactions, as testified by the low value of niche overlap indices between brown trout at low and high densities compared with the other comparisons. This was confirmed as vertical distribution between brown trout at low and high densities significantly differed (Fig. 4). Indeed, individual fish are expected to be ecologically more similar to their conspecifics than to other species (Fausch 1998). The divergent results between intra- and interspecific interactions were probably because of a differential selection of the water column, which maintained the interaction strength between rainbow trout and brown trout at a lower level than intraspecific interactions. Such results confirm the hypothesis of Kocik & Taylor (1995) suggesting that the impact of YOY steelhead trout (i.e., the migratory form of rainbow trout) on YOY brown trout was low compared with intraspecific interactions. It should be noticed that the niche shift induced on brown trout by rainbow trout had similar tendencies to that induced by an increase in brown trout density. In both cases, brown trout extended its habitat range. Such a pattern is quite unusual, as competitive interactions usually lead to niche partitioning rather than a niche expansion (Begon et al. 1996). Brown trout probably became established without potential competitors and adopted opportun-

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istic behaviour to exploit most of the available stream habitats. This hypothesis is consistent with previous considerations stipulating that streams are harsh environments in which community structure and function are determined by physical factors and stochastic events (Grossman et al. 1982, 1998; Resh et al. 1988). Therefore, introduction of fish (native or exotic salmonids) with habitat requirements similar to native brown trout tends to increase competitive interactions, but native brown trout could then reduce competition strength by extending its habitat.

In conclusion, the brook trout may represent a minor risk for native brown trout. On the contrary, the impact of rainbow trout may negatively affect native brown trout in European streams. Moreover, the strength of competition is known to be influenced by environmental characteristics such as fish density, water temperature or flow variability (Taniguchi & Nakano 2000; Fausch et al. 2001; Young 2004). Brown trout–rainbow trout interactions should therefore be placed within a framework of ecological processes (e.g., predation, environmental disturbances, life history plasticity and stochastic events) to determine long-term populations outcome.

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