

Do native brown trout and non-native brook trout interact reproductively?

J. Cucherousset · J. C. Aymes · N. Poulet ·
F. Santoul · R. Céréghino

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Abstract Reproductive interactions between native and non-native species of fish have received little attention compared to other types of interactions such as predation or competition for food and habitat. We studied the reproductive interactions between non-native brook trout (*Salvelinus fontinalis*) and native brown trout (*Salmo trutta*) in a Pyrenees Mountain stream (SW France). We found evidence of significant interspecific interactions owing to consistent spatial and temporal overlap in redd localizations and spawning periods. We observed mixed spawning groups composed of the two species, interspecific subordinate males, and presence of natural hybrids (tiger trout). These reproductive interactions could be detrimental to the reproduction success of both species. Our study shows that non-native species might have detrimental effects on native species via subtle hybridization behavior.

Keywords Introduced species · Salmonids · *Salmo trutta* · *Salvelinus fontinalis* · Hybridization behavior · Tiger trout

Introduction

Streams have little immunity to non-native species, and ecologists chiefly studied the most obvious impact of non-native fishes, leading to the decline of native species, i.e., predation and/or competition for food and/or habitat (Moyle and Light 1996) and introduction of novel diseases (Gozlan et al. 2005). However, less attention was paid to hybridization and its implications for species conservation (Allendorf et al. 2001).

The most frequently introduced freshwater organisms in Europe are fishes (reviewed in Copp et al. 2005; Garcia-Berthou et al. 2005). Because of their especially high recreational value for angling, salmonids have been widely introduced throughout the world including Europe, leading to many combinations of species in unnatural sympatry (Fausch 1988; Fausch et al. 2001). The competitive effects of salmonid introductions on native species are well documented, particularly outside of Europe (Cunjak and Power 1986; Fausch 1988; Nakano et al. 1998; Dunham et al. 2002; Quist and Hubert 2004; Baxter et al. 2004).

Of great interest in Europe is the unnatural sympatry of the North American brook trout (*Salvelinus fontinalis*, Mitchill) and the European brown trout (*Salmo trutta* L.). In many regions of North America, the adverse impacts of non-native brown trout on native brook trout have been demonstrated (e.g., Nyman 1970; Fausch and White 1981; DeWald and Wilzbach 1992). Amongst these effects are numerous reproductive interactions including attempted hybridization that may be partially responsible for the replacement of brook trout by brown trout in some locations (Sorensen et al. 1995; Essington et al. 1998; Grant et al. 2002). However, the reciprocal effect of brook trout introduction on native brown trout in Europe has received less attention and is still controversial. There is

J. Cucherousset (✉) · J. C. Aymes · F. Santoul · R. Céréghino
EcoLab, Laboratoire d'écologie fonctionnelle,
UMR 5245 (CNRS-UPS-INPT), Université Paul Sabatier,
bât 4R3, 118, route de Narbonne,
31062 Toulouse Cedex 9, France
e-mail: julien.cucherousset@cict.fr

N. Poulet
ONEMA, Office national de l'eau et des milieux aquatiques,
16 Avenue Louison Bobet,
94132 Fontenay-sous-Bois Cedex, France

J. C. Aymes
UMR Ecobiop, INRA,
Quartier Ibarron,
64310 Saint Pée sur Nivelle, France

evidence of long-term detrimental impact of brook trout on brown trout populations in boreal lakes of northern Sweden (Spens et al. 2007) and replacement of brown trout by brook trout in headwaters of Finland (Korsu et al. 2007). In South Europe, there is evidence of trophic interactions (Cucherousset et al. 2007), but Blanchet et al. (2007) suggested that brown trout growth and apparent survival are hardly affected by brook trout, indicating that other mechanisms are responsible. While existence of reproductive interactions and/or hybridization between these species in Europe has been suggested as a potential cause (Korsu et al. 2007; Spens et al. 2007), it has not been systematically studied.

The aim of the present study was to assess the reproductive interactions between the introduced brook trout and the native brown trout in a mountain stream of south-western France by monitoring spatial and temporal trends of reproduction and species-specific redd characteristics. Specifically, we addressed three questions: (1) Do these species spawn in similar river stretches and at similar periods?; (2) Do these species use similar micro-habitats for spawning?; and (3) Do these species hybridize?

Materials and methods

The Oriège River is a torrential stream in the Pyrenees Mountains (South France, 1°57' E, 42°39' N) that flows into the Ariège River at 815masl (Cucherousset et al. 2007). Discharge varies from 1 (winter and summer) to 15m³/s (spring thaw), and water temperatures range from 0°C to 13.5°C. The study was conducted in the upstream section of this river (1,480masl), in an area surrounded by 35ha of grassland, which is protected from angling and stocking. The studied stretch (700-m long) is the only part of the river where brown trout co-exist with a naturalized and self-sustained brook trout population. Only two fish species occur in this area, brown and brook trout. The latter species was introduced in the 1950s. Along the stretch, channel width and depth were uniform, averaging 5.1m (± 0.1 SE), 5.6m (± 0.2 SE), and 5.6m (± 0.2 SE) and 18.3cm (± 1.4 SE), 20.5cm (± 2.0 SE), and 26.0cm (± 1.7 SE) in the downstream, middle, and upstream areas, respectively. In the upstream area, water velocity was relatively low ($0.06\text{cm}^{-1} \pm 0.02$ SE), and the substrate consisted of silt (27.9% ± 6.6 SE) and pebble (23.6% ± 6.6 SE). The middle and downstream areas had a higher water velocity ($0.37\text{cm}^{-1} \pm 0.07$ SE and $0.51\text{cm}^{-1} \pm 0.08$ SE, respectively) and a substrate mainly composed of pebbles (37.0% ± 8.1 SE and 54.8% ± 6.8 SE, respectively) and stones (55.0% ± 8.7 SE and 21.7% ± 6.2 SE, respectively).

From 12 October 2005, the reproductive activity of these species was surveyed once or twice a week using direct

observations. Each survey consisted of walking from downstream to upstream along the same river stretch and localizing to the nearest 10m each active redd with reproducing fish. Active redds were defined by the presence of (a) sexually active female(s), (b) dominante male(s) and an excavated area in the stream bed (see Sorensen et al. 1995). Females and males were considered sexually active when they exhibited typical reproductive behavior (Liley et al. 1986a, b). Briefly, a female was considered sexually active if it was seen digging (displacing gravel to construct a nest), probing (dropping into the nest and pushing her anal fin into the excavation), covering (pushing gravel over eggs in a nest), or holding over a nest (maintaining position; after Liley et al. 1986a). Males were considered sexually active if they were courting or spawning with female (after Liley et al. 1986b). When observed, we carried out 10-min observations of fish with binoculars to determine the species and sex of fish present, as well the number of dominant or co-dominant (i.e., employing mate-guarding tactics) and subordinate males. Although some biases might arise during observations (e.g., fish frightening), maximal attention was paid. Surveys were always performed by the same operators, following the same procedure. This survey was completed on 19 December 2005 with the arrival of heavy snow (Fig. 1).

During the middle of the apparent reproductive season (November 23–December 1), all redd sites available were characterized. For each redd, a set of 15 micro-habitat parameters, previously suggested to be important in redd-sites selection of both species (Sorensen et al. 1995; Essington et al. 1998), was measured (details in Table 1). It should be noted that water column temperature (COLU_TEMP) and bottom temperature (BOTT_TEMP) were used to assess the presence of upwelling groundwaters characterized by a warmer BOTT_TEMP compared to COLU_TEMP. According to Zimmer and Power (2006), five parameters of redd-sites morphology and localization were also measured (Table 1). Finally, water temperature was recorded hourly using Tinytalk[®] dataloggers from October to December 2005, and mean daily temperatures were subsequently calculated.

To determine if hybrid trout might be present in this stream, we sampled the population both before spawning (on a weekly to fortnightly basis from July to October 2005) and then several months afterwards (July 2006, June 2007, and September 2007) using a backpack electroshocker (Type EFKO FEG 1500, details in Cucherousset et al. 2007). The tiger trout is the well-known hybrid of brown trout and brook trout (Blanc and Chevassus 1979), and hybrids were recognized on the field using coloration and vermiculation (Brown 1966; Allan 1977).

All data were evaluated for normality prior to data analysis. Differences in the number of subordinate males

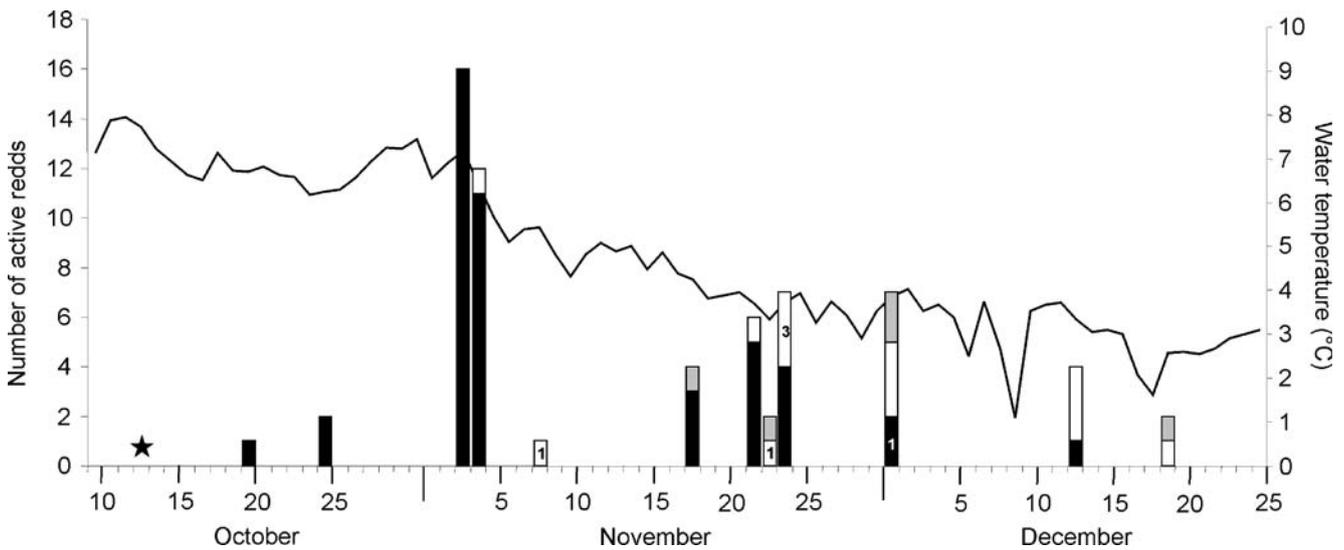


Fig. 1 Number of active redds for each day that observations were made in the River Oriège (France) from 20 October to 19 December 2005. Dark squares denote groups comprised of brook trout only, open squares denote groups comprised of brown only, and grey squares denote mixed groups that had more than one species (any

combination of sexes and species). The values within the histograms denote the number of active redds with interspecific subordinate males. A star denotes no activity. Mean daily water temperature (°C) is denoted by the solid line

Table 1 List of micro-habitat, morphological, and localization parameters (abbreviation and unit or categories) with mean (±SE) values of brown trout (n=9), mixed groups that had more than 1 species

(any combination of sexes and species, n=5), and brook trout (n=19) redd sites measured in the River Oriège (France) in 2005

Parameters	Abbreviation	Unit or categories	Brown trout	Mixed	Brook trout
Micro-habitat					
Water column velocity ^a	COLU_VELO	M s ⁻¹	0.26 (±0.03)	0.33 (±0.03)	0.15 (±0.03)
Water column temperature ^a	COLU_TEMP	°C	4.16 (±0.31)	3.65 (±0.69)	5.48 (±0.27)
Bottom velocity ^b	BOTT_VELO	M s ⁻¹	0.23 (±0.03)	0.26 (±0.02)	0.12 (±0.02)
Bottom temperature ^b	BOTT_TEMP	°C	4.64 (±0.33)	5.74 (±0.24)	6.10 (±0.20)
Dissolved oxygen ^a	OXYG_CONC	mg L ⁻¹	11.48 (±0.38)	11.01 (±0.32)	10.69 (±0.30)
Water conductivity ^a	WATE_COND	µS cm ⁻¹	34.22 (±4.22)	27.00 (±2.51)	29.26 (±0.52)
Small substrate (<3 mm)	SMAL_SUBS	%	17.78 (±3.64)	32.00 (±4.90)	33.68 (±2.67)
Medium substrate (3–20 mm)	MEDI_SUBS	%	56.67 (±4.71)	48.00 (±2.00)	42.63 (±1.68)
Large substrate (>20 mm)	LARG_SUBS	%	25.56 (±2.94)	20.00 (±4.47)	23.68 (±3.08)
Sun exposure	SUN_EXPO	%	75.56 (±8.01)	92.00 (±4.90)	95.79 (±1.92)
River width	RIVE_WIDT	M	5.04 (±0.37)	5.60 (±1.35)	4.50 (±0.46)
Substrate embeddedness	SUBS_EMBE	Low, medium, and high ^c	1.56 (±0.18)	2.00 (±0.00)	1.95 (±0.16)
Coverage of shelter	COVE_SHEL	Null, low, medium, and high ^c	0.56 (±0.18)	0.80 (±0.20)	1.53 (±0.23)
Coverage of aquatic vegetation	COVE_VEGE	Null, low, medium, and high ^c	0.22 (±0.15)	0.40 (±0.24)	1.84 (±0.30)
Coverage of vegetal detritus	COVE_DETR	Null, low, medium, and high ^c	0.89 (±0.20)	1.40 (±0.24)	1.37 (±0.19)
Redd-sites morphology and localization					
Distance to the nearest bank	DIST_BANK	m	1.38 (±0.37)	2.08 (±0.68)	0.97 (±0.14)
Distance to the nearest redd site	DIST_REDD	Low, medium, and high ^c	1.67 (±0.29)	1.00 (±0.00)	1.47 (±0.18)
Redd depth	REDD_DEPT	m	0.11 (±0.02)	0.20 (±0.02)	0.15 (±0.02)
Redd length	REDD LENG	m	1.04 (±0.09)	1.64 (±0.19)	1.20 (±0.12)
Redd width	REDD_WIDT	m	0.51 (±0.05)	0.83 (±0.04)	0.57 (±0.05)

^a Measured at 60% of the water depth

^b Measured at 3 cm of the river bottom

^c Numeric values used in the analyses: null 0, low 1, medium 2, and high 3

per redd was tested using non-parametric Kruskal–Wallis test, while differences in the proportion of active redds with subordinate males between the three species-specific groups was tested using Fisher's exact test. To address whether micro-habitats for spawning were different between species, we used a between-class principal components analysis (PCA). Between-class PCA is a particular case of redundancy analysis where there is only one qualitative instrumental variable (Dolédec and Chessel 1987; Dolédec and Chessel 1989; Pélissier et al. 2003). In our case, between-class PCA uses spawner type (i.e., brown trout, brook trout, and mixed group) as instrumental variable so that the analysis focuses on the differences between groups, seeking components that will best discriminate groups centroids. Prior to the analysis, among the 20 redd characteristics (Table 1), several variables of redd characteristics were log transformed (redd length REDD LENG, river width RIVE_WIDT, distance to the nearest bank DIST_BANK, water column velocity COLU_VELO, water conductivity WATE_COND) or square-root-transformed (redd depth REDD_DEPT) to improve normality, and the dataset was centered and normed. The difference between groups was tested using a Monte-Carlo permutation test with 1,000 permutations: Rows were permuted irrespectively to their class, and the between-class inertia was calculated each time, then the observed between-class inertia was compared to the distribution of the simulated values.

Results

Spawning commenced on October 20, 2005, and a total of 45 active brook trout redds and 14 active brown trout redds were encountered until the study stopped in 19 December 2005 (Fig. 1). On average, brook trout and brown trout groups were composed of $2.1 (\pm 0.1\text{SE})$ and $2.0 (\pm 0.0\text{SE})$ dominant or co-dominant individuals, respectively. Brook trout started to spawn in mid-October and brown trout 2–3 weeks later when water temperature was about 7°C (Fig. 1). The maximum number of active brook trout redds ($n = 16$) was observed on 11 November, while the maximum number of active brown trout redds ($n = 3$) was observed on three consecutive surveys from 24 November to 13 December. The two species continued to spawn through November and until mid-December, with a period of strong overlapping and with mixed groups (mid-November to early December, Fig. 1).

Five mixed groups (accounting for 7.8% of the total number of active redds) were observed. They were always composed of one dominant male and one female. Four mixed groups were composed of male brook trout with female brown trout. Consequently, 22.2% of all sexually active female brown trout (i.e., 14 in brown trout groups

and 4 in mixed groups) were courted by male brook trout, while only one sexually active female brook trout was courted by male brown trout.

No significant differences in number of subordinate males per redds were observed between the three species-specific groups (Kruskal–Wallis test, $KW = 1.10$, $p = 0.577$, $n = 64$) with, on average, $0.82 (\pm 0.19\text{SE})$ subordinate males were counted per active brown trout redds, $0.57 (\pm 0.22\text{SE})$ per active brook trout redds, and $1.40 (\pm 0.68\text{SE})$ per active mixed groups redds. As well, no significant differences in the proportion of active redds with subordinate males were observed between brown and brook trout (42.9% and 42.2%, respectively, Fisher's exact test, $p > 0.95$, $n = 59$). However, the proportion of interspecific subordinate males for brown trout (i.e., active brown trout redds with subordinate brook trout males, 35.7%) was significantly higher than for brook trout (i.e., active brook trout redds with subordinate brown trout males, 2.2%; Fisher's exact test, $p = 0.007$, $n = 59$, Fig. 1). In the five mixed groups, three had brook trout subordinate males.

Spawning activity was observed within ten areas of the river (hereafter called sub-sections A to J), and no active redds were observed outside of these sub-sections (Fig. 2). Among these sub-sections, the distribution of brown and brook trout redds differed markedly but overlapped in the middle part of the study area (Fig. 2). Brown trout redds were principally observed in the lower part, with 85.7% of redds located between section A and D. Sub-section C was the most used area of brown trout ($n = 5$ redds). The distribution of brook trout redds overlapped with

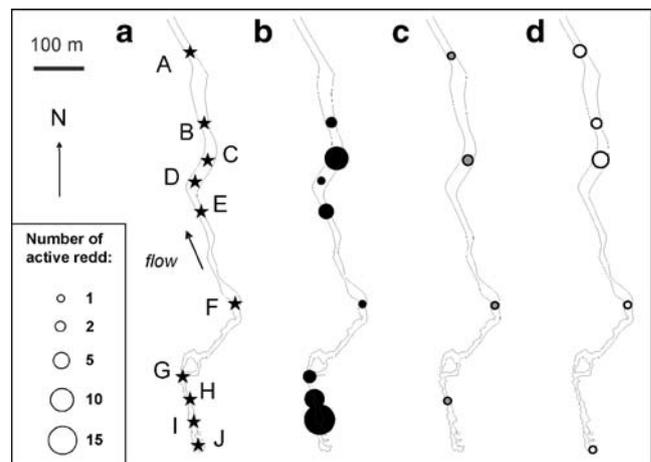


Fig. 2 Locations of active redds in the River Oriège (France) from 20 October to 19 December 2005 showing **a** sub-sections where active redds were encountered (A–J), **b** all brook trout redds (dark circles, $n=45$), **c** mixed groups that had more than one species (any combination of sexes and species, grey circles, $n=5$), and **d** all brown trout redds (open circles, $n=14$). The area of the circles is proportional to the number of active redds

brown trout in sub-sections B to F. The distribution of brook trout redds was more spatially extended than brown trout. Moreover, brook trout redds were principally observed in the upper part of the study area, with 62.2% of redds located between sub-sections F and I. Sub-section I was the most used area of brook trout ($n = 17$ redds). No consistent spatial patterns were measured for mixed group redds (Fig. 2).

Thirty-three redds, i.e., all redds available during the middle of the reproductive season, were measured for micro-habitat characteristics. Compared to brown trout redds, brook trout redds were characterized by warmer bottom temperature, finest substrate, more aquatic vegetation, and lowest current velocities (Fig. 3 and Table 1). The mixed redds showed a compromise between brook and brown trout redds environmental conditions but displayed large-sized redds (i.e., wider, deeper, and longer) and a low distance to the nearest redd. These characteristics certainly resulted from redd superimpositions, and redd superimpositions were also directly observed during the surveys.

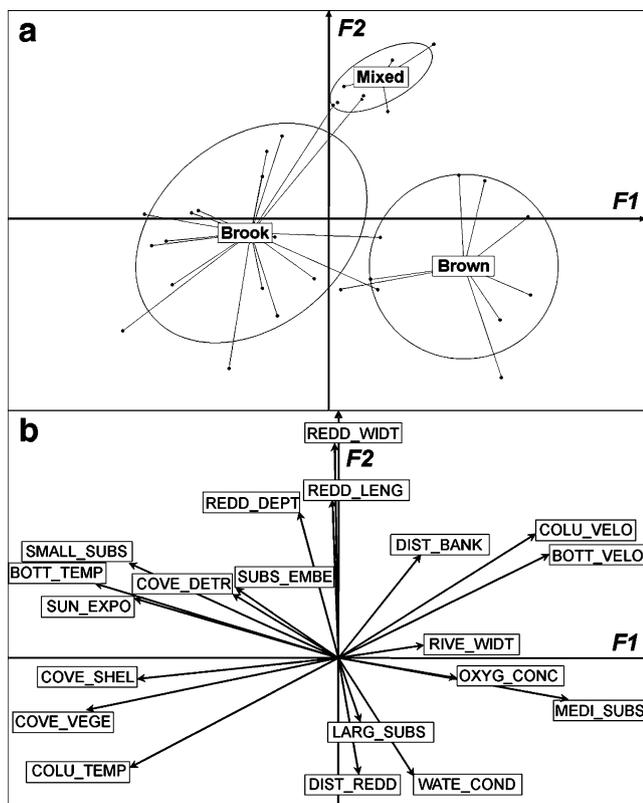


Fig. 3 Between-class PCA focusing on the redd-sites characteristics ($n=33$, see Table 1 for details) differences occupied by the brook trout, the brown trout, and mixed species ($F1$ first axis, 70% of the between-class inertia; $F2$ second axis, 30% of the between-class inertia): **a** species-group redds and **b** variables. An ellipse encloses 67% of the individuals of a given group. Between spawner groups = 19.5% of the total inertia (permutations test, $p < 0.001$)

Before spawning, 203 brown trout, 334 brook trout, and one tiger trout were captured (Fig. 4). After spawning (June 2006 and 2007), 242 brown and 254 brook trout were captured (no hybrid). In these last surveys, the mean total length of brown and brook trout was 139.2 mm ($\pm 3.7SE$) and 138.9 mm ($\pm 2.0SE$), respectively. In September 2007, a second tiger trout (aged 1+ that hatched during the reproduction survey) was caught among about a hundred fish sampled. In total, tiger trout comprised approximately 0.2% of the population.

Discussion

This study provides evidence that reproductive interactions between native and non-native fishes, a previously neglected area of research, may have important roles in the invasive biology of fishes (Sorensen et al. 1995; Hänfling 2007). In particular, we find extensive evidence that brook and brown trout interfere with each other's reproductive success in southern Europe, a phenomenon described previously in North America. Thus, although salmonid species usually spawn in different habitats and seasons, non-native salmonids species can disrupt this process and may lead to replacement of native species (Grant et al. 2002). Specifically, we found a high level of reproductive interactions due to a consistent spatial and temporal overlap in redd localizations and spawning periods and interspecific spawning interactions (mixed groups and interspecific subordinate males) resulting in hybridization during the monitored reproductive season in the study area.

As in North America, brook trout tended to spawn earlier in the season than brown trout in Europe with an overlap of about 4 weeks (Witzel and MacCrimmon 1983; Sorensen et al. 1995). Also, as in North America (Flebbe 1994; Essington et al. 1998) and elsewhere in Europe (Korsu et al. 2007), brook trout in our study stream used the upstream (i.e., pool-like) sections of the stretch while brown trout was in the downstream (i.e., riffle-like) sections, with an overlap area located in the middle of the studied stretch. In term of spawning micro-habitat, brown trout is known to use spawning sites with high flows, while brook trout preferentially use deep sites with lower flow (Witzel and MacCrimmon 1983; Essington et al. 1998). These species-specific preferences were observed in our study. However, upwelling groundwaters were preferentially selected by brook trout, while both species have been observed using sites with upwelling groundwaters to spawn (Witzel and MacCrimmon 1983; Sorensen et al. 1995). Nevertheless, the similarity of sex pheromone systems in these species (Essington and Sorensen 1996) and the attraction of females to sight of each others redds



Fig. 4 *S. trutta* × *S. fontinalis* hybrid (tiger trout, total length=205 mm, weight=78.6 g) captured in the Oriège River in 2005 (credit: P. Menaut, ONCFS)

(Essington et al. 1998) might explain partially hybridization behavior observed here.

The occurrence of mixed groups and redds superimposition is a common feature when brook and brown trout spawning ranges overlap (Witzel and MacCrimmon 1983; Sorensen et al. 1995; Grant et al. 2002). Although the number of observed mixed groups was relatively low ($n=5$, representing 7.8% of the total number of active redds), we found that these groups were principally composed of brook trout dominant males and brown trout females and that they superimposed their redds on existing redds (direct and indirect observations). Often, subordinate brook trout males occur with these mixed groups and 35.7% of brown trout groups had interspecific subordinate males. Together, these phenomena (i.e., attempted hybridization and superimposition) might act together to the detriment of both species (e.g., Hayes 1987). While these effects are likely to be particularly severe for native brook trout in North America (Sorensen et al. 1995), they might also affect brown trout reproduction success, which is native in Europe. For instance, the extensive hybridization activity of male brook trout might reduce the success of brown trout simply because it reduces female availability. As well, male brown trout may devote all their time to chasing subordinate male brook trout from nesting territories. However, the extent to which this impacts brown trout spawning success should be clarified.

Of particular interest is the capture of natural hybrids, which although relatively low in abundance, is significant because hybrid survival is low, so presumably leads to a severe underestimate of actual hybridization activity (Blanc and Chevassus 1986; Scheerer et al. 1987). While the

presence of tiger trout has been reported several times in North America (e.g., Brown 1966; Allan 1977; Witzel 1983; Sorensen et al. 1995), accurate reports of natural hybrids of brown and brook trout in Europe are scarce (but see Maitland 2004). In the present study, the proportion of tiger trout in the population was somewhat lower than in Sorensen et al. (1995) wherein tiger trout comprised approximately 0.5% of the population.

Although we do not have evidence of brown trout population decline or extinction due to the presence of brook trout in France, it has been reported to happen in North European lakes (Spens et al. 2007). In the River Oriège, trophic interactions have also been reported (Cucherousset et al. 2007), and the present study now reports the existence of reproductive interactions. Because the genetic stocks of brown trout are considered as threatened in many parts of Europe (Almodovar and Nicola 2004), the populations that still remain in head-water streams have high conservation value for the species. However, this is where brown trout is most likely to be affected by the presence of brook trout (Korsu et al. 2007). Consequently, more attention should be paid to the effects of brook trout on brown trout reproduction in Europe and to its long-term consequences on natural population ecology.

Reproductive interferences are a strong driver of species coexistence (Hochkirch et al. 2007). The reciprocal patterns of reproductive interactions between brook and brown trout in North America and Southern Europe might explain the invasion success of the two species. In North America, brown trout invasion might be facilitated by reproductive interactions (Grant et al. 2002), but in Southern Europe, these interactions might act as a form of biotic resistance that limit or halt brook trout invasion, although its potential threat on native brown trout and invasiveness can occur after a long lag time (Spens et al. 2007). Furthermore, there are now examples of non-native fish species, even with small introductions, altering the evolutionary pathway of native species by hybridization and subsequent introgression (Mooney and Cleland 2001; Hanfling 2007). Because unnatural sympatries between native and non-native species are more and more common, hybridization and its implications for native species conservation should be studied even if the invasiveness of the non-native species has not been determined yet.

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