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Evidence of two contrasting brown trout *Salmo trutta* populations spatially separated in the River Borne (France) and shift in management towards conservation of the native lineage

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A multidisciplinary study was made of brown trout *Salmo trutta* in the Borne River, a typical fast-flowing mountain stream in the Northern French Alps, in the geographical range of the Mediterranean lineages (ML). Information on (1) the proportion of stocked fluoro-marked fish in the angling harvest, (2) the introgression of introduced DNA microsatellite alleles into the native gene pool and (3) the demography of the population *in situ* in autumn revealed two contrasting populations separated by a physical barrier to upstream migration. A native *S. trutta* population (*c.* 10 000 adults) lives downstream of the barrier and is characterized by a large frequency of ML alleles (82–97%) and high densities (43–55 fish 100 m^{-2}). This population is maintained predominantly by natural recruitment of juveniles (51–82%). In contrast, the upstream population is characterized by a large frequency of Atlantic lineage (AL) alleles (78–100%) and low densities (1–2 fish 100 m^{-2}) and appears to be maintained by restocking (90–100%). The origins of these sharply contrasting populations appear to reflect isolation by an impassable barrier, catastrophic flooding, a downstream gradient in water quality, stocking and fishing pressure. The native downstream population has been resilient to large sudden floods and to intensive stockings of domesticated AL fish. The results of this study justify a shift in management towards conservation and rehabilitation of the native population.

Key words: conservation; freshwater; genetic; microsatellite; otolith; trout.

INTRODUCTION

Brown trout *Salmo trutta* L. is the most common salmonid in Europe and is of considerable socio-economic importance and heritage value because of its intra-species diversity. Bernatchez (2001) identified five evolutionary lineages in Europe (Atlantic, Mediterranean, Danubian, Adriatic and Marmoratus), each

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of which can be considered an evolutionary significant unit (Waples, 1995). In France, two evolutionary lineages can be distinguished with allozymes, mtDNA and nuclear (n) DNA markers: the Atlantic lineage (AL) occurs in the Atlantic catchment area and the Mediterranean lineage (ML) occurs in the Mediterranean catchment area (Guyomard, 1989; Bernatchez *et al.*, 1992; Launey *et al.*, 2003*a*; Cortey *et al.*, 2004). For more than a century, most hydrographic basins in France have been intensively stocked with domesticated AL trout (Krieg & Guyomard, 1985; Launey *et al.*, 2003*a*). This has led to massive introductions of AL trout into areas inhabited by native populations of ML trout and consequently to hybridization and to the decline or disappearance of native ML populations (Barbat-Leterrier *et al.*, 1989; Guyomard, 1989; Beaudou *et al.*, 1994; Largiader *et al.*, 1996; Poteaux *et al.*, 1998; Berrebi *et al.*, 2000).

Furthermore, a comprehensive review by 20 geneticists across Europe (Laikre, 1999) highlighted the ecological importance of the various lineages of *S. trutta* for preserving intraspecific diversity in this species. These authors stressed the need to manage *S. trutta* at the population level, rather than at the species level, to protect the remaining biodiversity and to preserve the long-term evolutionary potential of *S. trutta*. Many *S. trutta* populations inhabit high-altitude rivers and streams that present harsh environments to *S. trutta*. Native populations that survive these harsh conditions have a high conservation value for their ability to adapt. Hence, the study of these populations in their environmental and managerial context is of scientific interest.

With this perspective, a large-scale study has been undertaken over the whole hydrographic network (3800 km of river) of Haute-Savoie (Northern French Alps), located in the natural geographical range of the ML, to identify the remaining native populations and to assess the genetic effects of stocking. The Borne River was selected for a more detailed study because it has a history of intense stocking with domestic AL strains and has harsh conditions (flash floods, fragmentation by natural and artificial barriers, upstream pollution resulting from skiing tourism and cattle wintering) typical of rivers in the Northern French Alps. Geographical diversity among populations in the river was studied with genetic markers, physical marks, demography, angling records and habitat characteristics. The results of this study indicate that new practices, consistent with rehabilitation and conservation, should be used to manage native populations of *S. trutta*.

MATERIALS AND METHODS

STUDY SITES

The Borne River in the Northern French Alps is a major tributary of the Arve River, which is a tributary of the Rhône River, and lies within the geographical range of the Mediterranean *S. trutta* lineage (Guyomard, 1989; Bernatchez *et al.*, 1992; Estoup *et al.*, 2000; Launey *et al.*, 2003*a*; Cortey *et al.*, 2004). This fast-flowing, 32 km long mountain stream with a mean slope of 3·3% is typical of streams in the Northern French Alpine region. The river has a catchment area of 158 km^2 and ranges from 2750 to 400 m in elevation. The Borne River is fragmented by several artificial and natural impassable barriers that prevent the upstream dispersal of *S. trutta*. Three barriers are located in the main stream and two in the tributaries. Artificial barriers 1 and 3 (Fig. 1) are old watermill dams with small but impassable waterfalls (2–3 m high) without flow regulation. Barrier 2 is a small hydroelectric dam (9 m) with a water retention capacity of 10 000 m^3. The Borne River is completely isolated from the Arve River by impassable barriers 2 and 3 (Fig. 1). The two barriers in the tributaries of the Borne River (Fig. 1) are natural impassable waterfalls.

Salmo trutta can sporadically experience harsh conditions, such as severe flash flooding, in these fast-flowing streams. A major flooding event of a magnitude expected every 400 years occurred in the upper catchment area of the Borne River in July 1987. The river flooded after a violent storm (rainfall > 700 mm day^{-1}) in the upstream part of the catchment area, leading to flow rates >200 m^3 s^{-1}. By comparison, the annual average flow is 2 m^3 s^{-1}, and the value of the decennial flood is *c.* 75 m^3 s^{-1}. This violent flood led to 31 human deaths, major flooding of inhabited zones, numerous landslides and the destruction of roads and bridges. Additionally, water quality is substantially lowered by tourist and farm activities (long history of cattle wintering) in the upstream parts of the watercourse.

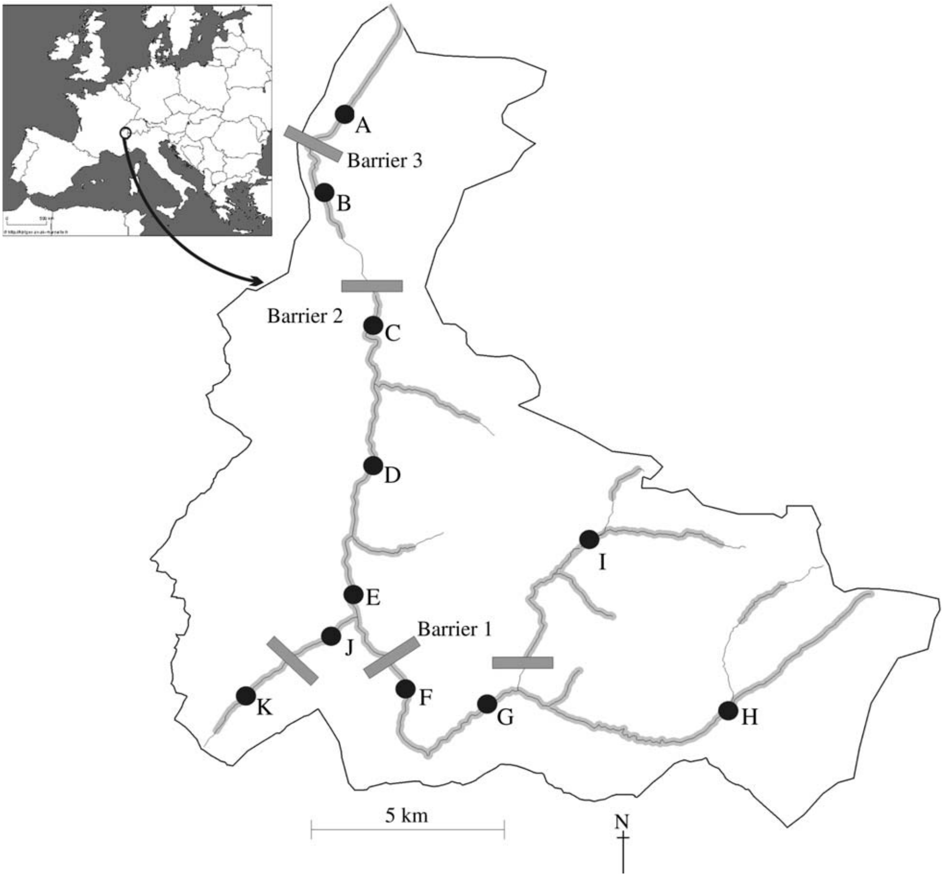

FIG. 1. Areas stocked with domesticated *Salmo trutta* (highlighted) and sample locations (●) in the Borne River catchment. ▬, Impassable barrier.

SALMO TRUTTA RESTOCKING

Stocking of *Salmo trutta* in the Borne River began in 1913 with the creation of a hatchery at Vizille (Department of Isère) that produced alevins. Initially, 20 000 alevins per year were stocked, but the number gradually reached several hundred thousand. Figure 2 shows the number of fish introduced after the major flood, between 1988 and 2004. In 1989, 1990 and 1991, the numbers of *S. trutta* introduced by the fisheries managers were markedly increased to offset the damage caused by the catastrophic flooding in 1987. Juveniles 4–5 cm in length were typically stocked before summer, after the snow has melted and when the hydrological conditions of the stream had stabilized. In the studied sections, fish had been released throughout the stream (Fig. 1). Allelic frequencies for the microsatellite loci Str541 and Str591 in the hatchery stock used to restock the Borne River (Vizille strain) were estimated by Launey *et al.* (2003*a*). These results showed that the Vizille strain belonged to the Atlantic *S. trutta* lineage (Launey *et al.*, 2003*a*).

CATCHMENT AREA STUDIES OF *SALMO TRUTTA* POPULATIONS

Contribution of restocked fish to stage 0+ and to anglers' catches

For three consecutive years, 2002, 2003 and 2004, the otoliths of alevins released into the Borne River (Fig. 1) were marked at the yolk-sac fry stage with fluorescence detectable alizarin red S (Caudron & Champigneulle, 2006).

To estimate the proportions of natural and stocked 0+ stage fish, samples of 0+ fish were collected by electrofishing in the Autumn of 2002. Fish were sampled at eight sites on the main stream of the Borne River and its main tributaries (Table I and Fig. 1). Each sampling site extended a few hundred metres to avoid sampling families and to provide a representative sample of the *in situ* population in different habitats. Fish within the size range likely to contain 0+ individuals were randomly sampled in each sector, euthanized with clove oil and stored at −18° C.

The contribution of restocked alevins to anglers' catches (legal size ≥23 cm) was estimated for three consecutive years, 2004, 2005 and 2006. Volunteer anglers provided information about their catches from March to October (date, exact location and size) and took the required samples (head and scales). The ages of fish sampled, both juveniles and adults, were determined by scalimetry to select only cohorts that were

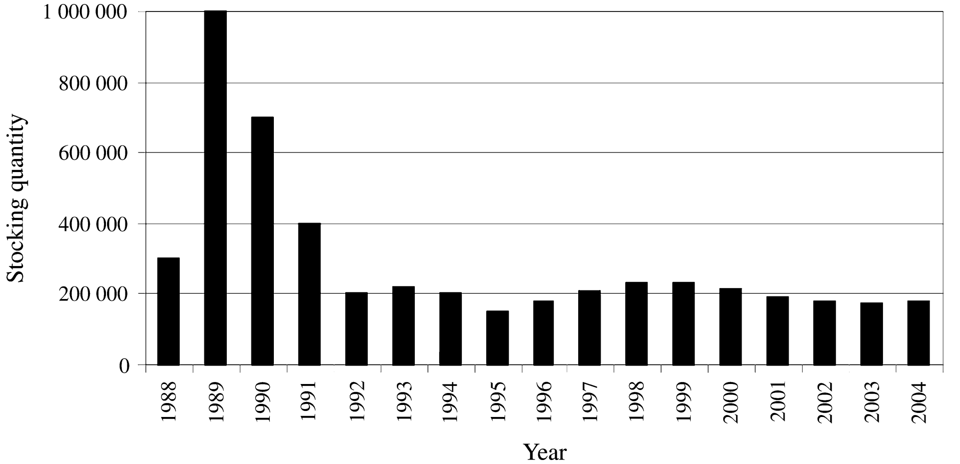

FIG. 2. Numbers of *Salmo trutta* released at alevin stage into the Borne River between 1988 and 2004.

TABLE I. River characteristics and investigations (X) of *Salmo trutta* carried out for each sector sampled in the Borne River

Location	Sector	Length (m) of the sector sampled	Stocking contribution	Genotyping	Demography
Main stream	A	650	X	X	X
	B	350	—	X	—
	C	300	X	X	—
	D	200	—	X	X
	E	500	X	X	X
	F	500	X	—	X
	G	400	X	X	X
	H	500	X	X	X
Tributaries	I	500	X	—	—
	J	200	X	X	—
	K	400	—	X	—

potentially marked. For each trout examined, the head was dissected and the otoliths (sagittae) were removed, prepared and examined for hatchery marking with the method of Caudron & Champigneulle (2006).

The contribution of marked individuals in a sample was expressed as a percentage, with 95% confidence limits (CL) calculated using tables of Beyer's (1986). Proportions of marked and unmarked fish were compared in a contingency table with the chi-squared statistic. The information from anglers was placed in a geographic information system using Mapinfo 7.0 software for spatial analyses (Mapinfo; www.mapinfo.com).

Identification of native ML populations by genotyping

Genetic samples were collected in nine sectors in Autumn 2002 by electrofishing; eight of these sectors were located at the same places surveyed for 0+ stage fish (Table I and Fig. 1). A fin clip was stored in 96% ethanol for genotyping. Ages were determined by scalimetry and 10 individuals at least 2+ in age were genotyped at two microsatellite loci, Str541 and Str591, per sector. Alleles at these loci unambiguously identify AL or ML fish (Estoup *et al.*, 1999, 2000). DNA was extracted using Chelex resin following Estoup *et al.* (1996). Polymerase chain reaction amplifications were carried out following Launey *et al.* (2003*b*).

The introgression rate for each sector was estimated from the mean frequency of the Atlantic alleles at Str541 and Str591 as the number of Atlantic alleles at Str541 and Str591 divided by the total number of alleles. These estimates provide only an approximation of the extent of introgression. Allele frequencies, observed heterozygosity (H_{obs}) and the unbiased expected heterozygosity (H_{nb}) were computed using GENETIX 4.05 (Belkhir *et al.*, 1996–2004).

Demographic characteristics of the population

In October 2004, the size of the population in the main stream was estimated by electrofishing at six stations (Table I and Fig. 1). Two sections of the main stream (B and C; Fig. 1) were not surveyed because the water was too deep for electrofishing. Fish were measured and weighed. Densities and biomass were estimated for each station using the two-removal method (DeLury, 1947). The total number of adults ($\geq$2+) was estimated for three parts of the main stream: downstream barrier 3, between barriers 1 and 2, and upstream of barrier 1, by extrapolating adult densities obtained by electrofishing and by scale analysis of samples from the various sectors.

RESULTS

The results prompted a separation of samples into downstream and upstream groups divided by barrier 1 in the main stem of the river (Fig. 1). 'Downstream' and 'upstream' zones of the Borne River will be frequently used in the text.

CONTRIBUTION OF *SALMO TRUTTA* RESTOCKING TO THE 0+ STAGE IN AUTUMN

In the four upstream sectors of the river (F, G and H in the main river, and I in a tributary), the contributions of restocked individuals to the 0+ stage in autumn were large, ranging from 90 to 100% (Table II and Fig. 1). In contrast, the proportions of stocked alevins in the downstream sectors A, C, E and J ranged from 0 to 49% and were lower than those of naturally recruited *S. trutta* (Table II). The percentage of stocked alevins were significantly ($P < 0{\cdot}01$) smaller than those in the four upstream sectors.

CONTRIBUTION OF STOCKED *SALMO TRUTTA* TO ANGLERS' CATCHES

The percentage of marked and unmarked *S. trutta* caught during the three angling seasons differed significantly ($P < 0{\cdot}01$) between the upper (100%, n = 31, 95% CL = 99–100%) and lower (22%, n = 291, 95% CL = 18–28%) parts of the Borne River catchment (Fig. 3). The age-class contributions to angling catches also differed between zones. In the upstream zone, most of the fish caught (88%) consisted of young age classes 1+ and 2+, whereas in the downstream zone, most of the fish caught (90%) belonged to age classes 2+ and 3+. The percentage of catches at 1+ stage was significantly ($P < 0{\cdot}01$) larger in the upstream zone (39%) than in the downstream zone (2%). In contrast, the percentage of 3+ trout was significantly ($P < 0{\cdot}01$) larger (52%) in the downstream zone than in the upstream zone (12%) (Fig. 3).

In the upstream zone, all *S. trutta* in the age classes examined had hatchery markings. In contrast, the number of marked stocked fish in the downstream zone was considerably lower. In this zone, the percentage of marked fish per age class was significantly lower ($P < 0{\cdot}05$) in the 3+ (7%) than in the 1+ and 2+ age classes (50% and 47%, respectively) (Fig. 3). In the 2002 cohort in the downstream zone, the percentage of marked 0+ fish (37%) did not differ significantly ($P > 0{\cdot}05$) from stage 2+ in anglers' catches (53%). However, the percentage of marked fish in the anglers' catches dropped significantly ($P <$ $0{\cdot}01$) to 11% at stage 3+ and to 0% at stage 4+ (Fig. 3).

RATE OF INTROGRESSION OF THE *IN SITU* POPULATION

Genetic analyses identified three Atlantic alleles and 10 Mediterranean alleles at Str591 and two Atlantic alleles and one Mediterranean allele at Str541 (Table III). The frequencies of Str541 and Str591 alleles in the hatchery stock (Vizille strain; Launey *et al.*, 2003*a*) used for out-planting appear in Table III. The low percentages of Atlantic alleles in six sectors (A, B, C, D and E in the

TABLE II. Restocking contribution of *Salmo trutta* measured at stage 0+ in autumn, introgression rate (% of Atlantic alleles) and estimates of density (total and adults) and biomass in each sector. The sector codes as in Fig. 1 *Sectors in tributary

				Demography			
River zone	Sector	Stocking contribution % (*n*), 95% CL	Introgression rate (%)	Surface (m^2)	Density (fish 100 m^{-2})	Biomass (kg ha^{-1})	Density of adults (fish 100 m^{-2})
Downstream	A	18 (28), 6–40	18	1755	14	53	1·3
	B	—	10	—	—	—	—
	C	43 (35), 26–61	3	—	—	—	—
	D	—	5	1475	43	200	6·9
	E	49 (70), 34–66	8	1060	55	267	5·2
	J*	0 (48), 0–7	10	—	—	—	—
	K*	—	100	—	—	—	—
Upstream	F	90 (20), 68–99	—	1860	14	73	0·5
	G	100 (49), ~100	100	1400	1	11	0·6
	H	100 (100), ~100	78	465	2	21	0·8
	I*	100 (42), ~100	—	—	—	—	—

CL, confidence limit.

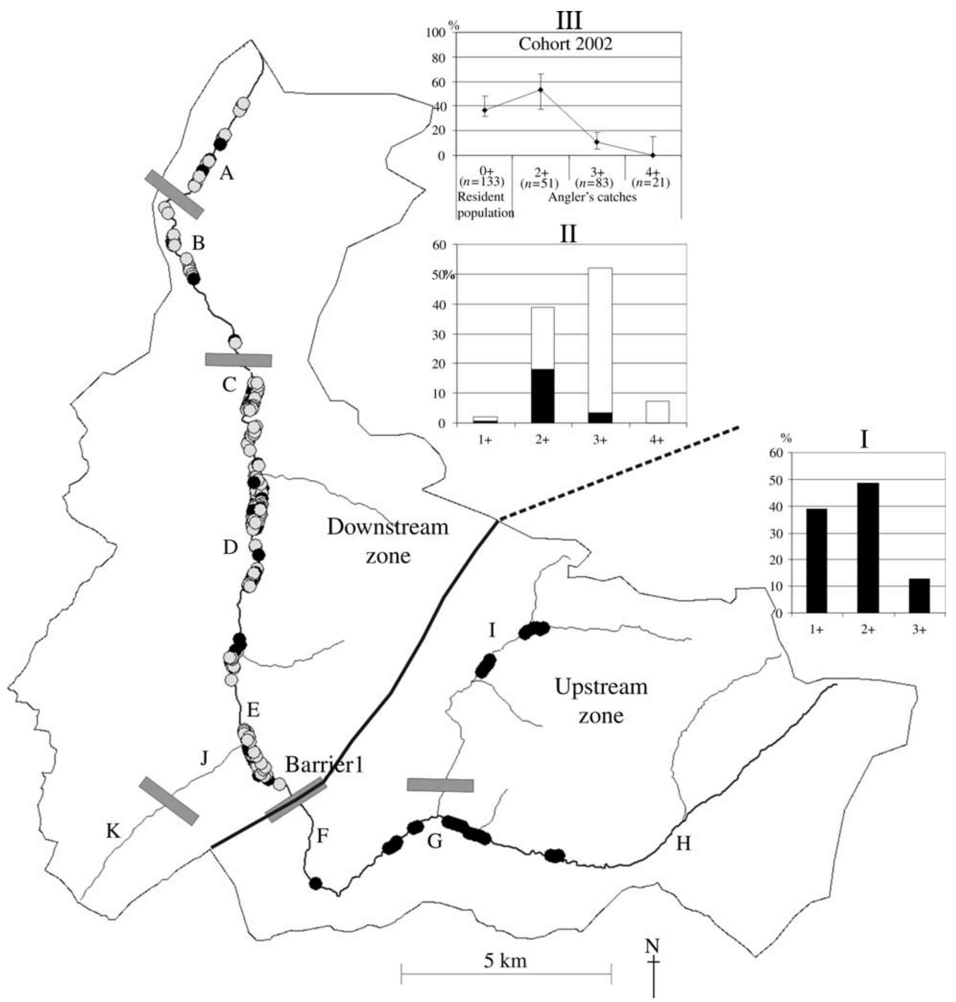

FIG. 3. Locations and characteristics of *Salmo trutta* caught by anglers during the fishing seasons of 2004, 2005 and 2006. (I) Distribution by age class of the trout angled on the upstream zone; (II) distribution by age class of the trout angled on the downstream zone and (III) change in the proportion of marked fish for the 2002 cohort at stage 0+ in the *in situ* population and at older stages in the anglers' catches on the downstream zone. ●, marked fish; ●, unmarked fish.

main stem, and J in the downstream part of a small tributary) in the downstream zone demonstrated the presence of a native ML population with little introgression in the downstream zone of the Borne River (Tables II and III). In contrast, the levels of introgression were high, ranging from 78 to 100% in the three upstream sectors (G, H and K) of the main river and were significantly larger ($P < 0{\cdot}01$) than the levels in the six downstream sectors (Tables II and III). Str591 and Str541 in sectors G and K were fixed for AL alleles 150 and 132, respectively (Table III). These results indicated that the native ML population was restricted to the downstream zone of the Borne River. In contrast, *S. trutta* in the upstream sectors were of Atlantic origin and were probably derived from restocking with domesticated AL *S. trutta*.

TABLE III. Allele frequencies at the Str591 and Str541 microsatellite loci in nine samples of *Salmo trutta* from the Borne River ($n = 10$ fish per sector) and in the Vizille hatchery (according to Launey *et al.*, 2003*a*). Alleles of Atlantic lineage origin are given in bold. H_{nb}, unbiased expected heterozygosity; H_{obs}, observed heterozygosity; n, mean number of alleles per population

		Samples								
Locus	Hatchery Stock	A	B	C	D	E	G	H	J	K
Str591										
150	**0·6333**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·8571**	**0·6000**	**0·0500**	**0·8000**
152	**0·3167**	**0·0556**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·1429**	**0·2500**	**0·0500**	**0·2000**
164	0·0000	0·1111	0·1000	0·1000	0·1000	0·1000	0·0000	0·0000	0·1500	0·0000
166	0·0333	0·2222	0·3000	0·2000	0·1000	0·1500	0·0000	0·0500	0·3500	0·0000
170	0·0000	0·0000	0·0500	0·0500	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000
176	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000	0·0500	0·0000	0·0000
188	0·0000	0·0556	0·0500	0·2000	0·3000	0·1500	0·0000	0·0000	0·0500	0·0000
190	0·0000	0·0000	0·0000	0·1500	0·0000	0·1000	0·0000	0·0000	0·1500	0·0000
192	0·0000	0·5556	0·5000	0·3000	0·4500	0·4500	0·0000	0·0000	0·2000	0·0000
194	0·0000	0·0000	0·0000	0·0000	0·0500	0·0500	0·0000	0·0000	0·0000	0·0000
200	0·0167	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000
216	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000	0·0000	0·0500	0·0000	0·0000
H_{nb}	0·5014	0·6601	0·6789	0·8368	0·7211	0·7684	0·2637	0·6000	0·8263	0·3368
H_{obs}	0·5333	0·5556	0·5000	0·6000	0·8000	0·8000	0·2857	0·8000	0·7000	0·4000
Str541										
130	**0·0333**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·0000**	**0·2000**
132	**0·9500**	**0·3000**	**0·2000**	**0·0500**	**0·1000**	**0·1500**	**1·0000**	**0·7000**	**0·1000**	**0·8000**
136	0·0167	0·7000	0·8000	0·9500	0·9000	0·8500	0·0000	0·3000	0·9000	0·0000
H_{nb}	0·0969	0·4421	0·3368	0·1000	0·1895	0·2684	0·0000	0·4421	0·1895	0·3368
H_{obs}	0·1000	0·4000	0·4000	0·1000	0·2000	0·3000	0·0000	0·2000	0·0000	0·4000
n	3·5	3·5	3·5	4·0	3·5	4·0	1·5	3·5	4·5	2·0

DEMOGRAPHIC CHARACTERISTICS OF THE POPULATION *IN SITU*

Only a small number of *S. trutta* were present in the two sectors (G and H) of the upstream zone in the main stream, where *S. trutta* densities were 1 or 2 individuals per 100 m^2 and *S. trutta* biomasses were 11–21 kg ha^{-1}. In contrast, the middle sectors D and E in the downstream zone had *S. trutta* densities that were 20–40 times larger (43–55 individuals per 100 m^2) and biomasses 10–20 times larger (200–267 kg 100 m^{-2}) than those in the upstream zone (Table II). Sector F, in the lower part of the upstream zone, had larger values than the middle and upper parts of the upstream zone. Sector F had a density of 14 individuals per 100 m^2 and a biomass of 73 kg ha^{-1}, but these values were still far below values in sector E, which was located <3 km downstream but below barrier 1. The intermediate results for sector A (14 individuals per 100 m^2 and 53 kg ha^{-1}) may reflect a deterioration of river habitat in an urban zone.

Densities of the various size classes (Fig. 4) in autumn after the fishing season indicated that population profiles in sectors A, D and E were similar with large

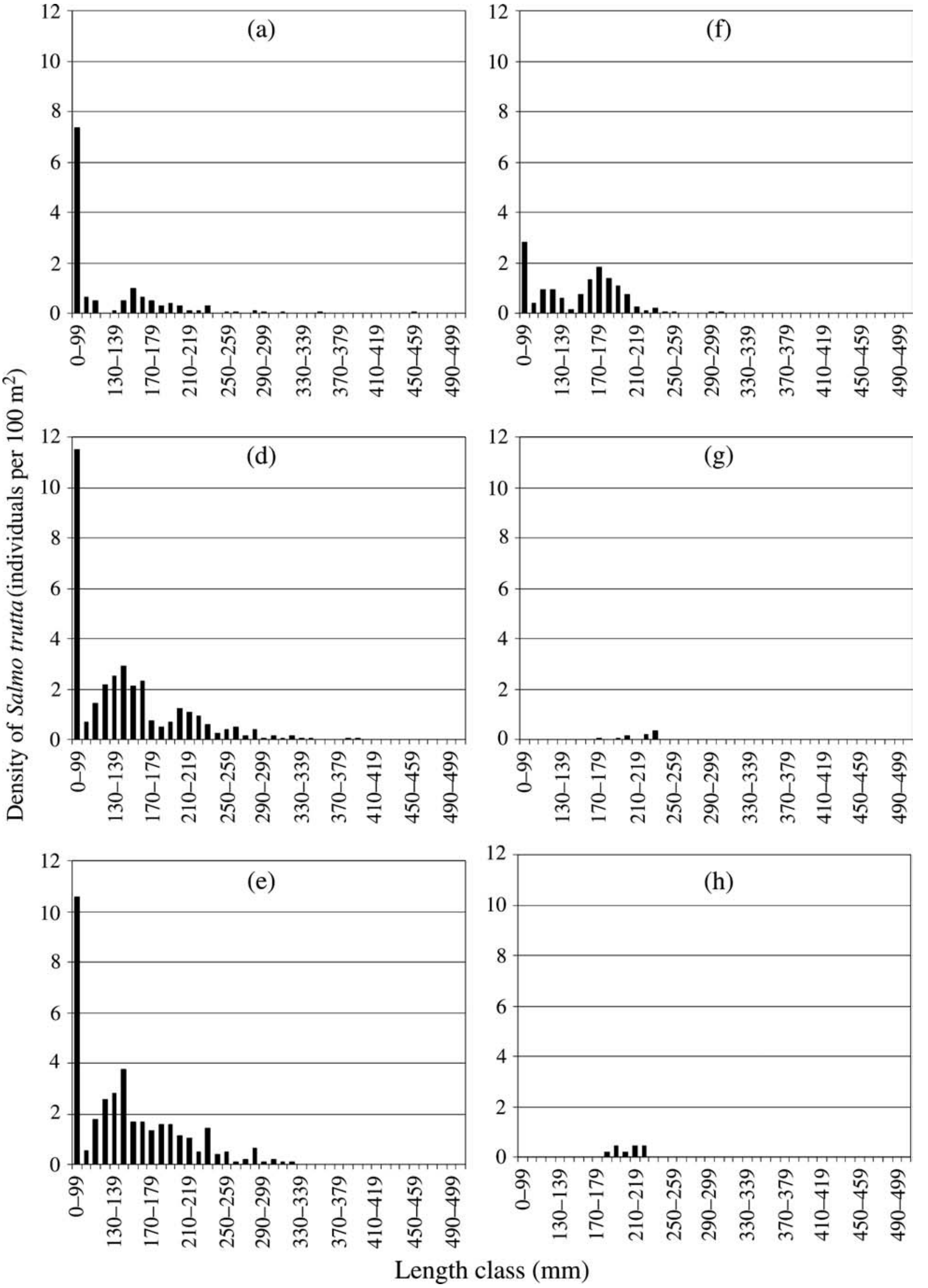

FIG. 4. Histograms of densities (fish per 100 m^2) by size classes of *Salmo trutta* caught by a two-passes electrofishing of the standing population at six stations of the Borne River. Letter codes as in Fig. 1.

densities (for a mountain mainstream) of young of the year <100 mm. Moreover, a substantial proportion of fish were larger than the minimum legal size of 230 mm in sectors D and E. In contrast, no juveniles were caught in sectors G and

H, and all fish present were between 170 and 239 mm in length. Extrapolations of the densities estimated in sectors sampled with electrofishing to the total area of the downstream zone produced an estimate a ML population of *c.* 10 000 adults ($\geq$2+). Most of this ML population inhabited the segment situated between barriers 1 and 2, with an estimate of 7800–10 300 adults. About 900 adults were estimated to be downstream of barrier 3. In the upstream zone, the extrapolation of densities produced a population size of only 500–700 stocked AL adults.

DISCUSSION

SPATIAL STRUCTURING OF POPULATIONS IN THE RIVER BORNE

The approach used in this study allows an assessment of the presence, status and characteristics of the resident trout populations in the Borne River catchment. The results included estimates of genetic composition, stock contribution, angling catches and size-class structure and revealed two distinctive *S. trutta* populations in the Borne River catchment area. A thriving native ML population, consisting of *c.* 10 000 adults, inhabits the downstream zone. Despite intensive stocking of AL *S. trutta* in this area, little introgression of AL alleles has occurred into the native population. In contrast, a small marginal population of AL *S. trutta* appears to be maintained by stocking. The boundary between these populations appears to be defined by an impassable physical barrier.

Several factors (alone or in conjunction) may have contributed to this structure. First, the impassable barriers may have isolated these populations. Second, a major flood in 1987 may have reorganized these populations. Third, early developmental stages of *S. trutta* may not be able to survive poor water quality in the upstream zone of the river. Fourth, intensive stocking with domestic AL strains and angling pressure on AL *S. trutta* at a young age may also have shaped the structures of these populations.

A sudden violent flood in July 1987 severely damaged the upstream zone and may have extirpated or greatly reduced population size. Recolonization of upstream areas with migrants from downstream populations was impossible because of impassable barriers separating the two zones. However, it is difficult to demonstrate that the low population level and the presence of AL *S. trutta* in the upstream zone resulted from this flood because no demographic and genetic profiles are available before and just after the 1987 flood. The restocking of large numbers of AL fish after the floods has failed to restore a functional AL population in the upper zone. Genetic and demographic profiles, anglers' catches and the locations of barriers suggest that a viable ML autochthonous population survived in the downstream zone despite the flood and intensive stocking with AL fish. Indeed, the major part of the ML population was located in the zone between barriers 1 and 2, which cannot be colonized by *S. trutta* from the Arve River because of two impassable barriers.

Major floods can have destructive effects on salmonid populations (Propst & Stefferud, 1997; Sato, 2006; Vincenzi *et al.*, 2008). When populations recover, it is difficult to determine whether some fish survived or whether the population was extirpated and re-established. Several examples of natural recolonizations have been reported after hydrological catastrophes for various salmonids, including *Salmo marmoratus* Cuvier (Vincenzi *et al.*, 2008), *Salvelinus fontinalis* (Mitchill) (Roghair *et al.*, 2002), Gila trout *Oncorhynchus gilae* (Miller) (Propst & Stefferud, 1997) and cutthroat trout *Oncorhynchus clarki* (Richardson) (Lamberti *et al.*, 1991; Swanson *et al.*, 1998). Beaudou *et al.* (1995) reported that a Corsican River devastated by flooding was recolonized by endemic *S. trutta* surviving in tributaries, rather than by the large-scale releases after the flood.

In the present case, apart from the exclusion of the native *S. trutta* from the downstream zone because of the barrier, the failure to develop a self-sustaining population in the upstream zone could also result from the poor water quality in winter, when early developmental stages are most vulnerable. Periodic monitoring beginning in 2006 (unpubl. data) shows that in sectors G and H ammonium and phosphate concentrations in the water at the time embryo–larval development exceed 1 mg l^{-1}, a value that can result in massive mortality of the eggs in the gravel beds (Rubin & Glimsäter, 1996; Massa *et al.*, 1998, 2000; C. Gillet, pers. comm.). The argument that poor water quality affects egg and larval survival is supported by the lack of natural recruitment of stocked AL *S. trutta* (100% of 0+ marked) and by the apparent normal growth of older alevins. Physicochemical assays show that the high concentrations of ammonium and phosphate gradually decrease downstream in sectors F and E to reach values ($<0{\cdot}3$ mg l^{-1}) low enough to allow normal embryo–larval survival. However, the details of the link between the upstream pollution and the level of viability of the *S. trutta* populations along the Borne River are still unknown. Whatever the link, water quality in the upstream zone is an important variable that should be taken into account to explain abundance of *S. trutta* in the river and to formulate conservation strategies to rehabilitate the native population.

The lack of natural recruitment of offspring from stocked AL *S. trutta* in the upstream zone may also be partly because of angling pressure. Reported statistics show that angling catches consist chiefly of young fish ages 1+ and 2+, and electrofishing results indicate the near absence of 3+ *S. trutta* in the autumn after the angling season. Thus, few potentially mature AL females are present in upstream areas during the spawning period.

SHIFT IN MANAGEMENT: CONSERVATION AND NATIVE POPULATION SUPPLEMENTATION

The results of this study have led to changes in the management of *S. trutta* populations in the Borne River. First, AL stocking in the whole Borne watershed was suspended to prevent the risk of further introgression of AL genes into the ML native population. A similar conservation measure to support native *S. trutta* populations has also been implemented in Spain (Araguas *et al.*, 2004, 2008; Almodóvar *et al.*, 2006) and Denmark (Hansen *et al.*, 1995), and these efforts appear to limit the amount of introgression (Almodóvar *et al.*, 2001; Araguas *et al.*, 2008). The downstream zone of the Borne River harbouring a ML population has been declared a sanctuary, but angling is still allowed. Several authors (Garcia-Marin *et al.*, 1998, 1999; Mezzera & Largiader, 2001; Champigneulle & Cachera, 2003) have suggested that introduced *S. trutta* and hybrids are much more easily caught than wild fish. A similar susceptibility to angling of stocked fish has also been reported for rainbow trout *Oncorhynchus mykiss* (Walbaum) (Dwyer & Piper, 1984) and *O. clarki* (Dwyer, 1990). The results for the Borne River also indicate that stocked AL fish have a tendency to be caught at the younger 1+ and 2+ stages. This implies that angling could help to reduce the proportion of AL genes in the Borne River and thus contribute to the conservation of the native ML population.

Other management interventions have focused on the upstream zone where, at the moment, management efforts are directed primarily at the rehabilitation of a large viable ML population. One goal is to extend the upstream distribution of the ML population that is now located downstream of impassable barrier 1. In addition, the recolonization of the upper tributaries of the Borne River would be a precautionary measure if a major accidental pollution of the main stream were to occur.

Population supplementation with native fish has been used successfully to preserve allelic diversity (Stockwell *et al.*, 1995) and evolutionary processes (Moritz, 1999) in several species. For example, translocation proved to be a viable strategy for maintaining populations of *O. clarki* in fragmented habitats (Schmetterling, 2003). In the Borne River, translocations of native *S. trutta* are being implemented before the construction of a fish passageway, scheduled in 2009, between the lower and the upper sections of the river. In agreement with the guidelines of Minckley (1995), 1600 *S. trutta* of various year classes were translocated from the downstream zone to the lower part of the upstream zone. However, a large 10 km upstream portion of the main river still remains to be colonized. Several authors have shown that colonization in this portion is crucial to establish a native population in the upstream portion of the river (Harig *et al.*, 2000; Hilderbrand & Kershner, 2000; Harig & Fausch, 2002). The proximity of the donor site to the recipient site also reduces the risk of introducing pests, including parasites, bacteria and viruses, into the upstream population (Leighton, 2002). Finally, translocations within the river are more conservative, less time-consuming and less onerous to implement than stocking *S. trutta* of native origin raised in a hatchery.

Regular monitoring of water quality has been implemented to assess the level of pollution in the river, especially in the upstream zone, where pollution is greatest and where improvement in water quality is expected. Finally, the spatio-temporal dynamics of demographic and genetic characteristics of Borne River *S. trutta* population are being monitored to assess the effects of the new management strategy and of improvements in water quality.

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