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RESEARCH ARTICLE

Genetic admixture between captive-bred and wild individuals affects patterns of dispersal in a brown trout (*Salmo trutta*) population

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Abstract

Genetic admixture between captive-bred and wild individuals has been demonstrated to affect many individual traits, although little is known about its potential influence on dispersal, an important trait governing the eco-evolutionary dynamics of populations. Here, we quantified and described the spatial distribution of genetic admixture in a brown trout (*Salmo trutta*) population from a small watershed that was stocked until 1999, and then tested whether or not individual dispersal parameters were related to admixture between wild and captive-bred fish. We genotyped 715 fish at 17 microsatellite loci sampled from both the mainstream and all populated tributaries, as well as 48 fish from the hatchery used to stock the study area. First, we used Bayesian clustering to infer local genetic structure and to quantify genetic admixture. We inferred first generation migrants to identify dispersal events and test which features (genetic admixture, sex and body length) affected dispersal parameters (i.e. probability to disperse, distance of dispersal and direction of the dispersal event). We identified two genetic clusters in the river basin, corresponding to wild fish on the one hand and to fish derived from the captive strain on the other hand, allowing us to define an individual gradient of admixture. Individuals with a strong assignment to the captive strain occurred almost exclusively in some tributaries, and were more likely to disperse towards a tributary than towards a site of the mainstream. Furthermore, dispersal probability increased as the probability of assignment to the captive strain increased, and individuals with an intermediate level of admixture exhibited the lowest dispersal distances. These findings show that various dispersal parameters may be biased by admixture with captive-bred genotypes, and that management policies should take into account the differential spread of captive-bred individuals in wild populations.

Keywords Genetic admixture · Dispersal · Brown trout · Microsatellites · Individual assignment · Captive breeding · Stocking · Hatchery

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Introduction

Captive breeding programs are a management practice that is commonly used to sustain endangered species and populations (Seddon et al. 2007; Frankham 2008), and/or to enhance populations in order to improve recreational activities such as fishing and hunting (Hansen et al. 2009; Burnside et al. 2016). However, captive-bred individuals can differ in their genetic and phenotypic characteristics from wild ones, mainly because captivity and the selective pressures associated with it strongly differ from natural environments (Frankham et al. 1986; Blanchet et al. 2008; Christie et al. 2016). Therefore, genetic admixture between wild populations and their captive-bred conspecifics is a major conservation and wildlife management conundrum (Randi 2008; Araki and Schmid 2010).

Genetic admixture between captive-bred and wild individuals can strongly influence individual fitness, notably through its consequences on behavioral, morphological and physiological traits (Geiser and Ferguson 2001; Stoinski et al. 2003). Among these traits, dispersal (which is defined here as all movements of individuals or propagules, potentially responsible for gene flow across space and time; Ronce 2007) is a determinant mechanism for population dynamics (Clobert 2012). Dispersal indeed plays a key role in the persistence of local populations and evolution of species' spatial distribution, in particular because dispersal enables gene flow among populations, underlies colonization and reduces extinction risk (Hanski 1998; Campbell Grant et al. 2010). Dispersal also directly benefits individuals' fitness in response to environmental changes, kin competition, and risk of inbreeding (Cressman and Křivan 2006). Moreover, differential dispersal (in terms of probability to disperse, distance travelled and characteristics of destination sites) among individuals varying in their genetic background (i.e. wild fish, admixed fish or descendants of captive-bred fish) could condition the spatial distribution of admixture.

The individual determinants of dispersal have been widely studied (Clobert 2012; Lowe and McPeek 2014) which permits generating predictions regarding how patterns of dispersal may differ between captive-bred, wild and resulting admixed individuals. For instance, Dingemanse et al. (2003) showed that individuals exhibiting higher exploratory behavior are more likely to disperse, and do so over longer distances. Similarly, more aggressive and bold individuals should disperse less, because they can successfully hold on to resources and to avoid costs of dispersal (Cote et al. 2010; Hudina et al. 2015). Given that captive-bred individuals tend to show a lower propensity for exploration (Robert et al. 1987; Johnsson and Abrahams 1991) and higher aggression and dominance levels (Kelley et al. 2006; Frumkin et al. 2016), we may expect captive-bred individuals to show a less pronounced dispersal behavior than wild ones. Alternatively, larger or heavier individuals with higher growth rate may show higher dispersal propensity and move over longer distances (Debeffe et al. 2014; Radinger and Wolter 2014; Dahirel et al. 2015). Because captive-bred individuals generally exhibit higher growth rates and higher body mass (Tymchuk and Devlin 2005), we may thus conversely expect captive-bred individuals to show a more pronounced dispersal behavior than wild ones. To sum up, captive-bred and wild individuals vary in many traits related to dispersal: clear predictions regarding differences between strains and admixed individuals (i.e. those sharing the genome of both captive-bred and wild individuals), in terms of dispersal propensity and distance, strongly depend on the relative importance of these traits on dispersal behavior.

Studies comparing dispersal differences between wild and captive-bred strains focus generally on immediate post-release movements. For instance, captive-bred fish released into a natural system are less likely to disperse (Symons 1969; Jorgensen and Berg 1991), but those that disperse do so over longer distances than wild ones (Bettinger and Bettoli 2002; Ebner and Thiem 2009). In birds, captive-bred individuals released in the wild tend to disperse less, and over shorter distances than wild ones, probably because of both shorter life span and lower migration speed in captive-bred individuals (Amar et al. 2008; Söderquist et al. 2013). To our knowledge however, no study has yet focused on the direct link between genetic admixture and dispersal in a population in which captive-bred strains have been implanted for a relatively long time, and in which admixture is thus a part of the population dynamics.

Here, we used a headwater stream fish, the brown trout (*Salmo trutta*), to test whether or not long-term admixture between wild individuals and captive-bred fish affects patterns of dispersal. We focused on a population residing in a small mountain watershed that was heavily stocked with captive-bred fish from 1972 to 1999, and in which we thoroughly sampled the whole watershed. By combining this fine scale sampling design and a series of tools derived from population genetics, we specifically aimed to (i) quantify genetic admixture of the supposedly wild trout with captive-bred trout at the individual level, (ii) test how admixture was spatially distributed within the river basin, and (iii) assess the effect of genetic admixture on individual dispersal parameters (dispersal probability, dispersal direction and dispersal distances), while simultaneously taking into account the effects of sex and body size on dispersal parameters (two characteristics having been identified as major determinants of dispersal; Pusey 1987; Gutiérrez and Menéndez 2003). We expected admixed fish and descendants of captive-bred fish to display different dispersal behavior than wild fish, and dispersal traits divergence between groups to increase with the increase in the proportion of allochtonous ancestry in the genome.

Materials and methods

Study area

The Neste d'Oueil is a snow/rain-fed river from the French Pyrenees (Fig. 1). Its source is at 1850 m altitude, it confluences with the Neste d'Oô River at 765 m, after a 9.2 km course, and it is situated ~500 km from the Atlantic Ocean mouth of the Garonne River (from which it is a tributary). With a 1.8% mean slope, its water flow varies from 0.4 to 1 $m^3 s^{-1}$. Its basin drains 30.7 km^2 and is composed of 14 tributaries, all shorter than 3 km in riparian distance. The river basin is fragmented by ten obstacles, among which eight weirs (four of them are lower than 0.5 m and the other four are between 0.5 and ~1.5 m high), a culvert and a natural waterfall (1.5 m high) (Fig. 1). According to local managers and a recent telemetric survey (unpublished data), all these obstacles are passable downstream, and upstream passage depends upon water flow conditions. Highest obstacles are passable (upstream) on rare high flow conditions, whereas smallest obstacles are passable during fall and spring normal high flows (Ovidio et al. 2015), which—overall—suggests that gene flow can occur across the whole river catchment. The fish community is dominated by sedentary brown trout (the population does not sustain anadromous individuals as the river is situated far too upstream to allow for saltwater migrations), with some rare bullhead individuals (*Cottus gobio*). The last brown trout stockings in the Neste d'Oueil occurred in 1999. Since 1972, these stockings were all done from a local trout hatchery (Soueich) that is administrated by the regional angling association (Fédération Départementale pour la Pêche et la Protection des Milieux Aquatiques de Haute Garonne) and used to stock most rivers in the area. This hatchery was created in 1971, and fish from this hatchery originated from crosses between Danish strains classically used in European hatcheries, and individuals from a neighboring river basin (the Ger River).

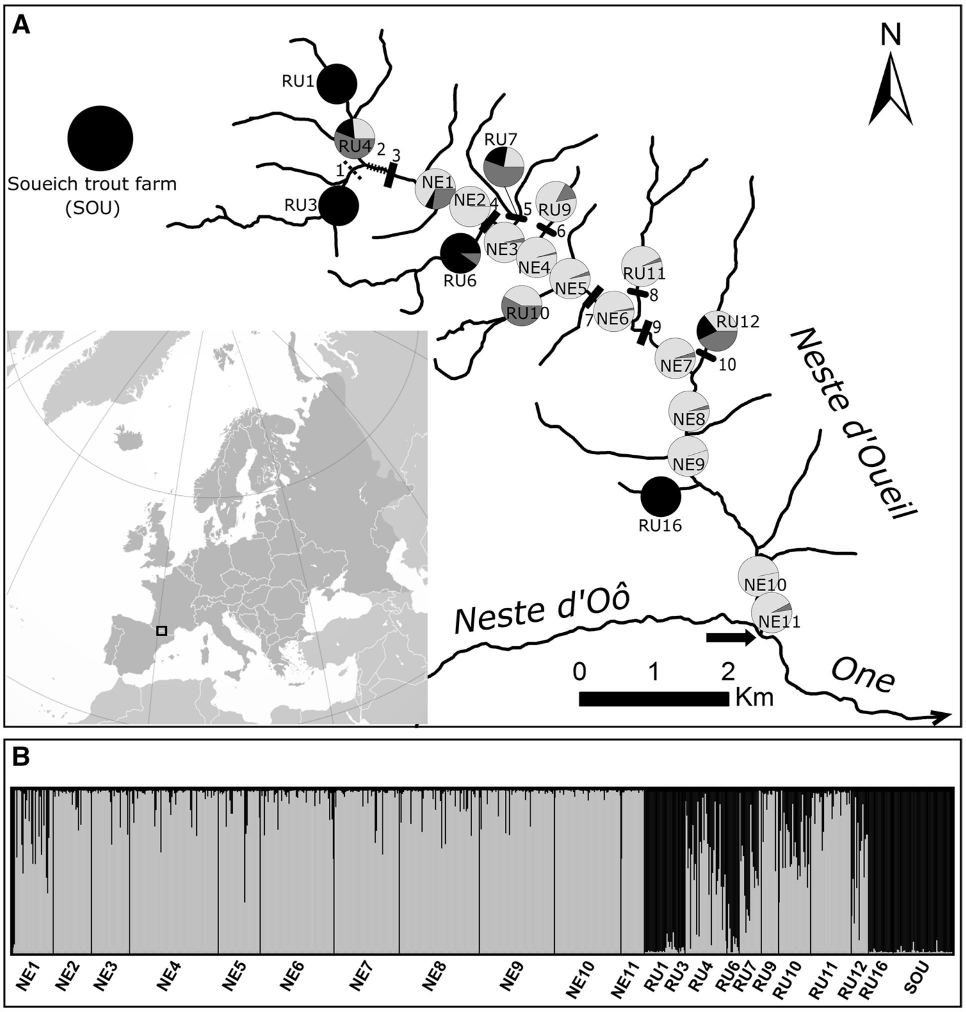

Fig. 1 **a** Maps representing the geographic situation of the Neste d'Oueil, as well as sampling sites, and obstacles (natural: square dashed line, culverts: rectangle dashed line, artificial weirs lower than 0.5 m: black rounded rectangles, artificial weirs higher than 0.5 m: black rectangles) in the river basin. Pie charts represent the proportions of individuals from each site that can be assigned to clusters "wild" (light grey), "captive-bred" (black) and "mixed" (dark grey) as inferred from Q-values. The black arrow indicates the location of the river mouth. **b** Classical bar plot for STRUCTURE results ("wild" cluster in light grey and "captive-bred" cluster in black)

Unpublished studies showed that these hatchery fish form a population being genetically distinct from wild populations from local rivers, even from the Ger River itself. Until 1999, yearly stocking in the Neste d'Oueil river basin mainly consisted in releasing juvenile fish (young-of-the-year) and/or in placing incubated eggs across the entire river basin, including the mainstream and tributaries. The local anglers associations in charge of the stocking aimed at releasing fish evenly in the river basin, and did not target any particular locations (personal communication). In some occasions (i.e. ~ once every 2 years), the downstream part of the mainstream was additionally stocked with adults for recreational activity (see Online Appendix S1).

Field sampling

Brown trout were sampled in July 2014, using electric-fishing from 21 sites in total, 11 on the mainstream ("NE" sites, Fig. 1), and 10 on tributaries ("RU" sites, Fig. 1). We failed to find brown trout in 4 out of the 14 tributaries sampled despite intensive sampling efforts, which indicated that they were probably fishless. We mainly sampled small individuals from the 1 year-old class age. In total, we captured 715 individuals, with sample sizes ranging from 5 (RU3) to 72 (NE4), and with an average of 35 ± 19 individuals per site (Online Appendix S2 and S3). We additionally sampled 48 fish from the Soueich trout hatchery to genetically characterize the captive-bred strain used in this river, and hence to quantify genetic admixture with captive-bred trout. Each individual was measured (total length in mm; see Online Appendix S2 for details), and a pelvic fin clip was taken for genetic analyses. All individuals were released alive to their original sampling site.

Genotyping

Individual multilocus genotypes were obtained at a total of 17 markers. Among these 17 markers, we used 16 microsatellite markers (BS31, One9, SsoSL311, SsoSL438, T3-13, Sfo1, Ssa064, Ssa417, Ssa103, Ots515NWFSC, Ssa-60NVH, Ssa-TAP2a, Ssa-UBA, Ssa14, Ssa85DU and SsoSL417; see Online Appendix S4 for details), and one sex-linked marker, Salmo-Sdy, which enables determination of the sex of each individual (Quéméré et al. 2014). The 17 markers were assembled in three PCR multiplexes.

Genomic DNA was extracted from the fin clips using a salt-extraction protocol (Aljanabi 1997). The loci were amplified using the QIAGEN Multiplex PCR Kit (Qiagen, Valencia, CA, USA). PCRs were carried out in a 10 µL final volume containing 5–20 ng of genomic DNA, 5 µL of 2X QIAGEN Multiplex PCR Master Mix, and locus-specific optimized combination of primers under the following conditions: 15 min at 95 °C followed by 30 cycles of 1 min at 94 °C, 1 min at 60 °C and 1 min at 72 °C and finally followed by a 60 min elongation step at 72 °C. Amplified fragments were then separated on an ABI PRISM 3730 automated capillary sequencer. Allelic sizes were called using GENEMAPPER v.4.0 (Applied Biosystems, Foster City, CA, USA).

Genetic diversity and differentiation

We performed preliminary analyses on all markers except for the one linked to sex. We first investigated large allele drop-out and null alleles using Microchecker V2.2 (Van Oosterhout et al. 2004). We then tested for linkage disequilibrium between loci using FSTAT (Goudet 1995), and we used LOSITAN (Antao et al. 2008) to determine whether or not some of these loci displayed signs of natural selection, as suggested by previous studies (Blanchet et al. 2009; Keller et al. 2011). We did not detect significant linkage disequilibrium among loci but one of the 16 markers (Ssa-UBA) displayed a strong deficit in heterozygosity, most likely because of the presence of null alleles (Online Appendix S3). Two loci appeared to be under potential selection (Ots515 NWFSC and Ssa14). Ssa-UBA, Ots515 NWFSC, and Ssa14 were therefore discarded from the database for subsequent analyses. Overall, our final genetic dataset thus comprises 763 individuals genotyped at 13 microsatellite markers (plus the sex marker Salmo-Sdy), with in total 1.48% of missing data.

Genetic diversity within each of the sampling sites was estimated over all loci by computing unbiased expected heterozygosity (He) using GENETIX (Belkhir et al. 2004), standardized allelic richness (i.e. the mean number of alleles corrected for the smaller sample size, Ar) after exclusion of small sample locations ($n < 14$; RU3, RU6, RU9 and RU12) using FSTAT, and the Fis index using GENEPOP (Rousset 2008). Departure from Hardy–Weinberg equilibrium within each sampling site and each locus was calculated using GENEPOP. Genetic differentiation was assessed by computing global Fst over all sites and pairwise Fst between sites using the adegenet R package (Jombart 2008).

Population structure and admixture extent

We assessed how *S. trutta* populations are genetically and spatially structured along the Neste d'Oueil, and whether there were differences in terms of spatial distribution between wild, captive-bred descendants and admixed individuals. We performed genetic clustering using STRUCTURE 2.3.1 (Pritchard et al. 2000) with the admixture model and the correlated allele frequency model, without prior population information. Runs were performed with a burn-in period of 200.000 and 200.000 subsequent MCMC repetitions. The number K of clusters ranged from 1 to 10 (five runs each). Log-likelihood plots and ΔK statistics were obtained via the Evanno's method (Evanno et al. 2005) using STRUCTURE HARVESTER (Earl and vonHoldt 2012), and they were used to infer the optimal K-value. Twenty runs were then performed with this optimal K-value and the ten best runs (the ones with highest LnP(D) values) were compiled using CLUMPP (Jakobsson and Rosenberg 2007) to get final averaged individual Q-values. Individuals were assigned to the cluster with the greatest Q-value, provided that value exceeded 0.7, as this has been done for other salmonid species (Hansen et al. 2001; Vähä and Primmer 2005; Valiquette et al. 2014). Individuals with intermediate Q-values (i.e. between 0.3 and 0.7) were considered genetically admixed. Graphical displays of STRUCTURE plots were generated using DISTRUCT software (Rosenberg 2003). We directly used the probability of assignment (individual Q-value) to the cluster containing all individuals from the Soueich trout hatchery as an estimate of individual genetic admixture with the captive-bred strain (Hansen et al. 2001).

In order to further describe the spatial structure of strains in the river basin, we tested the relationship between site distance to the river mouth (confluence between the Neste D'Oô and the One Rivers; Fig. 1) and admixture level (averaged at the population level and log-transformed). We also tested whether or not admixture level and distance to the mouth (and the resulting interaction term) were significantly related to mean allelic richness and population differentiation (mean Fst) respectively. Relationships were tested using linear models, and all variables were standardized. Finally, we tested to what extent geographic isolation and fragmentation by weirs affected the spatial distribution of strains by testing the relationships between difference in mean admixture between pairs of sites, pairwise riparian distance and number of obstacles between pairs of sites, using multiple regressions on distance matrices (MRDM; Smouse et al. 1986) coupled with regression commonality analyses (CA; Prunier et al. 2015).

Inferring dispersal from first generation migrants

We then aimed at identifying individual dispersal events by inferring "first generation migrants" (i.e. F0 immigrants) using GENECLASS 2 (Piry et al. 2004). We used Paetkau's method (Paetkau et al. 1995) to assign "first generation migrants" to their population of origin which involves calculating the expected frequency of each individual's genotype in each population (product of expected genotype frequency at each locus, based on the observed distributions of alleles) and subsequent assignment of each individual to the population where its expected genotype frequency is highest. We tested the null hypothesis that an individual was born in the population in which it was sampled using a Monte Carlo resampling method (Rannala and Mountain 1997; Cornuet et al. 1999). Rejection of the null hypothesis indicated an individual having dispersed from one site to another. The probability threshold for inferring first generation migrants was set to 0.01.

We tested the effect of level of admixture, sex and body length of each individual on four dispersal parameters (response variables): (i) the *individual dispersal probability* (obtained by transformation of the binomial variable "dispersal versus non-dispersal" using the *predict()* R function), (ii) the *individual dispersal distance* (i.e. geographic river distance between the site of origin and the site of destination), (iii) the *individual dispersal direction* (i.e. upstream or downstream-directed regarding the water flow), and (iv) the *probability of stream type of the destination site* (i.e. transformed binomial variable "dispersal to a site of the mainstream vs. to a tributary" using the R *predict()* function). We used generalized linear models (GLM; Gaussian or Binomial error terms depending on the response variable) and we standardized all continuous variables. We integrated the quadratic term for the level of admixture to test for potential non-linear relationships. For each of the four dependent variables, we then used a model selection procedure based on the Akaike information criteria (AIC) to identify the most parsimonious set of predictors.

Results

Genetic diversity and differentiation

Expected heterozygosity over all loci (He) ranged from 0.42 to 0.74 (mean = 0.65 ± 0.09), standardized mean allelic richness (Ar) varied from 4.49 to 9.39 (6.24 ± 1.21), and Fis within each site ranged from − 0.06 to 0.15 (0.053 ± 0.047) (Online Appendix S4). Eight out of 21 populations significantly deviated from Hardy–Weinberg equilibrium (Online Appendix S4). The mean genetic differentiation (Fst) estimated across sites and loci was 0.12 (± 0.07), and pairwise Fst values between sites ranged from 0 between NE8 and NE10 (geographically close sites) to 0.21 between RU1 and RU16 (geographically distant sites) with an average of 0.070 (± 0.023). Finally, the sex ratio in each site did not significantly differ from an equal ratio within sites (i.e. 50:50; $\chi^2 = 0.55$, d.f. = 1, p = 0.46).

Population structure and admixture extent

Individuals were assigned to two main genetic clusters. The first cluster (Cluster A, in light gray in Fig. 1) mainly regrouped individuals from the mainstream and from some of the tributaries (RU4, RU7, RU9, RU10, RU11 and RU12). All individuals from RU1, RU3, RU6, RU16 and from the Soueich trout farm were assigned to the second cluster (Cluster B, in black in Fig. 1), as well as a few individuals from NE1, RU4, RU7 and RU10. We therefore considered the first cluster as the "natural" population of the basin (hereafter "wild cluster"), and the second cluster as derived from past stocking activities (hereafter "captive-bred cluster"). We found that 79% of the fish were most likely assigned to the "wild cluster" (566 individuals with Q-value < 0.3), 11% were most likely assigned to the "captive-bred cluster" (77 individuals with Q-value > 0.7), while 10% were equally assigned to both the wild and captive-bred clusters. Moreover, within the captive-bred cluster, subclustering showed two different clusters (Online Appendix S5), with all individuals from the trout farm on the one hand and individuals caught within the river basin on the other hand, hence suggesting genetic drift and/or confirming a partial admixture with the wild population. We found a positive correlation between distance to the river mouth and level of genetic admixture with captive-bred trout (r = 0.55, d.f. = 19, P-value < 0.01), indicating that individuals strongly assigned to the captive-bred cluster were mostly found on a few upstream tributaries (Fig. 1).

Patterns of genetic diversity and admixture

Regarding patterns of allelic richness, we found a significant interaction term between admixture level (at the site level) and distance to the river mouth (Online Appendix S6, *allelic richness*). This indicated that, for an intermediate level of admixture, allelic richness was higher in upstream than in downstream sites (Online Appendix S6, S7 for the interpretation of model parameters in presence of a first-order interaction). This spatial trend held true at a low level of admixture (wild individuals) but not at a high level of admixture (Fig. 2): downstream sites associated with high admixture rates (notably RU16; Figs. 1, 2) were hence responsible for an inversion in the "natural" upstream increase in genetic diversity.

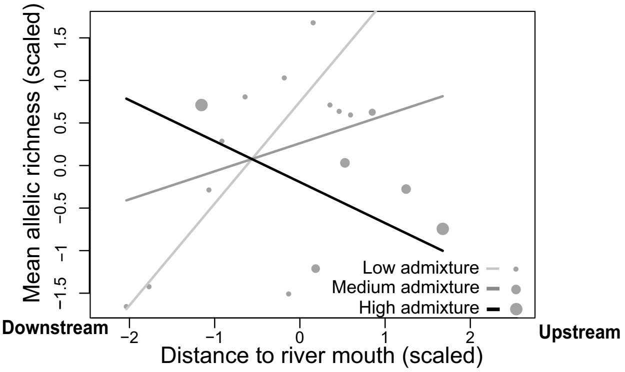

Fig. 2 Relationship between mean allelic richness and distance to the river mouth, depending on mean level of admixture at each site. In light grey, line for low admixture; in grey, line for average admixture; in black, line for high admixture

We further found a significant relationship between mean Fst measured at the site level and level of admixture: populations with a high proportion of fish assigned to the captive-bred cluster exhibited on average higher genetic differentiation (Online Appendix S6, *Fst*). Finally, we found that the number of obstacles significantly explained differences in admixture between sites (beta = 0.472, p-value = 0.004; unique contribution = 0.109, common contribution = 0.036), whereas riparian distance alone did not (beta = −0.127, p-value = 0.314; unique contribution = 0.008, common contribution = 0.036).

Inferring dispersal from first generation migrants

GENECLASS inferred 43 "first generation migrants" (24 females and 19 males) with a probability higher than 0.99, meaning that 5.6% of individuals dispersed. Twenty individuals dispersed upstream, 23 dispersed downstream. Thirty-one of these migrants dispersed towards a site of the mainstream whereas 12 dispersed towards a tributary. Individual dispersal distances ranged from 322.8 to 8062.1 m with a median of 1921.3 m (± 2124.4).

The best model retained to explain individual dispersal probability included both genetic admixture with captive-bred trout (simple term only) and trout body length (Table 1, A). As shown in Online Appendix S8_A, dispersal probability was positively correlated with the probability of assignment to the captive-bred cluster (individuals with a high proportion of allochtonous ancestry were more likely to undergo a dispersal event). We additionally found a slight tendency for smaller individuals to be more likely to disperse. The model retained to explain individual dispersal distance also comprised body length as well as the simple and quadratic terms of genetic admixture (Table 1, B). Individuals strongly assigned either to the wild or to the captive-bred cluster tended to disperse over longer distances than individuals with mixed assignments (Online Appendix S8_B). Moreover, smaller individuals tended to disperse over longer distances. The best model explaining destination stream type comprised genetic admixture only (Table 1, D). The probability to disperse towards a site of the mainstream rather than towards a tributary was negatively correlated with the probability of being assigned to the captive-bred cluster. Finally, the null (intercept only) model was the best at explaining individual dispersal direction (Table 1, C), indicating that factors other than sex, body length and genetic admixture could explain individual variations in dispersal direction. Interestingly, sex was never retained in final simplified models, indicating no differences between males and females in dispersal traits.

Table 1 Results from the final models retained for testing the role of sex, body length and admixture (along with the intercept) on the individual dispersal probability (A), the individual dispersal distance (B), the individual dispersal direction (C) and the type (i.e. mainstream or tributary) of the destination site of first generation migrants (D)

	A Dispersal probability			B Dispersal distance			C Dispersal direction			D Destination stream level		
	β	SE	P	β	SE	P	β	SE	P	β	SE	P
Intercept	−2.800	0.166	< 0.001**	$< 10e^{-6}$	0.135	1.000	0.191	0.310	0.538	1.062	0.392	0.007**
Sex	/			/			/			/		
Body length	−0.131	0.152	0.389	−0.338	0.151	0.031*	/			/		
Admixture	0.288	0.131	0.028*	−0.957	0.640	0.143	/			−0.966	0.365	0.008**
Admixture^2	/			1.274	0.628	0.049*	/			/		

Variables that were not retained in the final model are indicated by a slash bar

*p-value < 0.05; **p-value < 0.01

Discussion

Patterns of genetic admixture and genetic diversity at the basin scale

Although stocking was stopped more than 16 years ago (i.e. 6–8 trout generations ago), we found that 21% of individuals caught in the watershed were at least partially assigned to the captive-bred cluster. In particular, half of these individuals had a high assignment probability to the captive-bred cluster (> 0.7), suggesting either pure descendance from the captive-bred strain or back-crosses between admixed individuals and descendants from captive-bred fish. These results were difficult to compare to other systems because admixture rates between captive-bred and wild trout populations (and hence outcomes after stocking is stopped) are highly variable (Cagigas et al. 1999; Perrier et al. 2013).

Interestingly, the distribution of captive-bred genotypes in the watershed was not homogeneous. More precisely, some small tributaries, notably those situated in upstream parts of the basin, were exclusively populated with fish strongly assigned to the captive-bred cluster, whereas in the main river, fish strongly assigned to the captive-bred cluster were rare despite the homogeneous stocking effort in the watershed. This suggests that past stocking events significantly influenced the spatial distribution of alleles in this river basin. The persistence of fish strongly assigned to the captive-bred cluster in some tributaries could be due to the fact that these stretches were fishless or at very low density before stocking occurred: competition with the native strain was probably low, thus facilitating their settlement and reproductive success, enabling them to co-occur in parapatry with the original wild population. We also showed that obstacles partly explained differences in admixture between sites, and thus also probably contribute to favoring spatial segregation of the two strains in the basin. Indeed, some of these obstacles are difficult to cross upstreamwards at normal flow conditions, which may limit hybridization between wild and captive-bred individuals upstream of these obstacles. Nevertheless, additional information as to the historical spatial distribution of trout in this river system would be required to shed light on this spatial pattern.

Our results also suggested that past stocking activities and admixture with captive-bred trout affected spatial patterns of genetic diversity and genetic differentiation. We notably found an overall downstream decrease in allelic richness when levels of admixture were null to moderate (Fig. 2 and Online Appendix S6), contrary to the traditional expectation of a downstream increase in genetic diversity (Morrissey and de Kerckhove 2009; Paz-Vinas et al. 2015). This pattern has already been observed though (Cyr and Angers 2011; Conti et al. 2015) and, it could be explained by upstream-biased gene flow, higher effective population sizes in upstream stretches, and/or a historical colonization of the river that began upstream and ended downstream (Paz-Vinas et al. 2015). Conversely, allelic richness slightly increased downstream for high levels of admixture, indicating that the distribution of allochtonous genotypes introduced with stocking events differed from the distribution of wild ones. Overall, our findings demonstrated that stocking, even when it occurred several generations ago, can strongly affect spatial patterns of allelic richness while increasing genetic differentiation of populations carrying a high proportion of allochtonous genotypes (Marie et al. 2010; Valiquette et al. 2014), highlighting the necessity for stocking events to be taken into account in riverscape genetics studies (Prunier et al. 2018).

Captive breeding and genetic admixture affect patterns of dispersal

Although we expected a male-biased dispersal or at least higher male mobility (McGinnity et al. 2003) due to the polygamous and/or polyandrous mating system of trout and to the strong competition for mates, we here found no evidence for an effect of sex on dispersal. Possible explanations could be a lack of statistical power, the lack of sex-biased dispersal for immature (1+)-trout as mainly sampled, or the actual absence of sex bias in dispersal at such a small spatial scale. We did not find any significant correlation between fish size and dispersal probability either, although younger, and therefore smaller individuals, are generally more likely to disperse because their territory is not yet established (Andreu and Barba 2006; Gachot-Neveu et al. 2009). Nevertheless, the "first generation migrant" assignment approach indicated that smaller fish disperse further than larger ones, a pattern already observed in riverine fish (Skalski and Gilliam 2000). Since shorter dispersal can enhance survival by reducing mortality risk (Johnsson et al. 1999), larger and more dominant fish may chose not to disperse over long distances, forcing the smaller ones to disperse further (Vøllestad et al. 2012). It is noteworthy that previous studies on brown trout populations regularly mentioned environmental variables (Cucherousset et al. 2005), fish densities (Olsson et al. 2006) or physiological status (Rustadbakken et al. 2004) as major determinants of dispersal, which were not considered in our study.

On the contrary, a constant driver of dispersal probability and dispersal distance in our study was the probability of assignment to the captive-bred cluster. Indeed, we found that: (i) dispersal probability was affected by the probability of assignment to the captive-bred cluster, and (ii) dispersal distances covered by dispersing individuals were lower in individuals with a mixed assignment than in individuals assigned either to the wild or captive-bred cluster. It is noteworthy that this later relationship was not due to the fact that captive-bred individuals were confined to tributaries (that we might expect to be farther away from a neighboring population than a population from the mainstream) since tributary-neighboring populations were actually not significantly further apart than mainstream-neighboring populations (mean distance to neighboring site in the mainstream: 733 m versus mean distance to neighboring site in tributaries: 826 m; *t* test, $t = -0.63$, $df = 17.25$, $p = 0.53$). Our results further revealed that individuals with genotypes closer to those of the trout farm were more likely to disperse towards a tributary whereas individuals strongly assigned to the wild cluster were more likely to disperse towards a site of the mainstream, which may contribute to maintaining the spatial segregation of strains observed in the watershed. Importantly, these findings were confirmed using another independent analysis based on dispersal measured by reconstructing full sibling families (see Online Appendix S9 for further details). To our knowledge, our study is one of the first to reveal such a pattern of "admixture-biased dispersal", which has implications for understanding population dynamics in an environment being -or having been- subject to stocking by fish of non-native origin.

This "admixture-biased dispersal" can have diverse explanations. For instance, admixed individuals may show differences in behavioral dominance and/or body size (Edelaar and Bolnick 2012). However, we did not identify any link between admixture and size, a main trait of dominance (Miller and Frey 1972). Alternatively—and non-exclusively—the observed spatial distribution of admixture levels could result from differences in fitness between fish with a mixed assignment to the wild and captive-bred clusters (admixed fish per se) and pure (wild or captive-bred descendants) individuals (Johnson et al. 2010). Indeed, the average hybrid phenotypes have in many cases been shown to lie outside the phenotypic range of the parental ones, providing hybrid vigor or conversely hybrid depression (Facon et al. 2005; Rasmussen et al. 2012). These phenomena have been documented in salmonids (Wollebæk et al. 2012), although they are still ambiguous (McClelland and Naish 2007). Thus, predictions on the long-term genetic consequences of stocking is still a challenge, and the link between our results and these differential fitness outcomes remains unclear (Harrison et al. 2005), thus adding a hypothesis for explaining our results. However, this pattern has many counterexamples in which admixed individuals show strong fitness increases enabling them to be better colonizers (Drake 2006; Keller and Taylor 2010).

Local selection pressures (Edelaar and Bolnick 2012) and/or differential habitat matching choice between the two strains (Edelaar et al. 2008) could also help explain both dispersal differences between strains and the observed heterogeneous spatial distribution of strains in the watershed. In habitat matching choice, individuals with a given phenotype aim to settle in the environment in which their fitness is optimized (Edelaar et al. 2008). Conversely to what is usually expected as a consequence of high gene flow (i.e. lower genetic differentiation among demes), matching habitat choice through dispersal could increase and/or maintain among-habitat divergence between the two different strains (Bolnick and Nosil 2007). In that case, this may contribute to maintain—together with fragmentation by weirs or natural obstacles—the spatial segregation between the "captive-bred" and the "wild" populations. Evaluating the relative relevance of such a hypothesis (compared to fragmentation) would require further investigations on the habitat characteristics (tributaries vs. mainstream) used by captive-bred and wild individuals and on the relative fitness of "captive-bred" and "wild" individuals in their respective habitats.

Conclusions

We demonstrated that parameters of dispersal can be affected by the proportion of allochtonous alleles brought by stocking activity, and that these effects of admixture can be observed long after stocking activities ceased. Although the mechanisms sustaining differences in dispersal along this gradient of admixture are still unknown, this finding has important implications for understanding and predicting the spread, distribution and maintenance of allochtonous alleles in wild populations. For instance, we here revealed a strong spatial segregation between "wild" and "captive-bred" strains at the watershed level. This heterogeneous spatial distribution could be maintained over time because of the differences in dispersal direction observed between wild and descendants of captive-bred fish, which in the long term could limit the spread of allochtonous alleles. However, this distribution could also be the result of competitive exclusion, where the upstream populations act as sources of allochtonous alleles, which have trouble colonizing the downstream sites in which the wild strain is already present. We call for future studies completing these important findings and testing for underlying mechanisms. Indeed, it would be of interest to test whether differential dispersal parameters can affect the spatial dynamics of admixture in a watershed.

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Author contribution SB, NP and LT designed the experiment and coordinated the study; KSP, SB, NP, LT, OP, GL and CV conducted sampling; KSP, GL and CV carried out the experimental lab work; KSP and JGP ran the statistical analyses; KSP, JGP, SB, NP, LT, OP, GL and CV interpreted the data. KSP, SB, and JGP wrote the first draft of the manuscript. NP, LT, OP, GL and CV read, commented and corrected the initial draft, and all authors gave final approval for publication.

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Data Accessibility Raw data are deposited on figshare. https://doi.org/10.6084/m9.figshare.6886670.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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