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REVIEWS

Evaluation of strategies to conserve and restore intraspecific biodiversity of brown trout: outcomes from genetic monitoring in the French Alps

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Abstract Introduction of nonnative cultured fish is one of the most important threats to native salmonid populations. In brown trout, more than a century of stocking practices has led to a large hybridization between initially geographically isolated lineages, threatening native populations and thereby intraspecific diversity. In the French region of Haute-Savoie, managers and scientists implemented together three management strategies (genetic refuge, direct translocation of wild spawners and stocking with native fry) on 19 test sites for more than 15 years, in the aim to recover pure or nearly pure native populations. Here we propose an assessment of the different management strategies based on a synthetic analysis of the evolution of the introgression rate. While none of the implemented strategies completely achieves the initial objective to restore pure native populations, they differ in their efficiency: introgression rates tend to decrease quickly when direct translocation of native spawners of stocking with native fry strategies are used. The genetic refuge strategy shows slower and more heterogeneous changes of introgression rates. In general, pure nonnative fish are efficiently removed but at the cost of an increased presence of hybrids. Our results imply that intraspecific dynamics react quickly to management practices and that these changes are probably fueled by evolutionary feedbacks that are not yet well understood.

Keywords Conservation biology · Introgression · Intraspecific biodiversity · Conservation strategy · Brown trout

Introduction

Freshwater fishes are among the most imperiled faunas in the world (Cucherousset and Olden 2011). At the intra-specific level, introduction of non-native fish has constantly increased since the ninteenth century due to angling sport interest, in particular for brown trout which is one of the most widely introduced fish species in the world (Lowe et al. 2000). Advances in molecular genetics revealed high levels of intraspecific diversity in salmonids species thereby triggering efforts to conserve this biodiversity (Utter 1981, 2004;

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Allendorf and Ryman 1987; Waples 1991; Ryman et al. 1995). While negative effects of interactions between cultured and wild conspecific in populations of salmonids are well documented (Ryman et al. 1995; Utter 2004), far less attention has been devoted to the impact of resource managers' practices on intra-specific diversity. Additionally, practitioners rarely implement guidelines and recommendations outlined in scientific papers, despite a critical need for evidence-based conservation approaches (Latta 2000; Pullin et al. 2004; Sarewitz and Pielke 2007; Sutherland et al. 2009; Hart and Calhoun 2010).

In 1999, a comprehensive Europe-wide review on brown trout conservation and management involving 20 geneticists highlighted the ecological importance of the various native lineages for preserving intraspecific diversity in this species (Laikre et al. 1999). To do so, brown trout had to be managed at the population level, rather than at the species level, to protect its remaining biodiversity and to preserve the long-term evolutionary potential, and the management and conservation practices should be tested for their effectiveness. Genetic studies were since published specifying the phylogeny of the brown trout species in Europe and the genetic structure of populations within native lineages, comforting the previous points of view on the importance of intra-specific diversity (Bernatchez 2001). However, publications regarding the assessment of conservation strategies are still few. In the French Haute-Savoie area, a collaborative research between fishery managers and scientists was initiated in 2000 in order to efficiently conserve the remaining native Mediterranean brown trout populations threatened by introduced nonnative Atlantic brown trout (Caudron et al. 2012a). Following the recommendations of Laikre et al. (1999), the principle of evidence-based conservation was placed at the core of this research. More specifically, the goal was to assess the effects on wild populations of conservation strategies implemented by resource managers since 1993. Three different strategies were implemented: genetic refuge area where stocking were banned, stocking with native fry, and direct translocation of adult wild fish. This last decade, several outcomes were obtained from the application of these strategies and some of them were published as case studies (Caudron et al. 2006, 2011, 2012b). Here, in a broader approach, we synthesize the obtained outcomes on all targeted rivers and sites in order to bring out relevant common patterns. This approach includes already published data as well as new data on additional sites. In particular, we focus our work on how the genetic admixture between native and nonnative trout in the wild population changes over time in response to the implementation of different conservation strategies. The magnitude of genetic admixture change in relative short delays with respect to management strategies provides useful insights for conservation planning on native brown trout populations in particular, but it can also be informative for adjacent conservation efforts regarding intraspecific diversity of salmonids and other fish species.

Materials and methods

Study area

The Haute-Savoie area, located in the northern French Alps, belongs to the Mediterranean drainage and encompasses around 2800 km of rivers, streams and mountain creeks in an area of 4400 km^2. Despite being located within the geographical native range of the Mediterranean brown trout, this hydrographic network was massively stocked with nonnative domestic trout from Atlantic origin. Atlantic hatchery stocks used in France by fishery managers showed a high genetic similarity among them and a high genetic differentiation with the brown trout populations of the French Mediterranean catchment area (Krieg and Guyomard 1985; Beaudou et al. 1994; Presa et al. 1994; Largiadèr et al. 1996; Berrebi et al. 2000; Launey et al. 2003). In the present analysis, we used data collected on two main basins of the Haute-Savoie hydrographic network, the River Dranse basin and the River Borne basin (Fig. 1).

Story of brown trout management in Haute-Savoie area

At the end of the nineteenth century (approximately 1860–1880) resource managers began to stock rivers with brown trout from hatchery in order to develop recreational fisheries. Stocking has progressively increased to become an intensive method in the second half of the twentieth century. During this period, between 15 and 20 million of Atlantic trout have been stocked in the Haute-Savoie hydrographic

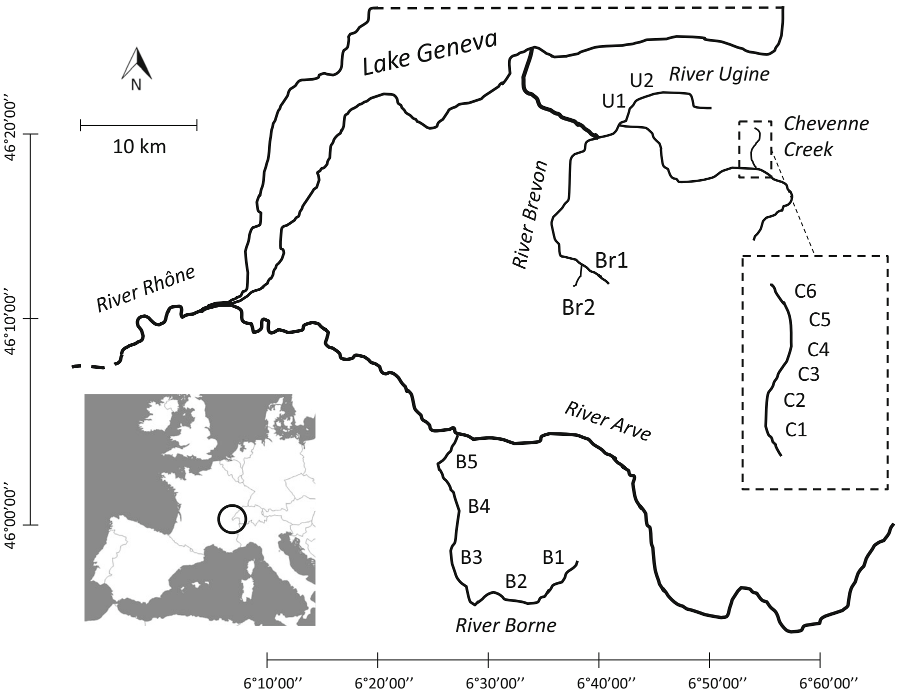


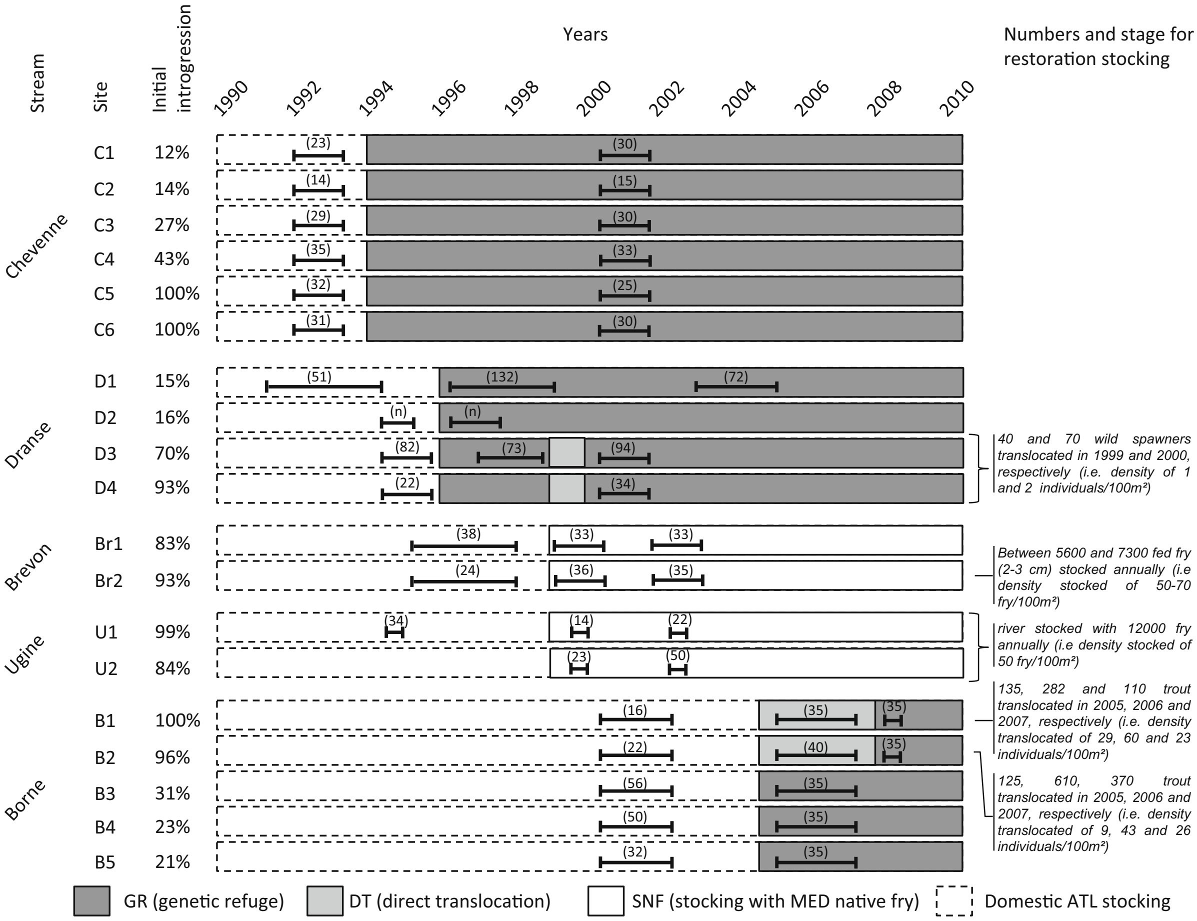
Fig. 1 Location of study sites on the Haute-Savoie hydrogeographic network. Nine sampling sites are located on the two main streams that are the River Borne and the River Dranse, 10 sites are located on three tributaries of the River Dranse (the Chevenne creek, the Serve creek and the River Ugine)

network per year at different stages (yolk-sac fry, fed fry and summerlings i.e. 4–6 cm in length). For example, in the single River Borne, the first documented practice of stocking dates back to 1913 and mentions the introduction of 20,000 fry per year produced from eggs of Atlantic origin. The number of stocked fry reaches several hundreds of thousands per year in the 1980s and 1990s with a peak at 1,000,000 in 1989 (Caudron et al. 2009). On the Dranse system, documents mention a first introduction of 48,000 fry of brown trout in 1903. In the late 1930s, more than 700,000 fry per year produced in local hatcheries with eggs from Denmark and Switzerland are stocked into the system. During the 1980s and 1990s, the number of annually stocked fry varies between 800,000 and 1,000,000 (Caudron and Champigneulle 2007). From the 1990s and mostly in the 2000s, the traditional stocking practices using nonnative trout were progressively abandoned. For instance, between 2000 and 2012, the number of fry released each year in the Haute-Savoie area decreases from 1,800,000 to 400 000, and the total length of rivers stocked decreases from 1000 to 450 km. Thus, during this two last decades, fishery managers replaced the traditional stocking by strategies for conserving and restoring native trout. This shift was allowed because fishery managers became progressively aware of the conservation issues of native brown trout (Caudron et al. 2012a).

Strategies assessed and study sites

For this synthesis, we selected 19 study sites where (1) strategies for conserving or restoring native populations were implemented by fishery managers and (2) genetic data were available before and after the change of management practices.

The 19 study sites are distributed on 5 different rivers in both Dranse and Borne basins. The Chevenne Creek (sites from C1 to C6), the River Ugine (sites U1 and U2), the River Brevon (sites Br1 and Br2), the River Dranse (sites D1 to D4) are located in the Dranse basin, while the River Borne (sites B1 to B5) is the main stream of the Borne basin (Figs. 1, 2).



40 and 70 wild spawners translocated in 1999 and 2000, respectively (i.e. density of 1 and 2 individuals/100m²)

Between 5600 and 7300 fed fry (2-3 cm) stocked annually (i.e density stocked of 50-70 fry/100m²)

river stocked with 12000 fry annually (i.e density stocked of 50 fry/100m²)

135, 282 and 110 trout translocated in 2005, 2006 and 2007, respectively (i.e. density translocated of 29, 60 and 23 individuals/100m²)

125, 610, 370 trout translocated in 2005, 2006 and 2007, respectively (i.e. density translocated of 9, 43 and 26 individuals/100m²)

Fig. 2 Presentation of the three different management strategies implemented and their duration for each site. The number of individuals sampled for genetic analysis is given between brackets

The three strategies assessed are defined as follows:

1. Genetic refuge (GR): managers stopped any fish introduction;
2. Direct translocation (DT): wild spawners (Caudron et al. 2011) or individuals of various age (Caudron et al. 2012b) were collected in pure or nearly pure native populations (introgression <10 %) and introduced in another site on the same river;
3. Stocking with native fry (SNF): native Mediterranean fry were produced from captive breeding stock founded with 98 families derived from native wild spawners caught in the Dranse d'Abondance River showing Mediterranean genotypes at three diagnostic markers, Str541, Str591 and Str791.

The GR strategy was implemented to conserve native populations lowly admixed by nonnative alleles (D1, D2, C1, C2, C3, B3, B4, B5) as well as to try to reduce nonnative allele rates in highly admixed populations (C4, C5, C6). This strategy represents a passive approach, i.e., 'just let time do the job'; at this time managers and scientists assumed that wild populations would purge 'themselves' of nonnative alleles. This point of view assumes that the non-native alleles could either be at neutral or non-neutral markers. The DT and SNF strategies represent active interventions. They were implemented by managers in order to replace nonnative populations (with high admixture rates, i.e. more than 70 % of nonnative Atlantic alleles) showing low densities (i.e. <10 individuals/100 m^2) by new native self-sustainable populations (sites D3, D4, B1, B2 for DT and sites Br1, Br2, U1, U2 for SNF). Originally, in the 1990s, the objective of managers was to fully replace nonnative ATL populations by native MED populations using a captive breeding stock. After the initial feedback from the scientists on the suggested restoration strategies, the objective was revised with managers, instead aiming to decrease the introgression. Several studies showed that native Mediterranean trout from the Dranse and Borne systems used for DT and SNF strategies present a high genetic differentiation with the nonnative brown trout receiving populations where they have been released (Largiader and Scholl 1996; Launey et al. 2003; Caudron et al. 2012a).

Sampling and genetic analysis

The data used from genetic monitoring available on brown trout populations before and after the change of managing practices in the different study sites are summarized in Fig. 2. At all sites, the samples of trout were collected continuously in autumn by electrofishing over a long stretch of river in order to be representative of the populations' structures. For each trout sampled, some scales and a fin clip were taken. The fin clips were stored in 95 % ethanol at ambient temperature for genetic analysis. Age was determined by scale reading. A total of 1715 individuals distributed among 46 sampling group (2 or 3 years of sampling per site) were used in our synthesis.

Samples were genotyped at two microsatellite markers Str541 and Str591 that are located on two distinct linkage groups (BT2 and BT7 respectively, Gharbi et al. 2006). These microsatellite loci have been shown to be diagnostic between Atlantic domesticated stocks and unstocked Mediterranean trout populations over a large part of the Mediterranean area including France, Italy, Greece and Spain (Estoup et al. 2000; Launey et al. 2003; R. Guyomard, unpublished data). The ability of these two markers to trace back each allele to its geographic origin (Atlantic or Mediterranean) has been validated through the genotyping at two microsatellites loci, Str542 and Str592, which are physically closely linked to Str541 and Str591 respectively. The rationale of this approach has been detailed in Estoup et al. (1999, 2000). Indeed, Str541 and Str591 belong to juxtaposed microsatellite systems (JMS), which are composed of two microsatellite repeat arrays separated by a sequence of <100 and >20 bp. The JMS notation for the loci Str541 and Str591 is JMS1-M1 and JMS2-M1 respectively. These JMSs were considered for their ability to provide diagnostic markers to measure the fraction of Atlantic origin in a native Mediterranean population (Estoup et al. 1999) and have been validated in numerous Mediterranean populations from France including samples in Dranse drainage, Italy, Greece and Spain and from farmed Atlantic strains used locally (Estoup et al. 2000; Launey et al. 2003; R. Guyomard unpublished data). The analysis of the two microsatellites loci associated to Str541 and Str591 (respectively Str542 or JMS1-M2 and Str592 or JMS2-M2) allowed to confirm the diagnostic character of these two microsatellite loci for the studied Mediterranean populations.

Methods for DNA extractions, PCR amplifications and genotypes determination for the different study sites are detailed in previous studies (Launey et al. 2003; Barnetta 2005; Caudron et al. 2006, 2011, 2012b). Additionally, and for the Chevenne Creek only, we analyzed variation at a diagnostic mitochondrial SNP in the various sections of the creek (C1 to C6) to discriminate the maternal origin of each sampled fish in 1995 and in 2003 (Apostolidis et al. 2007).

Data analyses

Our analysis focused on the temporal change in the genetic characteristics of the populations: level of introgression and genotypic composition. The introgression rate was estimated by the average frequencies of Atlantic alleles at the Str541 and Str591 loci (i.e. number of Atlantic alleles at Str541 and Str591 found in a sample divided by four times the number of individuals analyzed in this sample). Thereafter, the term introgression refers to the introduction of alien Atlantic genes and their incorporation into the native Mediterranean gene pool. Additionally, according to the observed number of hatchery specific alleles summed over the two diagnostic loci, each individual was given a hybrid index score between 0 and 4. Individuals were assigned to one of the three following categories describing their genotypic composition: pure nonnative Atlantic trout (ATL, 4 Atlantic alleles), pure native Mediterranean trout (MED, 0 Atlantic alleles) and hybrid trout (HYB, between 1 and 3 Atlantic alleles). For the mitochondrial approach on the Chevenne Creek, introgression was measured as the Atlantic haplotype proportion in each sample.

Results

Over time change of introgression rates (Fig. 3)

A clear decrease of the percentage of ATL alleles follows the implementation of DT and SNF strategies. The DT strategy induces an important decrease of the percentage of ATL alleles in a short time with the largest decrease from 94.3 to 11.8 % and the lowest decrease from 70.7 to 34.3 %. On the three sites where three samplings were available, the decrease appears to be steep during the first years and then reaches a plateau. For the SNF strategy the percentage of ATL alleles decreases also quickly with the largest decrease from 100 to 22.7 % and the lowest decrease from 85 to 46 %. As opposed to the DT strategy dynamics, sites with three samplings do not show a stabilization of the percentage of ATL alleles in the studied period. The GR strategy gives variable results. Three sites out of twelve show a negative change of the ATL allele percentage and 9 show a positive change. In any case, the magnitude of the changes was much lower than what was observed for the SNF and DT strategies (from 0.7 to 7.3 % for increasing trends and from 2 to 24.6 % for decreasing trends).

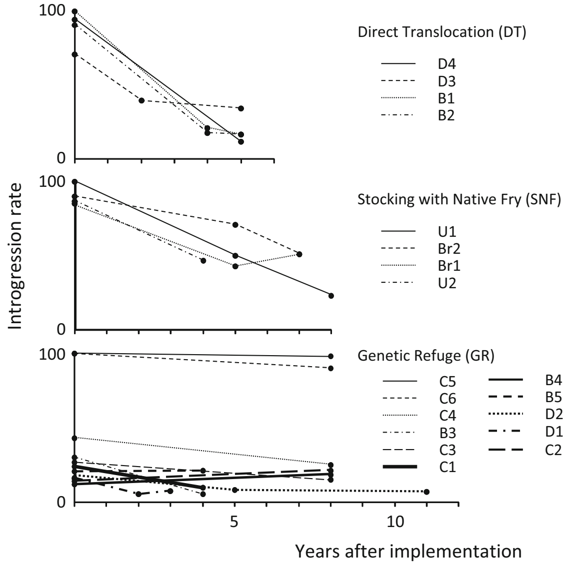


Fig. 3 Evolution of the introgression rate (calculated as the percentage of ATL alleles in the population) for each site according to the management strategy implemented

Change of the genotypic composition (Fig. 4)

In the DT strategy, the decrease of ATL genotypes percentage is stronger and faster compared to the other strategies over 4 or 5 years. The largest decrease of ATL percentage occurs from 100 to 0 % and the lowest decrease from 40.2 to 0 %. In this strategy, all sites show a clear increase of MED genotypes percentage (lowest increase from 3.6 to 20.2 % and largest increase from 0 to 76.5 %). For the three sites where three sampling dates were available, it appears that most of the variation happens during the first years following the implementation of the DT strategy, while a plateau in the variation is observed afterward. We also observe a very clear increase of HYB genotypes percentage in the four sites where DT strategy was implemented (largest increase from 0 to 54.4 % and lowest increase from 9 to 20.6 %).

The SNF strategy triggers a rapid decline of ATL genotype percentage (all sites show a decrease, with the largest variation from 100 to 16 % and the lowest from 7 to 0 %) that is not readily translated into an increase of MED genotype percentage (3 sites out of 4 show an increase but with the largest increase from 0 to 26 %). Consequently, in 3 sites out of 4, we observe a clear increase of HYB genotypes percentage.

Finally, the GR strategy generates the smallest changes in the genotypic partition: a general decrease of ATL genotypes is observed in most cases over relatively long durations (maximum of 11 years). The variation of MED genotypes percentage is highly heterogeneous among sites, with two trajectories showing a decrease while seven other sites present an increase. The largest increase in MED genotypes percentage occurs from 13 to 63 % and the lowest increase occurs from 41 to 63 %. Moreover, 8 sites out of 11 show an increase of the percentage of HYB genotypes percentage.

A focus on the Chevenne Creek (Supplementary Information 1)

In the Chevenne Creek, the introgression rates measured using the mitochondrial diagnostic SNP were almost always lower or equal to the introgression rates measured on nuclear microsatellite markers (Supplementary Information 1), either after the implementation of the GR strategy (1995) or even later (2003). Individuals designated as hybrids by their nuclear

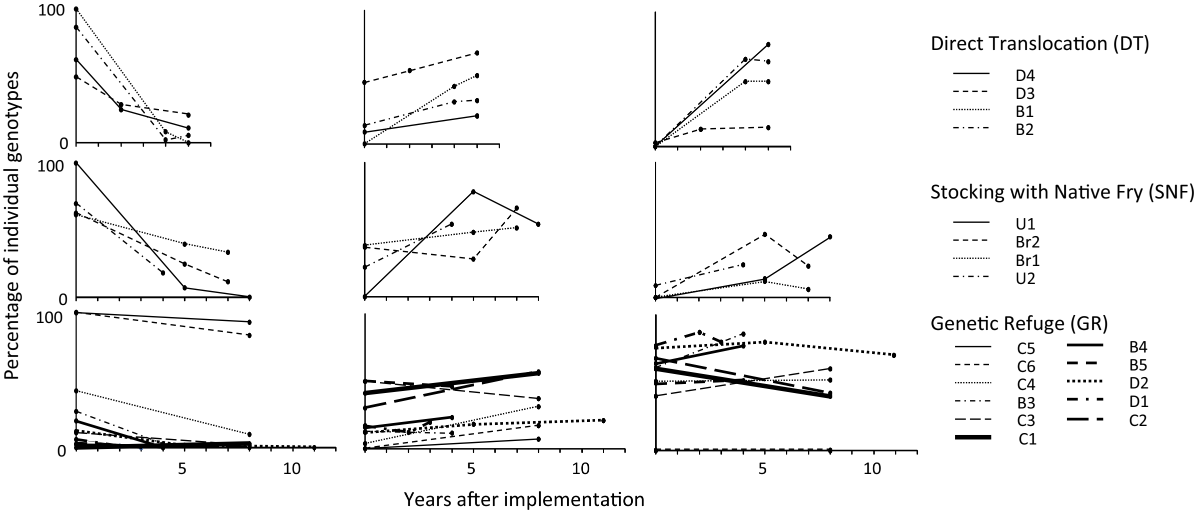


Fig. 4 Evolution of the percentage of individual genotypes. Three genotypes possible: ATL (pure Atlantic alien), HYB (hybrids) and MED (pure native Mediterranean), according to the observed number of hatchery specific alleles at the two diagnostic loci

alleles generally had a Mediterranean haplotype for the mitochondrial diagnostic SNP (32/34 in 1995 and 33/42 in 2003).

Discussion

Our result show that the three different management strategies (Genetic Refuge, Direct Translocation, and Stocking with Native Fry) all affect introgression rates and genotypic composition. In general, the strategies allowed to reduce pure Atlantic genotypes presence, while largely increasing the pool of hybrid individuals, all this on a remarkably short time period. There are however qualitative and quantitative differences between management strategies effects that we will now browse, in order to enlighten potential paths for further understanding of the dynamics of intraspecific diversity in relationship to management practices.

How efficient are the management strategies?

Efficiency as initially defined by managers was the restoration of nearly pure MED populations, and as such, only the DT strategy approached that objective, despite a small production of HYB genotypes in the population. This was achieved by introducing nearly pure MED spawners in sites where densities were very low and composed of ATL individuals. Mediterranean trout then appeared to invade efficiently the ecosystem and to reach much higher densities, while keeping hybridization at a relatively low level.

Presently, it is not possible to determine if this phenomenon is mainly due to a domestic *versus* wild or a MED *versus* ATL aspect, since the ATL individuals initially originate from a domestic strain in our case. In the first case, the inability of trout belonging to the ATL lineage to establish a population should be more due to the maladaptation of domestic strains to wild environment (Ruzzante et al. 2004; Hansen et al. 2009) and the important and fairly rapid decrease of fitness due to domestication (Araki et al. 2007; but see Feulner et al. 2013). In the second case this inability should be due to adaptive differences between both lineages. Keller et al. (2011) showed the existence of both neutral and potentially adaptive genetic differences between trout populations belonging to different lineages in the Rhine, Rhone and Po drainage basins in Switzerland and northern Italy, but they did not clearly tackle the relationship between lineage and adaptation to their native environment. The SNF and GR strategies have also led to a decrease of the percentage of ATL individuals but through an important increase of HYB individuals. In our case, SNF strategy corresponds to the introduction of pure MED fry in a pure ATL population. Therefore, the increase of HYB individuals could either be generated by a lack of pre-zygotic reproductive isolation between the two lineages and/or a lack of selection against hybrids in general. Our results regarding the effects of the GR strategy somehow show a consistent decrease of ATL alleles, but always in a lesser extent than the two other strategies. This indicates that the "self-purging" mechanism initially expected is not really efficient, at least in the studied populations, and for the markers considered. Meanwhile, the new genetic admixtures generated by the DT and SNF strategies appear to remain predominant within populations: in a sense, the most efficient strategies also generated a significant undesired collateral effect. Additional knowledge on introgression dynamics will be required to adapt the future management strategies. Alternatively, depending on the point of view, an increase of hybrids presence with a decrease of ATL pure genotypes can also be perceived as a relative success by the managers.

Feedback to the managers

Despite a relative failure to fully recover native MED populations, the results obtained after the implementation of these three different management strategies may already guide the managers. The GR strategy should not be considered as a unique conservation measure because of its disappointing results even in lowly introgressed populations. Allendorf et al. (2004) suggest applying genetic refuge to populations presenting an introgression rate under 10 %, and our results support their point of view. For populations with a percentage of ATL allele just above that threshold, we obtained variable results that may be driven by inter-sites environmental variation or connectivity differences. Thus, using a complementary measure could be more efficient (Araguas et al. 2008; Caudron et al. 2011). The systematization of the establishment of GR strategy before the implementation of any other conservation strategy is of primary interest to evaluate the ability of native lineages to maintain in the wild or to participate successfully to the reproduction (Laikre et al. 1999). We saw in the light of SNF and DT strategies' results the importance of this knowledge to avoid a massive creation of HYB individuals. Additionally, (Fernandez-Cebrian et al. 2014) predict negative long term consequences in terms of genetic homogenization for supplementation strategies such as SNF or DT. Conversely, in some other cases, implementation of management strategies have led to secondary problems such as inbreeding, decrease of heterozygosity or reduction in effective population size (Lusardi et al. 2015). Dunham et al. (2011) give a framework for the feasibility of translocation. This framework is based on two components, the ability of receiver environments to support the introduction of new fish in term of habitat and the ability of the donor population to support the removal of individuals. In the light of our results regarding DT and SNF strategies, we could add a condition: if hybridization is possible, the density of non-native resident fish and their ability to reproduce in the wild are crucial factors. In the case of a well-established ATL population, the implementation of DT or SNF strategies might bear the risk of a large hybridization process. The management of stream connectivity can here be used as an additional measure to ensure that genetic refuges are not affected by areas where hybrids have been produced (Fausch et al. 2009), although it does not always prevent gene flow and therefore hybridization (Loxterman et al. 2014).

Towards a mechanism oriented management?

The collapse of ATL individuals and the systematic increase of HYB individuals could be due to different combinations of evolutionary forces. The rapid creation of hybrids in relatively important proportions for SNF and DT strategies indicates that at least prezygotic isolation is not strong, as previously suggested (Largiader and Scholl 1996). Gil et al. (2015) recently found that female preference for male in the Dranse system (a hybrid zone) was targeted at phenotypic dissimilarity, a mechanism likely to promote heterogamy between lineages since they clearly diverge phenotypically (Aparicio et al. 2005). Simultaneously, differences in intrasexual competitive ability between gene pools could also condition access to sexual partners (Pearson and Rohwer 2000; Berger and Cunningham 1991), but available data do not evidence for such a difference for males at least (Gil 2015): therefore, intrasexual competition does not seem to increase prezygotic reproductive isolation. Such heterogamic mating system will likely increase the creation rate of hybrids at the expense of pure breeds.

However, as we observed in our data, the pure ATL genotypes are very rare while the pure MED genotypes seem to be more frequent, and such imbalance cannot be explained by the results found by Gil et al. (2015). Likewise, HYB genotypes appear to maintain even a long time after the end of ATL stocking in the case of the GR strategy for instance. Differences in survival between the ATL and MED individuals may explain the decrease of pure ATL genotypes, but in that case, HYB genotypes seem to fare as well as MED genotypes. As the mitochondrial data on the Chevenne Creek seem to indicate, gene flow appears to be different between sexes, with the maternal lineage of hybrids being usually Mediterranean, whereas the paternal lineage is mainly Atlantic. Such pattern has also been found in the hybrid zones between the marble trout and the brown trout (Bajec et al. 2015). A preliminary analysis of survival using different crosses between ATL, HYB and MED individuals indicates that offspring originating from MED mother may have a higher survival than those originating from ATL mother (Gil 2015). The same data may also indicate that hybrid offspring with an ATL father and a MED mother would always have the higher survival. This superiority in fitness could be explained by the inflow of a part of an alien genome (ATL) in the MED genome. For instance, mountains streams with a low connectivity and small populations are more submitted to the effects of genetic drift and can be genetically impoverished. In salmonids, hybridization between wild and domestic strains is usually considered to give low fitness hybrids (Miller et al. 2004; Wollebaek et al. 2012). But in the present case, several generations evolved since the end of domestic ATL stocking, possibly enough time to eliminate the genetic and non-genetic effects of domestication. This could be an explanation of the “all hybrids” situations we encounter with a lot of lowly introgressed hybrids.

It is also interesting to focus on the stage of introduction when comparing DT and SNF strategies: while DT strategy was implemented in very low density populations, the fact that adults were used could create a pre-zygotic isolation for the first reproductions, whereas the SNF strategy may dampen this effect because stocked fry will be raised in the same environment and in sympatry with their introgressed conspecifics. Such hypothesis could be tested by stocking native fry in highly introgressed sites with low density. A common interesting observation to both the disappearance of ATL genotypes and the increase of HYB genotypes is that these dynamics are fairly rapid, so the mechanisms controlling the creation of hybrids and the collapse of non-native individual should be strong, and therefore could be detected using adapted protocols *in natura*.

We just brushed the surface of a wide range of candidate mechanisms that may generate the observed dynamics. Our relative inability to pinpoint which ones are at work since the implementation of the management strategies underlines the necessity to improve our knowledge of the behavioral and selective processes that control for genes flow between the MED and ATL genes pools. And as a side note, it must be pointed out that gene flow will vary between loci, and recent approaches focusing on markers under selection could greatly broaden our understanding of the evolutionary forces at work.

Conclusion

This synthesis revealed the relative lack of efficiency of the implemented management strategies with regard for the initial expectations, but it also allowed to point at possible improvements in both practices and knowledge requirements. Managers and scientists should always implement several strategies simultaneously in order to increase the benefit gained from evidence-based approaches. This is the virtue of the path proposed by Sutherland (2004): it was possible in the present case to distinguish between management strategies effects thanks to replication, monitoring, and synthetic analyses.

As a result, we learned that the impact of the various management practices, while unsatisfactory, is often considerable and rapid: intraspecific dynamics can respond very quickly. Here, a side effect of the active management strategies is the rapid increase of hybrids between native and nonnative gene pools. This points directly at eco-evolutionary processes as a key to improve our management of intraspecific diversity. Although such a conclusion appears to be intuitive, very few management practices are actually based on actual knowledge of eco-evolutionary processes. This consideration is not specific to brown trout: it extends to a large number of freshwater fishes even beyond the salmonids. Surprisingly, studies of introgression patterns very rarely address the mechanisms leading to these patterns. As a consequence, we advise that in absence of knowledge about pre- and post-zygotic reproductive isolation processes, strategies aiming at restoring native intraspecific diversity should generally be implemented with great caution, so to prevent undesired and potentially irreversible hybridization process.

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