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Long-term species balance in sympatric populations: implications for Atlantic salmon and brown trout

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Abstract. The factors determining regional adaptation in salmonids are still unclear, but it is known that changes in their habitat imply changes in their population structure. In this preliminary study we integrate habitat data, molecular analyses (from both nuclear microsatellite and mitochondrial loci) and life-history traits (measured on archaeological vertebrae and modern scales) of two sympatric salmonid species: Atlantic salmon and brown trout. We propose that water temperature and geological characteristics changed the biogeographic patterns of these species through asymmetric migration and different (but complementary) population growth rates. As a consequence, differences in a life-history trait (mean number of years at sea) and population sizes were detected between regions, suggesting a process of substitution of Atlantic salmon by brown trout.

Keywords. archaeological vertebrae, biogeography, demography, life-history traits, *Salmo salar* L., *Salmo trutta* L.

Introduction

Climate and geology affect natural populations of salmonids. Both factors modify populations' structure through changes in water temperatures (Horreo et al. 2011a) and differences in geological substrate (Perrier et al. 2011). These changes disrupt the original local adaptations (Frankel & Soulé 1981) and their evolutionary potential (Koljonen et al. 2002), and can be especially important in small populations because the smaller the population size, the greater the chance of genetic drift occurring (Ellstrand and Elam 1993).

Environmental changes are the principal factors affecting life-history traits (LHTs) (Winkler et al. 2002), which may have direct effects on the evolution and biogeography of species. Major LHTs in salmonid fishes are age at first reproduction, number and size of offspring, and reproductive lifespan and longevity. Fish exhibit a large diversity of life-history strategies (Roff 1992), and salmonids appear especially flexible (Fraser et al. 2011). In the genus *Salmo*, phenological or LHTs such as run-timing and age at maturity vary with a clinal (latitudinal) relation to temperature at scales of hundreds to thousands of kilometres (Bernatchez

2004). Parallel evolution also has been detected at small scales of a few kilometres between ecotypes in different adjacent habitats (Taylor et al. 1996).

Relatively recent changes in habitat and management have altered the population structure of both Atlantic salmon *Salmo salar* (Horreo et al. 2011a) and brown trout *Salmo trutta* (Horreo et al. 2011b). Additionally, long-term climate change has shortened the mean generation time of both species (Turrero et al. 2012). Fraser et al. (2011) recently proposed an integration of classical and molecular approaches to understanding the variation in species' adaptations at different scales. Here we study the evolution of different sympatric populations of Atlantic salmon and brown trout in an area where Cape Peñas (northern Iberian Peninsula) marks a clear separation into two regions with very different geological conditions (Aramburu and Bastida 1995) and temperature regimes (colder in the western region; Dickson and Hughes 1981). We test whether water temperature and/or geological characteristics affect the biogeography of these Atlantic salmon and brown trout populations by integrating molecular and LHT data.

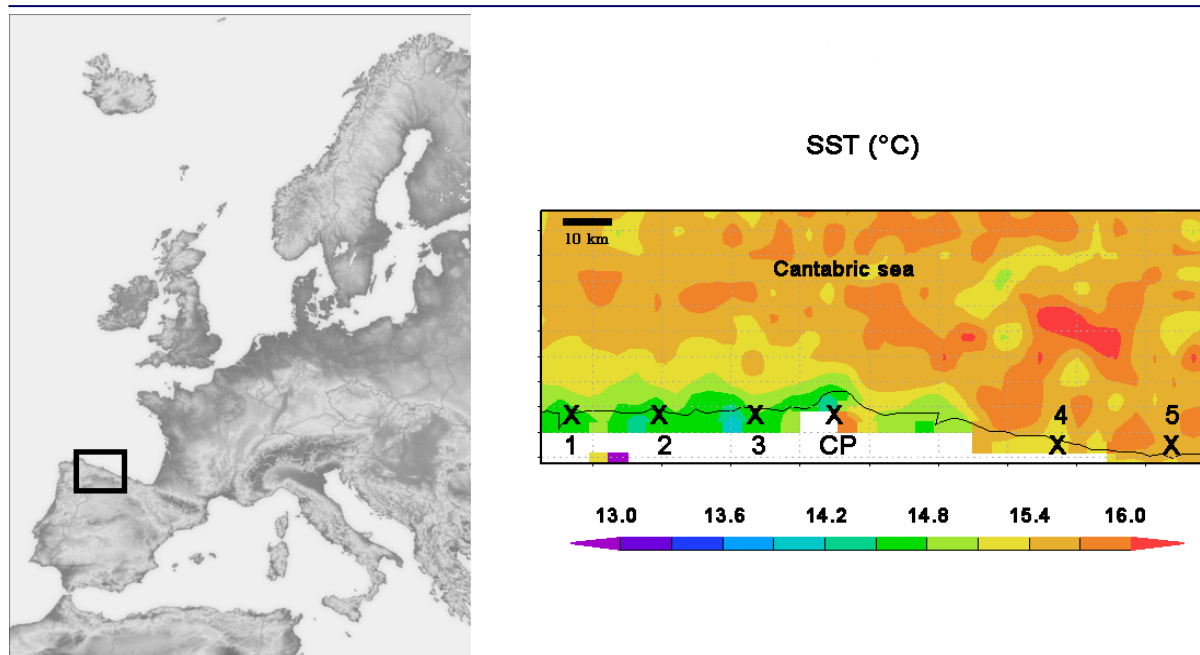


Figure 1. Map of the study area (Asturias, Spain) with sea-surface temperatures (in °C) averaged between January 2002 and December 2003. Cape Peñas (CP) and the studied rivers are marked with crosses (1-Eo; 2-Esva; 3-Narcea; 4-Sella; 5-Cares).

Methods

Salmonids at locations surrounding Cape Peñas (Fig. 1) currently are in the southernmost part of the natural Atlantic salmon distribution; these populations are in decline (Horreo et al 2011c). In total, 653 tissue samples of “modern” Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) from three different rivers west of the Cape (Eo, Esva and Narcea rivers) and two to the east (Sella and Cares rivers) were genetically analyzed (Table 1). For LHTs, 2151 “modern” scales and 45 archaeological vertebrae (6,000–20,000 years before present) of these species were analysed in the same areas ($n = 24$ and $n = 21$ in the western and eastern areas, respectively). Note that both species are considered together when treating

data obtained from bones (Turrero et al. 2012). Complete sampling details can be found in Supplementary Material S1.

Nuclear and mitochondrial DNA data were obtained from the “modern” salmonid samples. DNA extraction and microsatellite (8 loci) amplification followed protocols of Horreo et al. (2012a). Since the study of only one gene could provide enough information for evolutionary studies (Horreo 2012b), the mitochondrial control region (CR) was also amplified. These CR sequences (922 bp) already have been published and are available in GeneBank (see Turrero et al. 2012 for details).

Both nuclear microsatellite loci and mitochondrial CR datasets were employed to estimate several genetic diversity parameters. They were

Table 1. Sample numbers of Atlantic salmon and brown trout used to study the mitochondrial control region, microsatellite loci and life history traits (LHTs) to the west (Eo, Esva and Narcea rivers) and east (Sella and Cares rivers) of Cape Peñas.

		West			East	
		Eo	Esva	Narcea	Sella	Cares
LHTs	Atlantic salmon	174	135	664	664	431
	Brown trout	27	148	16	16	65
Control Region	Atlantic salmon	-	29	28	28	33
	Brown trout	-	27	33	33	22
Microsatellite loci	Atlantic salmon	49	46	50	50	50
	Brown trout	49	88	-	-	47

Table 2. Genetic variability and expansion tests of Atlantic salmon and brown trout populations of the western and eastern areas of Cape Peñas. AR: allelic richness; Pa: Private alleles; H_e : expected heterozygosity; H_o : observed heterozygosity; N_h : number of haplotypes; Ph: Private haplotypes; π : nucleotide diversity; H_d : haplotype diversity; F_s and D : Fu's and Tajima's expansion tests, respectively; r and SSD : Raggedness' r and SSD mismatch distributions, respectively; N_e : effective population size. Standard deviations are shown in parenthesis. *: $P < 0.05$.

	Atlantic salmon		Brown trout		
	West	East	West	East	
Microsatellite	AR	13.81 (8.56)	12.25 (5.56)	14.37 (4.34)	14.97 (4.44)
	Pa	21	17	31	9
	H_e	0.78 (0.10)	0.80 (0.09)	0.81(0.13)	0.77 (0.11)
	H_o	0.70 (0.08)	0.78 (0.09)	0.65 (0.09)	0.64 (0.10)
Mitochondrial	N_h	2	5	14	10
	Ph	0	3	10	5
	π	0.00004	0.00031	0.00270	0.00366
	H_d	0.003	0.269	0.824	0.782
Expansion indicators	F_s	-1.745*	-3.504*	-4.095*	0.330
	D	-1.089	-1.455*	0.086	0.830
	r	0.866	0.282	0.031	0.056
	SSD	0.000*	0.004	0.012	0.029
	N_e	228,000	72,000	178,000	214,000

also used to estimate the effective size (N_e) and demographic trends (in the last 10,000 years) of the area west and east of Cape Peñas, as well as the numbers of migrants (Nm) between them. Software and settings details can be found in Supplementary Material S3.

Results

The SST map of the study area (Fig. 1) showed differences in water temperatures (especially near the coast) of up to 2°C: colder in the western than in the eastern area of Cape Peñas. These differences were consistent across years (2002 and 2003) and particularly marked during the summer season (Supplementary Material S2). With respect to the genetic analyses, linkage disequilibrium and the presence of null alleles/large allele dropout were not present. Genetic variability was higher in brown trout than in Atlantic salmon in both nuclear and mitochondrial DNA (Table 2). Half of the demographic tests indicated population expansion in the western Atlantic salmon populations as well as in the eastern brown trout populations (Table 2); 75% and 100% of these tests indicated population expansion in the west for brown trout and in the east for Atlantic salmon, respectively.

The number of migrants per generation (Nm) between both sides of Cape Peñas ranged between 1.01 and 8.52 when estimated with microsatellite data and between 2.44 and 9.44 when estimated with mitochondrial DNA (Table 3). Additionally Nm was asymmetric, being always more intense from west-to-east than in the opposite direction.

Atlantic salmon mitochondrial data (Fig. 2A) showed a star-shaped haplotype genealogy with one central haplotype (H3) present in both western and eastern areas in similar frequency, and four other haplotypes derived from this one, three of them present only in the eastern area. In brown trout (Fig. 2B), four more frequent haplotypes (H1, H3, H6 and H10) were present in both western

Table 3. Long-term mean number of migrants per generation (Nm) between the western (W) and eastern (E) areas of Cape Peñas (Northern Iberia).

Nm	Direction	Atlantic salmon	Brown trout
Mitochondrial	W to E	6.92	9.44
	E to W	2.44	4.48
Microsatellites	W to E	8.58	15.47
	E to W	2.72	1.01

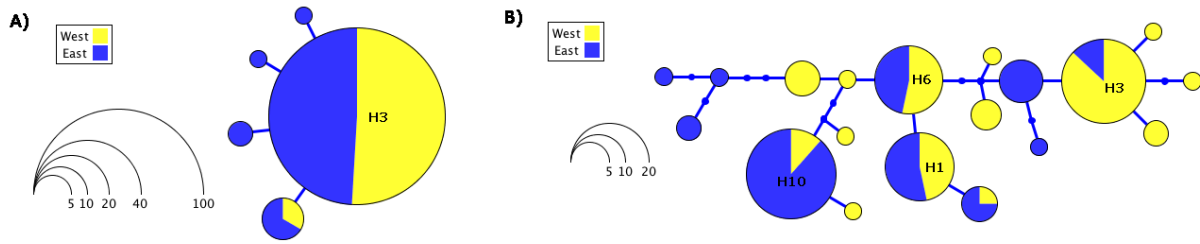


Figure 2. Haplotype genealogies representing the intra-specific haplotype distribution and their relative frequencies (circles are proportional to frequencies, see scales in the figures) in the sampled areas (western area: yellow, eastern area: blue) of Atlantic salmon (A) and brown trout (B). Branches are proportional to mutation steps.

and eastern areas in different frequencies; there were also singletons derived from the four main haplotypes, and intermediate haplotypes between them. Low-frequency haplotypes were found mainly in the east for Atlantic salmon, while more singletons were found in the west for brown trout.

The most common age classes (Fig. 3) were always 1.1 (one year in the river, one year at sea) and 1.2 in both western and eastern areas. In both species the 1.1 age class was less frequent in the west than in the east. Mean generation time was 2.81 years and 2.55 years for western Atlantic salmon and brown trout respectively, and 2.71 and 2.09 years (same order) in the east. When river and sea ages (i.e. time spent by the fish in rivers and the sea, respectively) were individually analysed, river age was similar in all cases (one year), but the mean number of sea years was always higher in the western area: 1.74 (s.d. = 0.06) in the west and 1.65 (s.d. = 0.03) in the east for Atlantic salmon and 1.61 (s.d. = 0.58) in the west and 1.29 (s.d. = 0.03) in the east for brown trout (t-values significant in both cases, $P = 0.014$ and 0.003 , respectively).

The archaeological samples showed a higher proportion of older individuals (2.2 and 1.3 age classes) in the western area (Fig. 3). Considering only two age classes, i.e. 4 and <4 year old individuals, the prehistoric samples were significantly different in the western and the eastern areas (contingency Chi-square = 8.37, $P < 0.01$, 1 d.f.). River age in these samples was similar to modern samples, and mean sea age also followed the same trend (average sea age in western samples: 1.99 years, average in eastern samples: 1.80 years; not significant, $P = 0.29$ in a t-test).

Sex ratio was different between grilse and multi-sea-winter (MSW) (i.e. individuals that have spent one or more than one year at sea, respectively) in both species (Fig. 4). There were proportionately many more females within MSW individuals than within the grilse in all cases, meaning that most males return to the river after only one year at sea while most females return after two or more years (all comparisons, based on contingency Chi-squares, were highly significant, $P < 0.01$). Sex-ratio differences between MSW and grilse were greater in the west in Atlantic salmon and in the east in brown trout.

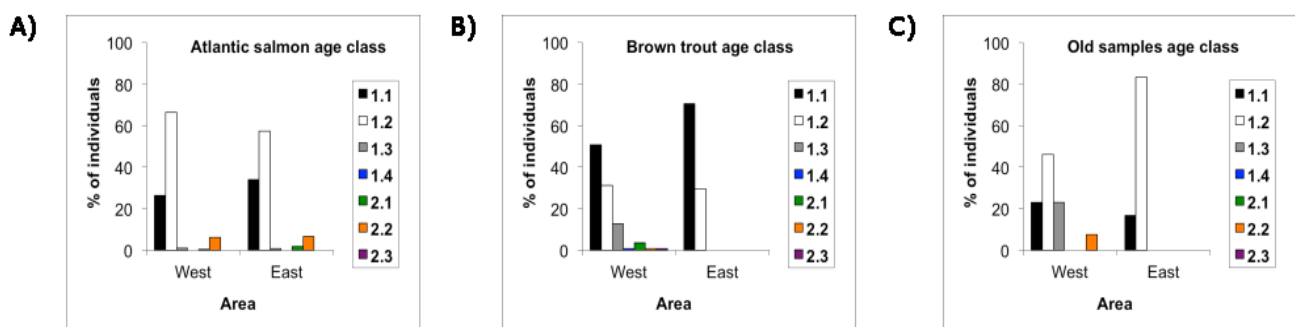


Figure 3. Percentages of Atlantic salmon (A), brown trout (B) and archaeological salmonid vertebrae (C) age classes (river age.sea age) in the western and eastern areas of Cape Peñas. Percentages within each area sum to 100% in each panel.

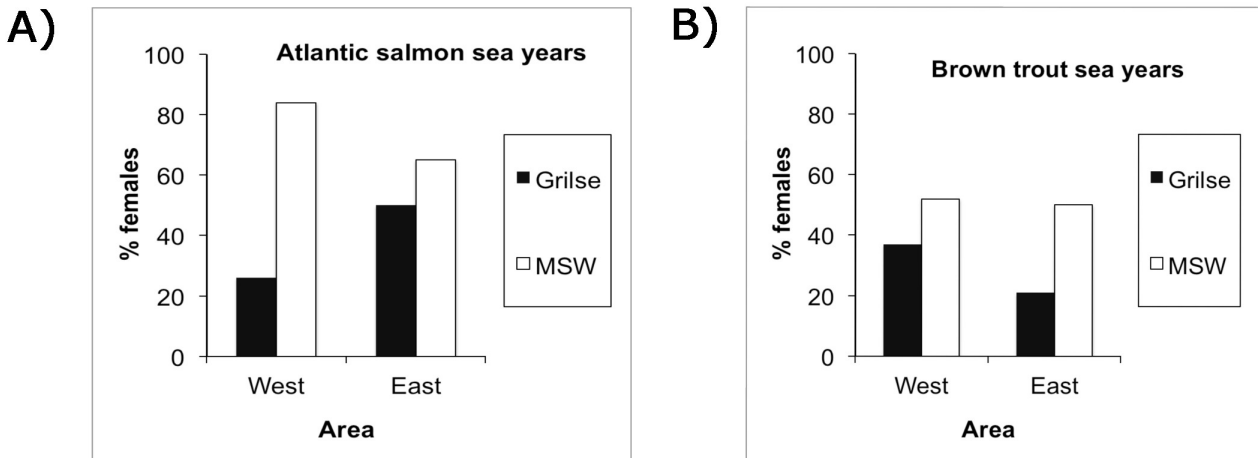


Figure 4. Proportion of females (in %) found in multi-sea-winter (MSW) and grilse (1 year spent in the sea) Atlantic salmon (A) and brown trout (B) in the western and eastern areas of Cape Peñas.

Analyses of past demographic trends (Fig. 5) showed positive Atlantic salmon population growth rates (differences in population size in a period of time) in both areas, with an intense decline recently in the western area. Brown trout population growth rates were relatively stable both sides of Cape Peñas, with small positive trends in the west and negative trends in the east; these rates have recently increased to reach positive values. Bayesian Skyline Plot (BSP) shapes were similar in the western and eastern regions within each species, and complementary between species.

The mean generation time was used to estimate N_e values (see Supplementary Material S3 for details). N_e were slightly higher in the eastern

than in the western area in brown trout, and more than two times higher in the western than the eastern area in Atlantic salmon (Table 2). Anadromous brown trout populations were larger than Atlantic salmon populations in the east, whereas the opposite trend occurred in the west.

Discussion

We have found subtle but clear regional and complementary differences in population genetics and life history in both Atlantic salmon and brown trout populations that can be attributed, at least partially, to spatial environmental differences at quite a small scale (in a range of a few hundred kilometres). The differences in population genetics are not related to the genetic population structure

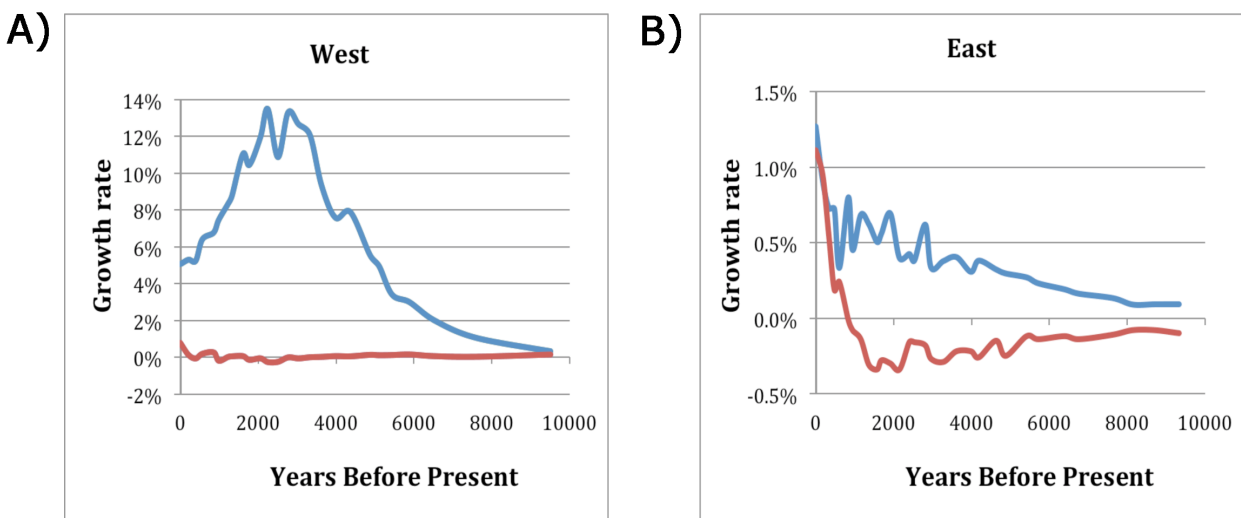


Figure 5. Atlantic salmon (blue) and brown trout (red) population growth rates (in %) in the last 10,000 years before present estimated with BEAST software to the West (A) and East (B) of Cape Peñas.

of the species because Cape Peñas has no influence on this (Horreo et al. 2011a). Life-history traits (LHTs), such as sea age and sex ratio, as well as population growth and migration directionality, are known to have been affected by these environmental differences since the Upper Palaeolithic.

Several factors, such as fishing pressure, fish density, geological characteristics of the bedrock and water temperature, can affect LHTs. The first two are the same across the whole study area due to fishing legislation and ecological and meteorological conditions, and therefore they cannot explain the east–west differences found. Bedrock characteristics have a great influence on river habitat (Frissell et al. 1986). Concretely, Perrier et al. (2011) described geological substrate as a major environmental factor influencing gene flow and local adaptation among Atlantic salmon populations; populations inhabiting rivers with different geological substrates therefore have genetic differences among them. In the present case, there are differences in the geological substrate on opposite sides of Cape Peñas, the proportion of carbonate rocks being much higher in the eastern area than in the western area (Aramburu and Bastida 1995). This produces population differentiation in both species on both sides of the cape. As mentioned above, the coastal water temperature difference is the other main factor. A precise 2°C difference (as occurs in this area; Fig. 1) is enough to change salmonids' LHTs through delays in Atlantic salmon sea-run timing (Valiente et al. 2011). This is indeed what happens in this location with Atlantic salmon (while the opposite occurs in brown trout; Fig. 3), because these water-temperature differences are highly marked during the summer when the Atlantic salmon are returning to their home rivers. Additionally, sex-ratio differences between MSW and grilse were greater in the west in Atlantic salmon and in the east in brown trout, suggesting more intense selection for this LHT in Atlantic salmon and brown trout in those areas. In sum, both factors—geological substrate and water temperature—influence the studied salmonids' LHTs.

Migration rates (Nm) were higher than one migrant per generation (OMPG) in all cases,

thereby affecting population structuring because values higher than OMPG imply population homogenization. Despite this, all Nm values among the western and eastern areas (except west-to-east brown trout migration) were much lower (Table 3) than Nm values in the whole area during the same year ($Nm=11.34$ – 12.70 ; Horreo et al. 2011a). This could mean that factors relating to the presence of Cape Peñas produce, in some way, a decrease in gene flow between these areas. West-to-east migration would be favoured by the Bay of Biscay streams, as occurs with horse mackerel and albacore (Lavin et al. 2007). Although brown trout migratory routes at sea are unknown for northern Spanish populations, these results suggest that there is a sea corridor/sea trout stream that communicates with both sides of Cape Peñas, with trout migrating more intensely toward the east.

Estimates of Nm also showed similar mitochondrial and nuclear estimates for Atlantic salmon, which indicate similar male/female migration habits. In the case of brown trout, females were shown to be more migratory than males, as suggested for this species in other latitudes (e.g. Jonsson 1985, Piechuch et al. 2007). Brown trout Nm values were also in general higher than values for Atlantic salmon, which accords with the stricter homing instinct of Atlantic salmon and with the generally more plastic migratory habits of brown trout—which makes the latter species highly adaptable (Valiente et al. 2010). This trout plasticity is key to its colonizing capacity and could contribute to maintaining the less-favoured populations of the eastern area, as they do at a smaller scale (Ayllon et al. 2006).

Genetic variability determines a population's evolutionary potential (Frankel and Soulé 1981). Current brown trout populations fit better in the west, as deduced from the high genetic variability of that area and the asymmetric migration between it and the eastern area. Their intricate haplotype genealogy suggests a long-term, well-established population in the whole region, with west–east differences and interchanges between areas. In Atlantic salmon, however, it is not so easy to determine which area has been histori-

cally better for this species' adaptation. The mitochondrial star-shaped genealogy of haplotypes suggests population expansion after a bottleneck (Mirol et al. 2008), but there are fewer haplotypes in the western area than in the eastern one. Since microsatellite variation in Atlantic salmon is similar in both areas, differences in haplotypes could indicate that female Atlantic salmon fit better in the colder (western) area.

Atlantic salmon and brown trout share their habitats, reproduce in the same areas and compete for the same resources (Heggenes et al. 1999). Such interspecific competition is reflected here in a complementary evolution of population growth rates (Fig. 5). Effective population sizes seem to be in concordance with this, being very much higher in trout than in salmon in the east, and vice versa in the west. Subtle contrasting patterns of LHTs were also found for both species across the region, leading to the conclusion that water temperature and geological characteristics may change the long-term balance among sympatric populations of Atlantic salmon and brown trout, as well as the evolution of their LHTs. Interaction between these two species, as shown by complementary population fluctuation and population sizes, probably influences their future biogeography.

This information is useful for the conservation and management of both species and highlights on how small a scale local adaptation differences in salmonids can be produced. As mentioned above, the phenotypic plasticity of brown trout represents its main adaptive advantage (e.g. Valiente et al. 2010), and this species is predicted to replace Atlantic salmon due to global climate change (Brander, 2007). Therefore, protection of the more-fragile species in sympatric species pairs and preservation of marine corridors to facilitate the migration of anadromous species between rivers could be two useful measures to take at this time of accelerated global climate change.

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Supplementary Materials

The following supplementary materials can be found online:

S1. Sample collection and LHT details

S2. Sea Surface Temperature (SST) maps

S3. Data analysis details

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