

Reproductive strategies explain genetic diversity in Atlantic salmon, *Salmo salar*

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Synopsis

We investigated the relationship between conservation status and genetic variability in European and North American Atlantic salmon, *Salmo salar*, populations, many of which have suffered severe bottlenecks. A negative north–south cline exists for the status of population conservation in this species. A literature review of genetic variability and demographic parameters of wild Atlantic salmon populations resulted in no statistical associations between population conservation status and genetic variation at enzyme or VNTR loci. We found however, a negative relationship between male parr maturation rates and geographical latitude for both American and European populations. The increase in effective population size due to participation by mature male parr and the increased proportions of these males in smaller (southern) populations could explain the lack of expected relationship between genetic variation and conservation status.

Introduction

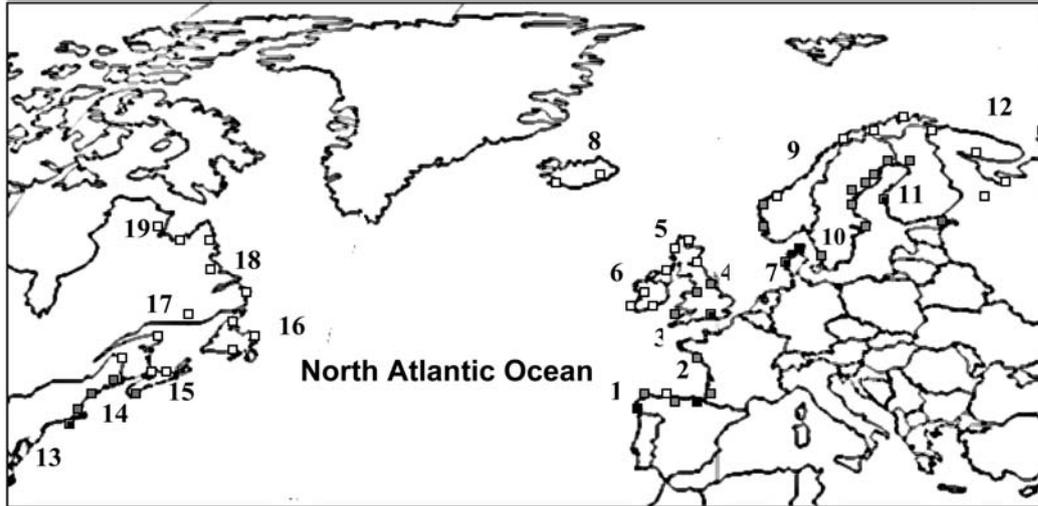
The conservation status of natural populations is generally related to genetic variability (Frankham 1996). Populations suffering bottlenecks for long periods are expected to have reduced genetic variability, at least at neutral loci. In species exhibiting migratory behaviour, the biological definition of a particular population is not very evident because *a priori* the migrants could reproduce in non-native habitats. But when the homing instinct exists, as in the case of Atlantic salmon, *Salmo salar*, each river – or even each tributary – can be considered a population unit.

Atlantic salmon is a species with essentially anadromous populations (i.e. Sedgwick 1982). The juveniles, also called parr, stay 1 or more years in the natal river before smolting and migrating to

the sea. The marine phase lasts for a period between 1 and 4 years, when they grow rapidly until sexual maturation. Then, normally in spring or early summer, they return to their natal river for breeding in the autumn and early winter. Most salmon die after spawning.

Atlantic salmon is distributed on the two Atlantic coasts in the northern hemisphere, with a diversity of anadromous census counts likely due to marked differences in the status of each population and their habitats (Parrish et al. 1998). A major factor that affects population size in this species is usually habitat loss. Populations inhabiting rivers located at the northern edge of the natural distribution (58–70° N) are generally stable, with large censuses and good habitats (Figure 1). Populations located in the middle of the distribution (51–60° N) have suffered a general

□ Stable; ■ Declining; ■ Extirpated-Restored; ■ Extirpated



1. Spain	Mandeo Esva Bidasoa Ason Cares	Pas Sella Eo Porcia Narcea	13. United States	Connecticut Kennebec Sheepscot Ducktrap Penobscot Narraguagus Pleasant Machias Dennys	
2. France	Nivelle	Loira		14. Nova Scotia	Salmon LaHave Martin's Mushamush Gold St. Croix Wells Petite Gaspereau East St. Mary's West St. Mary St. Mary's Country Harbour Isaac's Harbour Stewiacke Philip Margaree
3. England & Wales	Test Itchen Usk Wye Teifi	Dyfi Rhyd-hir Dee (Cheshire) Lune Hodder	15. New Brunswick		Maguadavic Big Salmon Hammond St. John Bartholomew
4. Scotland	Langa Nith Tweed Beaully Conon Tay Orchy Creran Dee (Aberdeen)	Spey Ewe Shin Polly Kirkaig Helmsdale Grimersta Dionard Thurso			Miramichi Resigouche
5. North Ireland	Tyne Roe Glendun	Bush Lower Bann			
6. Ireland	Inney Blackwater (Co. Cork) Slaney Shannon Doonbeg Corrib Screebe Sneum Varde	Boyne Burrishoole (Co. Mayo) Moy Spaddagh Foyle Faughan Storaa Gudena			
7. Denmark					

Figure 1. Map showing the conservation status of the main Atlantic salmon populations in the native distribution range of the species (northern hemisphere). Specific locations are listed in Table 1.

	Skjern			
8. Iceland	Geirlandsá	Hrútafjardará/Siká	16. Newfoundland	North Harbour
	Thjórsá	Núpsá		Salmonier
	Hvítá	Flekkudalsá		Little Codroy
	Sogid	Austurá		White Bear
	Stóra-Laxá	Vesturá		Northeast
	Ellidaár	Fáskrúd		Come by Chace
	Úlfarsá	Midfjardará		Conne
	Bruará	Laxá á Hrútafirði		Highland
	Leirvogsa	Krossá á Skardsst		Expoits
	Namsen	Bakkaá		Terra Nova
	Laxá í Kjós	Blanda		Gander
	Bugða	Vídidalsá/Fitjaá		Middle Brook
	Brynjudalsá	Hvoísá/Stadarh		Dog Bay
	Leirá	Vikurá		Humber
	Laxá í Lsveit	Vatnsdalsá	Aides Stream	
	Edlida	Svariá	Lomond	
	Andakílsá	Laxá á Ásuml	Indian	
	Grímsá	Hrófá	West	
	Flókadalsá	Saemundará	St. Genevieve	
	Dvina	Húseyjarkvísl	Forteau	
	Langá	Hofsá	Pinware	
	Älftá	Vídidalsá	Eagle	
	Reykjadalsá	Laxá-Ytri	Hunt	
	Hvítá	Isafjardará	Madeleine	
	Gjúfurá	Fnjóská	Bonaventure	
	Hitará	Langadalsá	Cascapedia	
	Tlivreá	Selá	Matane	
Nordurá	Vopnafirði	York		
Breiddalsá	Skjáfandafljót	San Lorenzo		
Hafjardará	Hvanriadaísá	Trinité		
Straumfjardará	Vesturdal	Godbout		
Fródá	Laxá í Adaídal	Moise		
Hördudalsá	Fossá	Natashquan		
Midá í Dölum	Laugardalsá			
Laxá á Skógst	Midfjardará	18. Labrador	Sand Hill	
Haukadalsá	Fljótaá		Michaels	
			Flowers	
9. Norway	Ímsa	Saltðalselva	19. Ungava	George
	Oyreselv	Näätamö		Koksoak
	Hopselv	Neidenfjord		
	Strynselva	Alta		
	Namsen	Repparfjord		
Beiarelva	Teno			
10. Sweden	Lagan	Lögdeälven		
	Ätran	Ümeälven		
	Dalälven	Skellefteälven		
	Ljusnan	Byskeälven		
	Örstaelva	Oulujoki		
	Ängermanälven	Luleälven		
Bondalsalven	Kalixälven			
Índalsälven	Tornionjoki			
Sokna				
11. Finland	Kymijoki	Simojoki		
	Iijoki	Kemijoki		
12. Russian	Neva	Tuloma		
	Dvina	Kola		
	Varzuga	Bolshaya Zapadnaya		
	Nilma	Kachkovka		

Fig 1. (Continued)

decline due to human – induced habitat damages and overfishing (Parrish et al. 1998). Populations located at the southern areas (40–52° N) are severely endangered and many of them are extinct (Prouzet 1990, Braña et al. 1995). Reasons for the decline of southern populations are human – induced but also include effects of habitat change such as droughts, probably associated with global climate change in the last few decades (Parsons & Lear 2001).

From this general perspective Atlantic salmon is an ideal species with which to examine the association between genetic variability and population conservation status throughout their whole geographic range. We hypothesize that a north–south cline should exist for genetic variability, associated with a decrease in the population conservation status with latitude. We will test this hypothesis using published studies of genetic variability for the species, both at enzymatic and VNTR loci (minisatellites and/or microsatellites). With some possible exceptions such as the malic enzyme MEP-2* (Verspoor & Jordan 1989), or microsatellites hypothetically involved in diseases, both allozyme and VNTR variation could be considered neutral. Genetic diversity could also be affected by the presence of mature male parr which can contribute to spawning in this species (Saunders & Schom 1985, Myers et al. 1986, Hutchings & Jones 1998, Garcia-Vazquez et al. 2001) and by genetic exchange between populations through straying (Rieman & Dunham 2000) which can be common in Atlantic salmon (Quinn 1993, Jonsson et al. 2003). We therefore also test for latitudinal trends in parr maturation and straying.

Materials and methods

We searched all publications reporting genetic variability and life history trait variation in wild Atlantic salmon populations using the databases BIOSIS, ISI, Medline and Science Direct. The geographic regions considered, their latitudes, the number of rivers from which we obtained published data and the references are summarized in Table 1. The range of latitudes considered was 42° 02'–70° 47'.

The conservation status of the main Atlantic salmon populations in their native distribution

area can be observed in the map in Figure 1. The status was based on censuses of adult individuals by direct observation or counting in traps in consecutive years. We considered the following status categories: stable-sea run has not decreased in recent years; declining-sea run has been decreasing for some years, extirpated-restored-natural sea run was interrupted for some years and Atlantic salmon stocks were introduced in the river for restoration allowing new sea run, extirpated-sea run no longer exists.

With respect to genetic variation, we considered two types of loci: enzyme-coding loci and VNTR loci. The parameters of genetic variability considered for analysis were: the mean heterozygosity per locus expected under Hardy–Weinberg conditions (H_e), for both enzyme and VNTR loci; and the mean number of alleles per locus (N_A), only for VNTR loci. The mean number of migrants per generation (N_{em}) was estimated based on published F_{ST} values (Wright 1978), to understand the degree of gene exchange between population within a given geographic region. Regions of similar size were considered, to prevent biased conclusions due to the effect of between-river distance into N_{em} and straying rates.

The population parameters chosen for analysis were: male parr maturation rate in the river, and straying rate (percent of anadromous individuals returning to a river different of the natal one) determined by physical tagging.

The relationship between latitude and status of wild populations in Europe (from 42°N to 70° 47' N) and America (from 42° 03' N to 58° 39' N) was tested using non-parametric Kruskal–Wallis tests, attributing arbitrary numeric values to each status as follows: stable, 1. declining, 2. extirpated-restored, 3. extirpated, 4. We used linear regression for testing association between latitude and parameters of genetic variability (H_e for enzymatic loci, H_e for VNTR loci, and N_A for VNTR loci) as well as the percent of mature male parr aged 1+, and multiple regression to test for an association between latitude (dependent variable) and the biological parameters considered (rate of male parr maturation as a representative of life-history trait and mean number of alleles per locus as a representative of genetic variability (independent variables)). A rank correlation test was employed to investigate the

Table 1. Populations considered in this work.

Continent	Area	Latitude		N	References
		from	To		
America	United States	42° 02'	44° 54'	17	1, 2
	New Brunswick	44° 14'	48° 02'	10	4, 13, 19, 20, 21
	Nova Scotia	44° 10'	46° 34'	15	1, 4, 15, 16, 22, 23
	Québec	48° 10'	58° 30'	24	3, 4, 5, 6, 7, 8, 9, 10, 11, 12
	Newfoundland	47° 00'	53° 28'	22	1, 3, 4, 13, 14, 15, 16, 17, 18
	Labrador	53° 35'	56° 10'	3	1, 3, 4
Europe	Spain	42° 00'	43° 34'	11	1, 3, 24, 28, 34, 35, 36, 37, 38, 39, 40
	France	43° 22'	47° 42'	3	36, 41, 42, 43, 44
	England & Wales	50° 23'	54° 59'	17	29, 30, 31
	Ireland	51° 56'	55° 43'	38	1, 7, 13, 24, 25, 26, 27, 28
	Scotland	54° 28'	58° 36'	25	1, 24, 25, 28, 32, 33
	Denmark	55° 24'	56° 29'	5	45
	Sweden	56° 29'	65° 48'	18	1, 52, 53, 54
	Norway	60° 00'	70° 47'	43	46, 47, 48, 49, 50, 51
	Iceland	64° 26'	66° 08'	2	1, 13
	Russia	64° 36'	69° 11'	13	46, 47, 55, 56
	Finland	65° 24'	65° 42'	2	53

N = number of populations considered in each area.

1, King et al. 2001; 2, Letcher & Terrick 1998; 3, Verspoor et al. (in Jordan et al. 1997); 4, Verspoor 1988 (in Jordan et al. 1997); 5, Landry & Bernatchez 2001; 6, Fontaine et al. 1997; 7, Garant et al. 2000; 8, Schiefer 1971 (in Myers et al. 1986); 9, Riley et al. 1984; 10, Randall & Power 1979; 11, Schiefer 1969 (in Myers et al. 1986); 12, Gibson (in Myers et al. 1986); 13, McElligott & Cross 1991; 14, Beacham & Dempson 1998; 15, McConnell et al. 1997; 16, Marshall, Department of Fisheries and Oceans, Halifax, N.S. (in Myers et al. 1986); 17, Dalley 1979 (in Myers et al. 1986); 18, Daley et al. 1983; 19, Ståhl (in Jordan et al. 1997); 20, Randall Department of Fisheries and Oceans, Moncton, N.B. (in Myers et al. 1986); 21, Schofield & Peppar 1982; 22, McConnell et al. 1995; 23, O'Reilly et al. 1996; 24, Sánchez et al. 1996; 25, Wilson et al. 1995; 26, Crozier & Moffet 1989; 27, Galvin et al. 1996; 28, Stone et al. 1997; 29, Hovey et al. 1989; 30, O'Connell et al. 1995; 31, Hurrell & Price 1993; 32, Jordan et al. 1992; 33, Jordan 1990 (in Jordan & Youngson 1992); 34, Morán et al. 1994; 35, Vázquez et al. 1990; 36, Martínez et al. 2001; 37, Pérez et al. 1997; 38, Morán & Garcia-Vazquez 1998; 39, Braña et al. 1995; 40, Utrilla & Lobón-Cerviá 1999; 41, Guyomard 1987; 42, Baglinière & Champigneulle 1986; 43, Héland & Dumas 1994; 44, Dumas & Prouzet 2003; 45, Nielsen et al. 1999; 46, Skaala et al. 1998; 47, Koljonen 1989; 48, Elo et al. 1994; 49, Ståhl & Hindar 1998 (in Jordan et al. 1997); 50, Cross & Healy (in Jordan et al. 1997); 51, L'Abée-Lund 1989; 52, Ståhl 1987; 53, Koljonen & McKinnell 1996; 54, Ryman & Ståhl 1981; 55, Studenov et al. 2001; 56, Martynov et al. 1994.

association between the straying rate and $N_e m$. The significance of the rho parameter (r_s) was estimated by a *t* test.

Results

Conservation status and latitude

Stable populations are mostly located in the northern part of the species distribution, both in Europe and America, whereas southern populations are generally declining or extirpated. This trend is statistically significant for European ($n = 183$, $\chi^2 = 32.99$, $p < 0.001$) and North American ($n = 69$, $\chi^2 = 42.99$, $p < 0.001$) populations, and when both continents are analyzed together ($n = 252$, $\chi^2 = 47.18$, $p < 0.001$).

Genetic variability and latitude

Mean heterozygosity expected under H-W at enzyme loci ranged from 0.009 (Nova Scotia, Canada) to 0.469 (north of Brittany, France). We found no significant association between mean heterozygosity and geographical latitude for North America ($r = 0.032$, $p = 0.926$, $n = 15$) or Europe ($r = 0.063$, $p = 0.511$, $n = 99$) populations (Figure 2a). Similarly, no relationship was found between these parameters at VNTR loci analysed in 57 populations (for North America $r = 0.3$, $p = 0.137$, $n = 26$; for Europe $r = 0.089$, $p = 0.63$, $n = 31$) (Figure 2b), with values ranging from 0.28 (Scotland) to 0.88 (Nova Scotia).

We only considered the mean number of alleles per locus (N_A) for VNTR loci because the

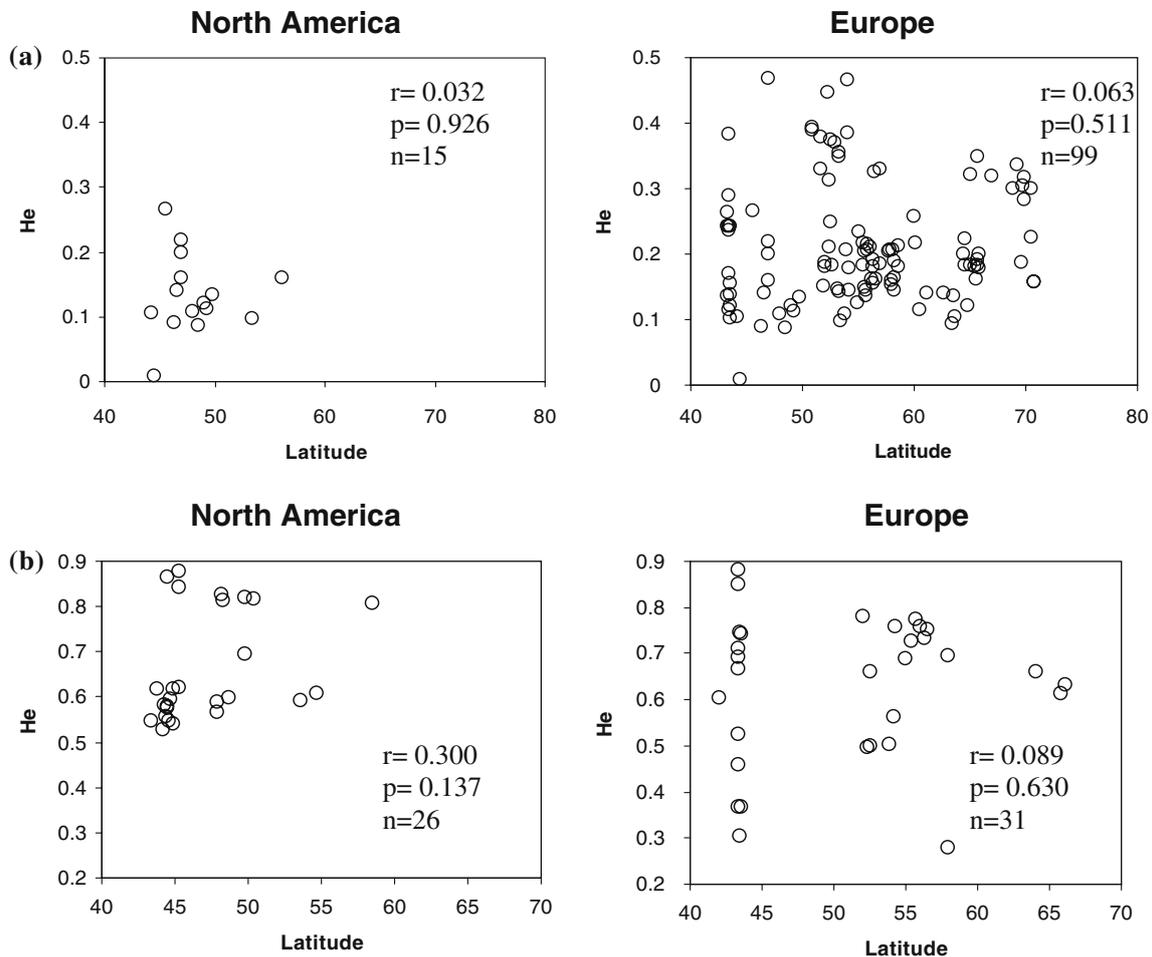


Figure 2. (a) Heterozygosity expected at enzyme loci in North American (left) and European (right) populations. (b) Heterozygosity expected at VNTR loci in North American (left) and European (right) populations. R values for the association between heterozygosity and latitude (r), statistical significance (p) and number of populations analyzed (n).

variation at enzyme loci is very low for this species (Davidson et al. 1989). In the 60 populations analyzed, N_A ranged from 3 (Spain) to 17.8 (France), with Canadian populations exhibiting higher N_A than European populations. Similar to our results using mean heterozygosity as a measure of genetic variability, we found no statistical association between N_A and latitude ($r = -0.084$, $p = 0.691$ for North America; $r = 0.055$, $p = 0.771$ for Europe) (Figure 3).

Male parr maturation and latitude

We found a significant negative association between parr maturation rate and latitude on both

sides of the Atlantic Ocean ($r = -0.905$, $p < 0.01$, $n = 9$, and $r = -0.761$, $p < 0.05$, $n = 23$ for Europe and North America respectively) (Figure 4). Results of the multiple regression that included both parr maturity and genetic variability showed that only parr maturity was significantly associated with latitude ($p = 0.04$ for parr maturation rate, $p = 0.72$ for mean number of alleles per locus).

Gene flow and latitude

We found no association between straying rates and latitude ($r = -0.239$, $p = 0.859$) or between straying rates and N_{em} in these regions ($r = -0.170$, $p = 0.748$) (Table 2).

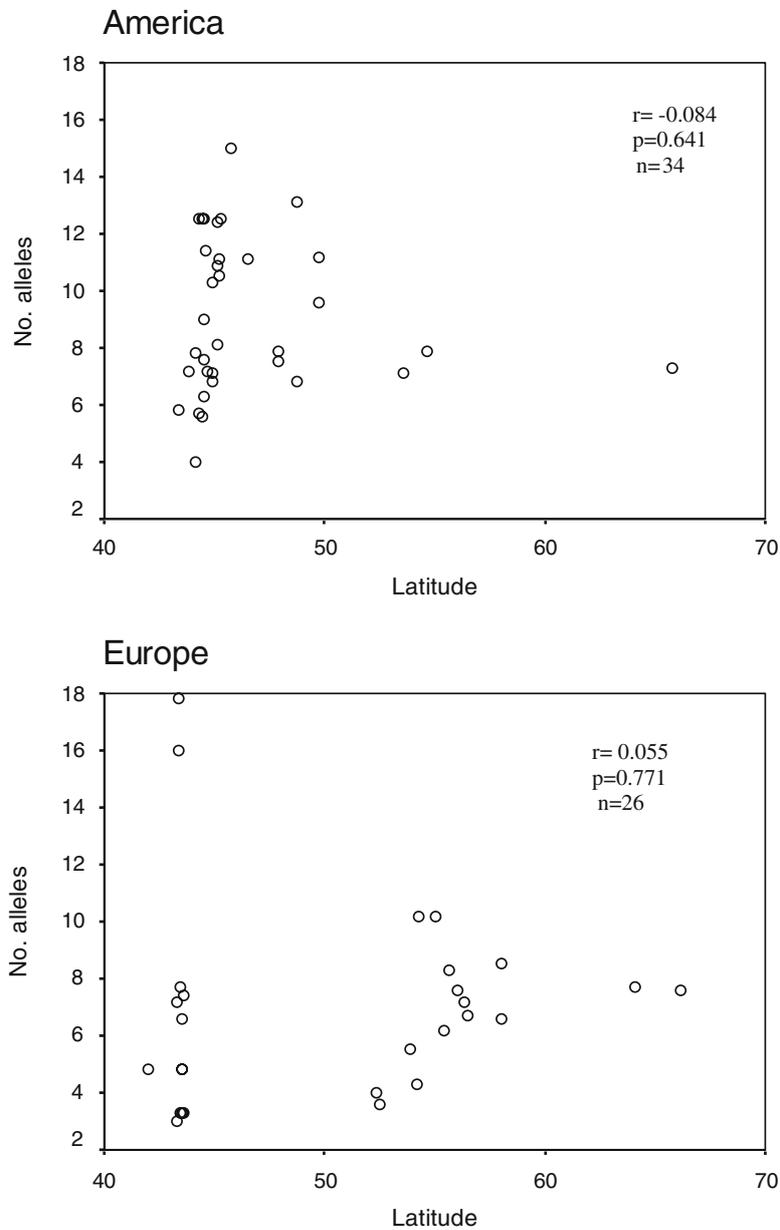


Figure 3. Mean number of alleles per locus (No. alleles) at VNTR loci in North American (above) and European (below) populations located at different latitudes. R values for the association between mean number of alleles and latitude (r), statistical significance (p) and number of populations analyzed (n).

Discussion

Contrary to expectation, we found no latitudinal trend in the genetic variability of wild Atlantic salmon populations throughout their range despite the strong latitudinal cline in conservation status. Populations at the edge of the salmon distribu-

tional range exhibit relatively high levels of genetic variability both at coding (enzyme) and at non-coding (VNTR) loci, in spite of the fact that they are small and often endangered (Sánchez et al. 1996, Martínez et al. 2001). This result seems to be a genetic paradox because genetic drift in such small populations usually leads to loss of genetic

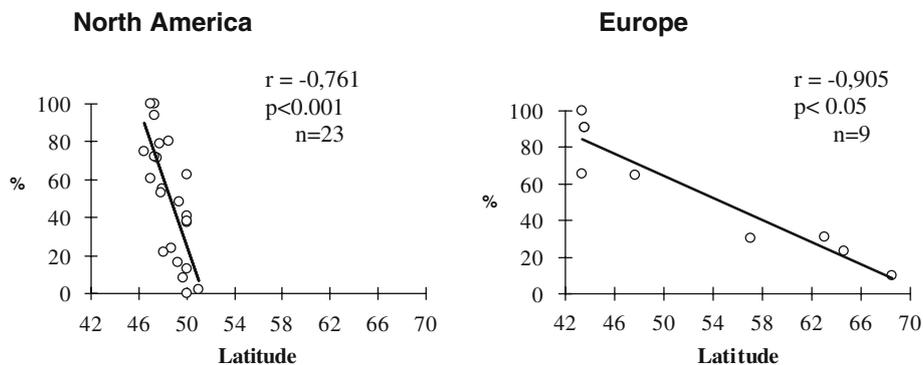


Figure 4. Maturation rate at age 1+ in North American (left) and European (right) populations located at different latitudes. R values for the association between maturation rate and latitude (r), statistical significance (p) and number of populations analyzed (n).

Table 2. Values of straying rate and mean number of migrants per generation ($N_e m$).

Latitude	Area	Straying	$N_e m$	References
43° 30'	Spain	9.0	7.6	1, 2
53° 30'	Ireland	3.0	5.6	3, 4
56° 30'	Scotland	2.7	15.4	5, 6
58° 30'	Norway	15.4	14.5	7, 8
60° 30'	Sweden	2.0	2.5	9, 10
63° 00'	Baltic	7.3	2.3	11, 12
65° 00'	Iceland	2.1	–	13

1, García de Leániz et al. 2001; 2, Moran et al. 1994; 3, Hawkins 1979; 4, Jordan et al. 1992; 5, Went 1969 (in Thorpe & Mitchell 1981); 6, McElligott & Cross 1991; 7, Toft 1975 (in Thorpe & Mitchell 1981); 8, Koljonen 1989; 9, Rasmuson 1968 (in Koljonen 1989); 10, Ståhl 1981; 11, Jonsson et al. 2003; 12, Jordan et al. 1997; 13, Johannsson et al. 1998.

variants and decreased genetic variability (i.e. Caballero 1994).

Moran & Garcia-Vazquez (1998) attributed unexpectedly high genetic variation in southern European Atlantic salmon to the contribution of male parr that could considerably increase effective population sizes, particularly in small populations (L'Abée-Lund 1989, Martinez et al. 2000, Jones & Hutchings 2001). In this study we have shown that the maturation rate of males in freshwater before sea migration is a life-history trait associated with latitude. This association, previously reported for Canadian rivers in a narrower geographical context (Myers et al. 1986), is here confirmed for the entire range of the species. Moreover, maturation of male parr aged 0+ was reported only for rivers at the southern limit of the geographic distribution, both in America (17% in the Connecticut River, USA; Letcher & Terrick 1998) and Europe (42–53% in Spanish rivers, Nicieza & Braña 1995, Utrilla & Lobon-Cervia

1999; 18% in French rivers, Dumas & Prouzet 2003).

Parr maturation is not synonymous with parr contribution to spawning. Although there are many studies reporting parr maturation rates, little information exists on the effective contribution of male parr to spawning in different latitudes, likely due to the difficulty in conducting such experiments in natural conditions with Atlantic salmon. These experiments involve typing and monitoring of anadromous adults in sites where male parr, previously genotyped, are naturally present; as well as embryo sampling and paternity analysis. There are only two relevant studies with these conditions corresponding to three different latitudes. In the River Aberdeenshire-Dee (Scotland, 57° N) a mean contribution of 10.8% to spawning was reported for mature male parr (Jordan & Youngson 1992). In the River Nivelle (France, 42° N) this contribution was 65% (Martinez et al. 2000). Other experiments have been conducted in

semi-natural or controlled conditions involving different parr densities, with variable results emphasising the important contribution of male parr to spawning (Myers & Hutchings 1987, Hutchings & Myers 1988, Moran et al. 1996, Thomaz et al. 1997, Jones & Hutchings 2001). Their results are not applicable to the question addressed here because they do not correspond to natural situations with a 'normal' density of mature parr in wild river areas. From the two experiments conducted in the wild we could infer a higher contribution of mature parr in southern latitudes but it is evident that it is not statistically sound. Jones & Hutchings (2001) found a negative relationship between total parr reproductive success and intensity of anadromous male competition and suggested that the increase in the effective number of males is most pronounced in natural populations when the number of anadromous individuals is low. Thus, the higher contribution of parr to spawning found in the River Nivelles could be due to a scarcity of anadromous males rather than a high density of mature male parr due to a high maturation rate. This issue can not be solved with the data currently available.

Alternative/complementary explanations for the maintenance of genetic variability in southern populations, such as higher straying rate or higher gene flow between rivers in southern areas are not supported by our study. Although it seems reasonable to expect that salmon might lose strict homing when faced with droughts or very low water discharge situations (e.g. Unwin & Quinn 1993) which are more frequent in southern latitudes, we found similar straying rates across latitudes. Latitudinal variation in straying rates could also be linked to population size (Quinn 1984) such that larger (northern) populations might be expected to have higher straying rates. This clinal pattern may be balanced by the tendency for higher straying rates with increased duration of the oceanic migration (Quinn et al. 1991, Jonsson et al. 2003) or with parr maturation rates, both of which would predict higher straying rates in southern populations. Clearly other factors, such as parr contribution, should be invoked to fully explain high genetic variability in southern Atlantic salmon.

There is some evidence to suggest that male parr maturation is not genetically determined, or at

least does not have a strong genetic component. Parr maturation can be chemically induced (Henry et al. 1998), and parr maturation rates are a function of winter temperature and feeding regimes in experimental conditions (Herbinger & Frias 1992). In the field, parr maturation rates increase following habitat alterations such as floods (Letcher & Terrick 1998). Increases in the proportion of mature parr are also explained by variation in growth alone (Myers et al. 1986). When Scottish individuals are transplanted to Spanish rivers they mature and can contribute to spawning as Spanish native parr do (Moran et al. 1994). If environmental conditions can induce or modify parr maturation a strong environmental determination of this life-history trait should be acknowledged.

Evidence supporting the environmental determination of parr maturity has important implications for management of wild populations. Male parr naturally contribute to wild spawning (i.e. Saegrov & Urdal 1993, Erkinaro et al. 1994) and are responsible for much genetic variation of wild populations as shown here. Their male offspring would mature as parr only in response to environmental stimuli (Letcher & Terrick 1998), not as a consequence of the early maturation status of the father. The use of male parr as breeders for enhancing captive stocks should therefore be considered in future management of Atlantic salmon.

Other implications for management may concern habitat conservation. Gross (1991) demonstrated increased reproductive success of coho salmon, *Oncorhynchus kisutch*, jacks (mature parr) with increased stream debris, that can provide refuges used by jacks for sneaking. Habitat clearing by government and citizens, usually practised for aesthetic purposes in many areas, may modify mature parr reproductive success also in Atlantic salmon. This aspect should be carefully considered in the future given the importance of mature parr for increasing population sizes in small populations.

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