

Reproductive strategies in small populations: using Atlantic salmon as a case study

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Abstract – Wild salmonid populations with only a few breeding adults may not exhibit a significant reduction in genetic variability compared with larger populations. Such an observation suggests that effective population sizes are larger than population size estimates based on direct adult counts and/or the mating strategy maximises outbreeding, contributing to increased heterozygosity. In the case of wild Atlantic salmon *Salmo salar* populations, stratification by age classes and sexes on the spawning grounds avoids inbreeding and increases genetic variability. We studied the breeding composition of four Spanish salmon populations. Over a 7-year period we concluded that the probability of within-cohort mating is very low: females generally reproduce after two sea-winters whereas males reproduce mostly as one sea-winter (*grilse*) and/or mature parr. Considering different levels of contribution of mature parr to spawning derived from field surveys, we developed a simple model for estimating effective population sizes and found that they doubled with 65% parr contribution expected for rivers at this latitude (43°N), and ranged from 100–800 individuals. The effect of between-cohort mating was modelled considering different ranges of differences in allele frequencies between cohorts and resulted in 28–50% increases in heterozygosity when considering a 65% parr contribution. The complex mating strategy of Atlantic salmon contributes to explain the high levels of genetic variability found for small populations of this species. This model can probably be extended to other animal species with mating strategies involving different cohorts.

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Introduction

Fish populations are in decline in many parts of the world (Pauly et al. 2003; Hutchings & Reynolds 2004). This decline is of additional concern because of the potential reduction in genetic variability that can occur in small populations especially at the edges of species distributions (Frankham 1996). However, wild salmonid populations with only a few breeding adults may not exhibit a significant reduction in genetic variability compared with larger populations (Moran & Garcia-Vazquez 1998; Martinez et al. 2000; Valiente et al. 2005). This unexpected result suggests that effective population sizes are larger than

population size estimates based on direct adult counts and/or the mating strategy maximises outbreeding, contributing to increased heterozygosity.

Salmonids exhibit large variation in life history traits, including age at maturity which can range from <1 year to 10 years (Power 1969; Letcher & Terrick 1998). As a consequence, reproductive stocks consist of a mixture of cohorts spawning in the river so that the breeding populations are composed of individuals of different ages (reviewed in Hutchings & Jones 1998). The reproductive strategy of anadromous salmonids consists mostly of semelparity with overlapping year classes (Fleming 1998). At the southern edge of its distribution, the breeding populations of

Atlantic salmon include anadromous females and a mixture of anadromous and nonanadromous males (Nicieza & Braña 1993). Many male parr mature during the fluvial phase before migrating to sea, even during the first year of life (Letcher & Terrick 1998; Utrilla & Lobon-Cervia 1999). Mature parr fertilise around 65% of eggs in wild south European populations (Martinez et al. 2000), then smolt, migrate to sea and return to reproduce again, whereas females only reproduce when returning from the sea. A small proportion of adults survive spawning and return to spawn in subsequent years (Braña et al. 1995).

The breeding system of Atlantic salmon may affect the genetic variability of wild populations in different ways. Population genetic variability is usually measured in two ways: as the number of alleles (genetic variants) and as heterozygosity. Bottlenecks affect both parameters, but the number of alleles usually decreases first whereas heterozygosity is reduced in further generations (Cornuet & Luikart 1996). The reproductive system of Atlantic salmon probably influences both measures of genetic variability. First, mature parr may directly increase the effective population size, thus avoiding losses of genetic variants (number of alleles). Secondly, the combination of a number of cohorts simultaneously reproducing in the river may also increase heterozygosity, if: (i) some genetic differences exist among generations (e.g. because of drift) and (ii) mating is not classed within cohort.

The demographic and genetic consequences of parr maturity have been explored by modelling but without prior knowledge of the extent of mature parr genetic contribution (Caswell et al. 1984; L'Abée-Lund 1989). The increase in the effective number of breeders because of a high contribution of alternative male phenotypes to spawning (Garcia-Vazquez et al. 2001) may be lower than expected because a great variance appears in experimental arenas in individual mature parr reproductive success (Jones & Hutchings 2002).

The potential increase in heterozygosity that could be derived from between-cohort matings (BCMs) has been less well explored. Variation in age at maturity for both males and females has been reported for south European Atlantic salmon populations (Nicieza & Braña 1993). Although individual sizes can be positively related to reproductive success for either males or females (Garant et al. 2001), males of different sizes, cohorts – have alternative routes to gain access to mating (Fleming 1998; De Gaudemar et al. 2000) and crosses between individuals from different age classes are expected.

Here we describe the breeding structure of four wild Spanish salmon populations, and then explore the possible effects of field-derived levels of genetic contribution of mature parr and age structure of

breeders for these salmon populations using a simple model to describe: (i) potential levels of within-cohort mating (WCM) and (ii) potential increases of effective population size. We also explore the consequences of BCM for genetic variability (heterozygosity) by considering different ranges of genetic differences among cohorts.

Material and methods

Salmon populations analysed

Spanish Atlantic salmon populations are declining or extirpated because of the construction of dams without fish passage, industrial pollution and flow depletion from withdrawals for industrial, domestic and agricultural use. The central part of the Cantabric Coast, Asturias (Bay of Biscay, North Spain), is the only Spanish area where stable Atlantic salmon populations still exist (Parrish et al. 1998). The Esva, Narcea, Sella and Cares rivers support the largest self-sustained populations in this area. Because there is available information on the demographic and genetic conservation status of these rivers (Moran et al. 1993; Braña et al. 1995; Perez et al. 1997), we have chosen these four populations as test cases for highlighting the effect of reproductive strategies on the genetic variability of wild Atlantic salmon populations.

Fish samples

Adult Atlantic salmon entering the Esva, Narcea, Sella and Cares rivers from 1993 to 1999 were caught by rod-and-line during the angling season (March–July), and by electrofishing during the spawning season (November–January). An intense sampling effort was made during these years, thus problems of poor censuses requiring mathematical transformations of raw data are not expected (Holmes 2001). Scale samples for age determination and blood from the caudal vein for sex determination were taken from each individual.

We surveyed parr each year by electrofishing in the spawning areas of these rivers during the spawning season to determine the breeding component of mature male parr. Parr were anaesthetised, maturity was assessed by gently stripping all individuals sampled to assess sperm production, and some scales were sampled from each mature parr to determine age. A minimum number of 200 parr were sampled per year.

Age and sex determination

Age was determined by scale reading following Baglinière (1985). For anadromous fish the number of years in the river and the number of years at sea are

given (i.e. 1.1 means 1 year in the river and 1 year at sea). For parr only the number of years in the river is given (1+ and 0+ indicate that the individuals are 1 year + some months, and several months old, respectively). Sex determination was based on the detection by immunoagglutination of the serum vitellogenin of females (Le Bail & Breton 1981).

Constructing the models

The abundance of mature parr in the spawning areas does not indicate their actual contribution to spawning *per se*, that is, their real effect on the genetic composition of the next generation. For southern European rivers, a 65% contribution of mature parr to spawning has been reported (Martinez et al. 2000). Other relative contributions have been reported by other authors (see Introduction); for our model we also chose 20% as an intermediate estimate (found in a Scottish river; Jordan & Youngson 1992). In addition we also consider the situation of no contribution by mature parr, that is, only anadromous adults reproduce.

Estimates of the effective number of breeders N_b were made employing the expression $1/N_b = 1/4N_m + 1/4N_f$ where N_m is the effective number of males and N_f the effective number of females, following Crow & Denniston (1988). Estimates of the effective population size N_e (based on Waples 1990; Tajima 1992) were made as $N_e \approx gN_b$, where g is the generation length or average age at spawning weighted by age-specific fecundity. Age-specific fecundity for Atlantic salmon females inhabiting the studied rivers was 4867 ± 243 eggs/female for one sea-winter (known as *grilse*) and 8780 ± 311 eggs/female for two sea-winter females (Nicieza & Braña 1993). For males, g was estimated based on the average individual reproductive success of anadromous and mature parr, reported to be 11 and 3.9 offspring respectively in this geographic area (Martinez et al. 2000). Although a large variation in individual reproductive success is expected for both anadromous and mature parr, we employed these values in our model because they are the only available estimates for this European latitude (43°N).

Estimates of heterozygote increases because of BCM were obtained using the following rationale. Suppose a situation where all females belong to a cohort X and all males to a cohort $X + 1$ with a heterozygosity value H_o . Under Hardy–Weinberg conditions each cohort is composed of males and females in equal proportions and the heterozygosity value is H_e . The difference $H_o - H_e$ will depend on the absolute difference between the allele frequencies of males and females s . To simplify the model we considered only two alleles. Assuming equal number

of males and females, the frequency of an allele will be $p + 0.5s$ for one sex and $p - 0.5s$ for the other, p being the average frequency for the whole population. The observed proportion of heterozygotes in a situation of compulsory BCM (all males from a cohort, all females from another) will be:

$$\begin{aligned} H_o &= (p - 0.5s)(1 - p - 0.5s) \\ &\quad + (p + 0.5s)(1 - p + 0.5s) \\ &= -2p^2 + 2p + 0.5s^2 \end{aligned}$$

The heterozygosity expected under Hardy–Weinberg conditions if each cohort is composed of both males and females in equal numbers is:

$$H_e = 2pq = 2p(1 - p) = 2p - 2p^2.$$

Thus $H_o - H_e = 0.5s^2$

Thus the increase in heterozygosity will be proportional to the square of the difference between male and female allele frequencies.

Results

Table 1 presents the description of the adult samples collected for the period 1993–1999, classified by sex and returning year within each cohort. The individuals which hatched in a given year (a cohort) returned to the river as adults over two or three different years, as 2-year old after spending only one winter at sea (*grilse*), or as 3-, or even 4-year olds. The distribution of sexes by return age differed within each cohort: females tended to return after 2 years at sea whereas males returned mostly after only 1 year at sea (i.e. as *grilse*). This trend was similar in all four studied rivers and suggests that there are both anadromous females and males from three cohorts during the spawning season in the four Spanish rivers we studied. However, mature male parr need to be included in this breeding system because they were abundant in the spawning areas of the four rivers every year. The majority of the mature male parr present in the four rivers during the spawning season were the young of the year (0+), but a proportion (up to 26%, Cares River in 1996) were more than 1-year old. Only three adults (two females and one male) returned to spawn a second time based on spawning marks on scales (Baglinière 1985; Perez et al. 2005); the females are effectively semelparous, males spawn once as parr and once again as adults.

Constructing the model

The breeding schemes of our four populations for the 1995, 1996 and 1997 spawning seasons are shown in Fig. 1 as a function of variation in male contribution

Table 1. By-cohort and sex composition of the anadromous component of the four studied populations for the period considered (1993–1999).

Year	Cohort 1991		Cohort 1992		Cohort 1993		Cohort 1994		Cohort 1995	
	F	M	F	M	F	M	F	M	F	M
River Esva										
1993	46.4%	84.2%								
1994	46.4%	14.2%	15.5%	79.8%						
1995	7.2%	1.6%	82.2%	11.9%	8.7%	46.7%				
1996			2.3%	8.3%	86.9%	48.9%	37.3%	73.7%		
1997					4.3%	4.4%	60.5%	26.3%	10.6%	50%
1998							2.2%	0	89.4%	50%
1999									0	0
<i>N</i>	140	120	129	84	92	45	46	19	47	16
River Narcea										
1993	21.8%	72.9%								
1994	68.8%	19.5%	15.2%	69.6%						
1995	9.4%	7.6%	82.9%	29.6%	19.4%	48.8%				
1996			1.8%	0.8%	79.4%	48.8%	27.3%	70.4%		
1997					1.1%	2.3%	69.3%	26.5%	10.4%	60.3%
1998							3%	3.1%	83%	34.2%
1999									6.6%	5.5%
<i>N</i>	266	210	433	358	175	86	198	98	259	73
River Sella										
1993	46%	64.3%								
1994	40.4%	22.1%	56.2%	81.3%						
1995	13.6%	13.6%	37.7%	15.9%	8.7%	0%				
1996			6%	2.8%	79.6%	86%	29.2%	45.5%		
1997					11.7%	14%	66.7%	54.5%	63.6%	27.3%
1998							4.1%	0	30.7%	66.6%
1999									5.7%	6.1%
<i>N</i>	161	235	281	252	103	43	72	33	140	33
River Cares										
1993	27.8%	63.8%								
1994	70.4%	34.6%	40.9%	84.9%						
1995	1.8%	1.5%	55.2%	12.4%	13.9%	43.1%				
1996			3.8%	2.7%	82.6%	52.3%	20.7%	66.7%		
1997					3.5%	4.6%	79.3%	33.3%	51.1%	68.4%
1998							0	0	48.9%	31.6%
1999									0	0
<i>N</i>	162	130	105	113	115	65	58	18	45	19

Results are presented as the per cent of individuals of each cohort returned to the river each year, within sex. *N*, total number of individuals of each sex and cohort, per river.

(from only anadromous to 65% by mature parr). The relative proportion of males and females of a given cohort varied depending on rivers and years. However, the composition of the breeding populations was not identical, or even similar, for males and females, thus allowing for a large proportion of BCM.

Estimating within-cohort mating

From the age composition of the breeding populations of Atlantic salmon, we next calculated the proportion of WCM under the three different hypotheses of different relative contributions of mature parr stated above: high (65%), low (20%) and none (0%). In Table 2 we present the estimated proportion of WCM expected under these three situations. Our results clearly show that most possible crosses occur between females and males of different cohorts. With 65% contribution of mature parr, the highest WCM rate was

22% of the total matings (Cares River, 1996). If mature parr fertilised 20% of the ova, the highest WCM was 50%. Finally, 62% WCM is expected for the Cares River 1996 if male parr are not considered. WCMs increase when male parr contribution decreases, and vice versa. But even if male parr did not contribute to breeding (0%), most expected WCM rates are under 50%, with a mean proportion of 0.436 across all rivers and years.

Estimating effective population sizes

In Table 2 we present estimates of effective population sizes following Waples (1990) and Tajima (1992), under three different hypothetical scenarios. In this particular case, the final value of N_e depends not only on the absolute numbers of males and females but on the relative fertility of each type, which depends on the age (females) or on the reproductive strategy (parr or

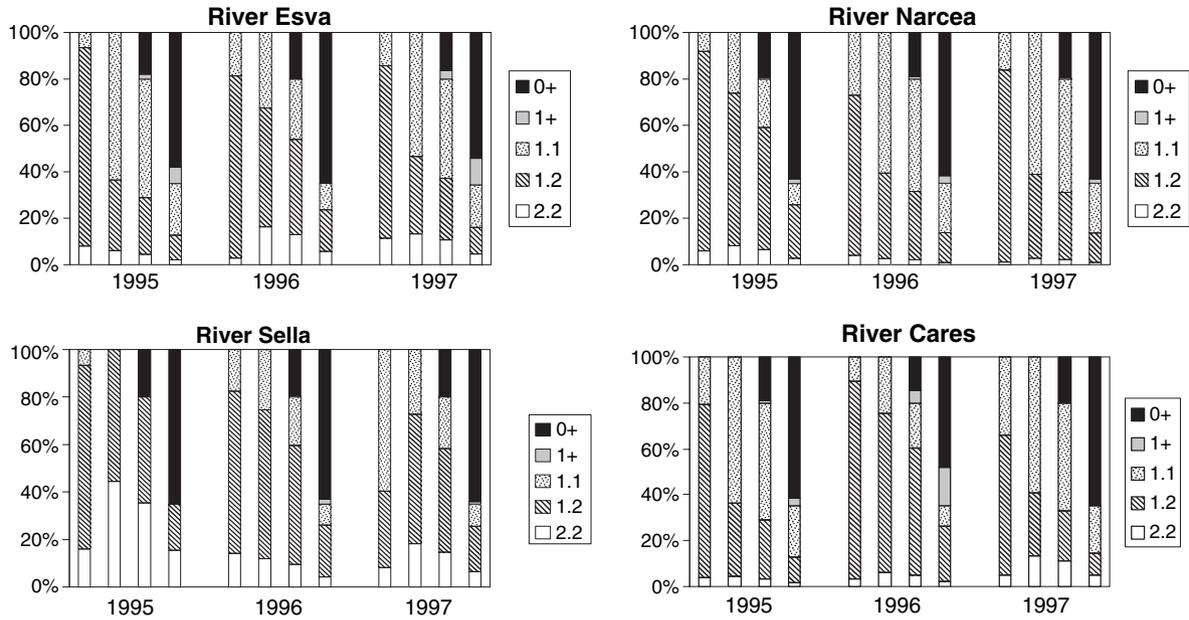


Fig. 1. Anadromous adults constituting the breeding population of each river for three consecutive years. The results are presented as the proportion of breeders of each age class (2.2, 1.2, 1.1, 1+ and 0+) expected per sex and year, for each river. Within each year, columns are (from left to right): females; only anadromous males; males with 20% mature parr contribution and males with 65% mature parr contribution.

Table 2. Sex-ratio (males/females), effective population size (N_e) and proportion of within-cohort mating (WCM) of salmon in each river during the spawning season from 1995 to 1997, assuming 65%, 20% or 0% mature male para contribution to paternity.

River	Year	Male parr paternity								
		65%			20%			0%		
		Sex-ratio	N_e	WCM	Sex-ratio	N_e	WCM	Sex-ratio	N_e	WCM
Esva	1995	0.760	208.09	0.107	0.333	120.36	0.244	0.266	101.26	0.305
	1996	1.204	204.38	0.163	0.527	129.2	0.373	0.421	110.95	0.467
	1997	1.226	73.11	0.119	0.537	46.39	0.271	0.428	33.75	0.339
Narcea	1995	1.100	810.67	0.207	0.481	502.42	0.473	0.385	430.23	0.591
	1996	1.620	437.7	0.147	0.709	293.63	0.334	0.567	256.16	0.418
	1997	1.232	342.11	0.139	0.539	217.06	0.318	0.431	186.73	0.398
Sella	1995	1.496	318.86	0.176	0.657	210.9	0.402	0.525	183.26	0.502
	1996	1.405	258.35	0.171	0.614	189.67	0.379	0.492	145.88	0.489
	1997	0.633	169.51	0.123	0.277	94.83	0.282	0.221	79.3	0.353
Cares	1995	1.632	173.31	0.131	0.714	116.46	0.299	0.571	101.63	0.373
	1996	1.261	235.71	0.218	0.552	150.27	0.498	0.441	129.43	0.623
	1997	0.828	116.68	0.131	0.362	68.45	0.299	0.289	57.84	0.374

anadromous males). Although there is variation among rivers and years, it is evident that the effective population sizes (N_e) almost doubled if 65% of embryos were fertilised by mature male parr. The estimated N_e for the total period considered (harmonic mean of the three brood years, following Hartl & Clark 1997) ranged from 61.9 (only anadromous contribution) to 128.4 (65% mature parr contribution) for the Esva River; from 259.1 to 465.8 for the Narcea River under the same assumptions; from 120.5 to 232.6 for the Sella River and from 86 to 161.3 for the Cares River. Bottleneck effects are not expected for these large population sizes over the studied period,

particularly when mature parr contribution is considered.

Effect of between-cohort mating on heterozygosity

The estimates of heterozygosity increases for different BCM situations (Table 3) changed greatly depending on the difference between male and female allele frequencies. The ratio of BCM existing in a population is also decisive for an effective increase in heterozygosity. In Table 3 five different situations are considered. One (BCM = 1) implies that females and males are from different cohorts, thus all the mating events occur

Table 3. Estimates of heterozygosity increase expected for different situations of between-cohort mating (BCM) and differences in allele frequencies between males and females (*s*).

Situation	BCM	<i>s</i> -values		
		1	0.5	0.1
Reference	1	0.5	0.125	0.005
65% male parr contribution, Esva River 1995	0.893	0.4465	0.1116	0.0045
65% male parr contribution, Cares River 1996	0.782	0.391	0.0978	0.0039
0% male parr contribution, Esva River 1995	0.695	0.3475	0.0869	0.0035
65% male parr contribution, Cares River 1996	0.377	0.1885	0.0471	0.0019

between different cohorts. In this situation the maximum increase in expected heterozygosity is 0.5, i.e. all offspring are heterozygotes, in contrast to a Hardy–Weinberg situation where both males and females are homozygotes for different alleles and will mate at random. The other four situations correspond to 65% contribution of male parr in two extreme real cases (BCM = 0.893 and 0.782, corresponding to the Esva River in 1995 and Cares River in 1996 respectively) and 0% contribution of male parr (BCM = 0.695 and 0.377 for the same rivers and years). A considerable increase in heterozygotes can be obtained even if the contribution of male parr was 0%. The main factor that determines heterozygosity values over those expected from Hardy–Weinberg is the difference in allele frequencies between cohorts. The relative effect of the contribution of male parr depended on the particular sex-ratio and age composition of each cohort. For example, for the small Esva River population the increase in heterozygotes for a 65% contribution of male parr was only 28% higher than that estimated for a null contribution of these reproductive forms. However, for the Cares River the increase in heterozygotes doubled for a 65% male parr contribution with respect to the situation where only anadromous individuals reproduced in the system.

Discussion

Our results suggest that the breeding strategy of southern European Atlantic salmon populations including four to five cohorts of males and two to three cohorts of females tends to minimise losses of genetic variability, in different ways. Garcia-Vazquez et al. (2001) have proposed that the mechanisms involved include an increase in the number of breeders and BCM. Here, we expand on those ideas and provide a more complete analysis of these mechanisms using field data and simple modelling.

Realistically, and taking into account that male parr actually fertilise a large proportion of ova, most

possible crosses occur between females and males of different cohorts (Table 2). It is worth noting that the smallest population from the Esva River also presents the lowest range of potential WCM. WCM has such a low probability of occurring that full-sib mating can be considered negligible (except in cases of much reduced population sizes). Furthermore, as females are generally semelparous, mother-son crosses can be discarded. Males fertilise eggs as 1- or 2-year-old parr and generally return after 1 year at sea, when their daughters are still immature in the river. Even if they returned after 2 years at sea, their daughters would probably still be at sea because females return later than males to reproduce. Therefore inbreeding because of endogamous mating can be practically discarded and outbreeding is likely favoured by the simple cohort composition of the breeding stock, even if mature male parr contributed only 20% to paternity in these rivers.

A combination of males and females of different cohorts maximises outbreeding, providing a very small proportion (if any) of inbred crosses. Clearly, the *F*-value in a population is determined by the finite population size, and not to an additional increase of homozygotes from inbred crosses. The expression $(1-F_{IS})(1-F_{ST}) = 1-F_{IT}$ (Hartl & Clark 1997) is reduced to $(1-F_{ST}) = (1-F_{IT})$ if F_{IS} tends to zero. The effects of mating between close relatives being $1-F_{IS}$ and the fixation index because of limited population size being *F*. However, it is not clear that this strategy has significant long-term effects on N_E . In a Pacific salmon hatchery programme, Waples & Do (1994) demonstrated that broodstock practices such as sib-avoidance mating had little permanent effect on the level of inbreeding. A BCM schema could contribute to explain high values of heterozygosity in small populations but not to preserve the number of variants in a population. As the older breeding cohorts are composed mostly of females and the younger (adults, mature parr) mostly of males, high heterozygosities can be explained, at least partially, on the basis of this outbred mating between different cohorts. This effect is maximised in small populations, as the main factor increasing heterozygosity over expected Hardy–Weinberg values is the difference between cohorts in allele frequencies (Table 3). In very small populations a heterozygote excess in offspring is expected, because genetic drift produces differences in allele frequencies between breeding cohorts. This hypothesis is supported by the high levels of heterozygosity we found which is consistent with other small endangered populations at this latitude (Perez et al. 1997; Moran & Garcia-Vazquez 1998; Martinez et al. 2000; Valiente et al. 2005).

Effective population size is a key parameter used to understand population viability and thus can have

important consequences for conservation (Anthony & Blumstein 2000). Here we show that the contribution of male parr also leads to an increase in effective population size (Table 2). For example, the effective population size was doubled in many situations when the contribution of parr was 65%, a typical value for South European populations (Martinez et al. 2000). The consequence of the increase in effective population sizes is the maintenance of genetic variability in populations, avoiding losses/fixation of alleles because of increases of F . Based on the censuses presented in Table 1, F -values expected for the four populations in the studied time period can be calculated following Hartl & Clark (1997) as $F = 1 - (1 - 1/2N_e)$ each generation. F ranged from 0.048 (Esva River in 1997) to 0.0019 (Narcea River in 1995) if only returning adults were considered but from 0.0068 (Esva 1997) to 0.00061 (Narcea 1995) if mature parr are included as the 65% of male breeders, resulting in considerable reductions in F . These values are small and no significant loss of genetic variability is expected in the four populations. Effective population size increases less if there is variation in male reproductive success between parr and adults (Jones & Hutchings 2002). Nevertheless, the genetic variability found in our small populations suggests that the actual increase in effective population size is enough to avoid allele losses. The contribution of mature parr may thus explain the latitudinal pattern in genetic variability found for Atlantic salmon in both North America and Europe (Valiente et al. 2005).

These results also suggest different strategies for males and females which can have important evolutionary consequences (Fleming 1998). Females smolt earlier, stay at sea longer, come back at larger body sizes and are essentially semelparous. Males grow fast in streams and mature early, smolt later, and tend to stay at sea for only 1 year, but are iteroparous. Because of the higher mortality rates of males, sex ratios are female-biased as adults (Table 1, Perez et al. 2005), but return near one when mature male parr are considered (Table 2).

There are other implications of this breeding system for the preservation of Atlantic salmon populations from the southern edge of their distribution. In these marginal populations, extreme environmental conditions such as high water temperatures and droughts can be limiting for the species (Parrish et al. 1998). However, even if alevin survival is very poor in 1 year, the negative effect of a lower adult return 2 and 3 years later is not totally detrimental for the population as the breeding stock is composed of many cohorts. Thus, a one-cohort failure may be compensated for by other cohorts and mature parr, to maintain the breeding stock and occupy spawning areas.

In conclusion, in this study we have found that the structure of the Atlantic salmon breeding stocks maximises outbreeding because sexes return to reproduce at different ages, and tends to increase effective population sizes because of the participation in spawning of male parr. The consequence of this breeding system is the maintenance of genetic variability in wild stocks, which are preserved in marginal distributional areas in spite of the diverse environmental threats they are subjected to. Future work should validate the results of our model using molecular data (Waples 1989) and consider whether the model presented for this anadromous species can be extended to other fish species at the edge of their distribution.

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