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GENETIC VARIATION AND AGE AT MATURITY IN POPULATIONS OF ATLANTIC SALMON OF NORTHERN SPAIN.

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ABSTRACT

The main features of the life history of Atlantic salmon have been analyzed in a number of studies and reviews. (Shearer, 1992). Natural salmon populations exist as discrete stocks, maintained through precise homing, spawnig time and migration and showing locally adapted peculiarities.

In Spanish rivers, Atlantic salmon begin to enter in the river in February-March, spawn in December- January and the young fish spend 1 or 2 years before migrating to the sea. Salmon return to their nursery river as mature adults 1 to 3 years later (Martin-Ventura, 1987 Nicieza et al. 1990). As in other countriesp the proportion of fish returning as grilses (1SW) had a considerable increasing in Spanish river in last year. So, grilses represent among 7.47 to 8.12 % of total catches in 1970 and between 24.4 and 35.14 in 1989.

Different hypotheses were made to explain these phenomena. In this work we analyze the relationships between genetic variability (using the six most polymorphic protein-coding-loci detected in Atlantic salmon : IDPH-3*, mMEP-2*, IDDH-1*, IDDH-2*, sAAT-4* and MDH-3,4*) and the age of maturity of adults' salmon (estimated as number of years spent in sea water before return to the river).

Our results show that grilses (1SW) has a significantly higher frequency of heterozygotes on mMEP-2 locus and lower frequency of heterozygous on MDH-3,4 locus than in salmon (2 or 3 SW). However, grilses shows a lower mean heterozygosity over six polymorphic loci than salmon group.

These data suggest a variable association between genetic variability and age at maturity and a selective influence of some particular locus.

Introduction

The life history and biology of Atlantic salmon have been analyzed in a number of studies and reviews (Shearer 1992). Reproduction and early juvenile rearing are in fresh water but juvenile migrate to the sea for feeding until maturity and them return to their natal river to spawn, after a period that varies widely through their geographical range.

Natural salmon populations exist as discrete stocks, maintained through precise homing, spawning time and migration showing locally adapted peculiarities.

The rivers of northern Spain, constitute the southern limit distribution of Atlantic salmon (*Salmo salar L.*) in Europe. These rivers are generally short and their populations, usually small, are exploited only by recreational fishermen who use rod and line. Atlantic salmon begin to enter in these rivers in February-March and spawn between late November to mid January. Juvenile salmon spend one o two years in fresh water before becoming smolts and migrate into the sea. Salmon return to their nursery river as mature adults 1 to 3 years later (Matin-Ventura,1987: Nicieza et al.,1990).

The Atlantic salmon stocks of these rivers mainly consist of 2 SW salmon (50-90%) but, as in others countries, a considerable increasing of fish returning as grilses (1SW) and , in parallel, a general decline in the proportion of fish with 3SW or more, were observed in Spanish rivers in last years (Matin-Ventura,1987:Nicieza et al.,1990; Nicieza & Braña,1993).

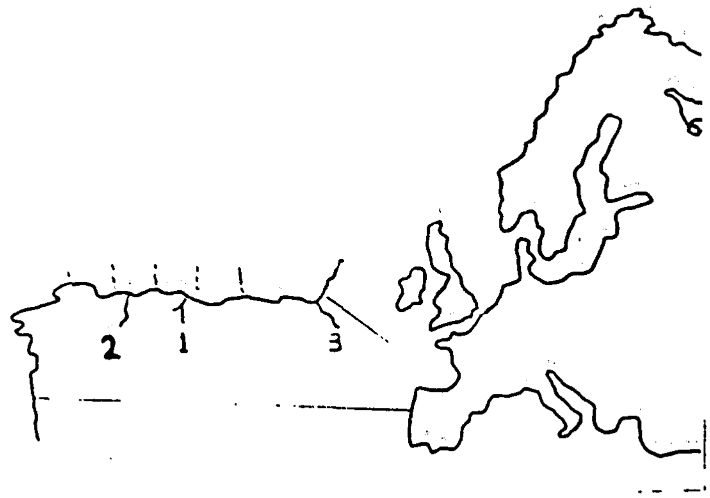
Age at maturity is a very important parameter in the dynamics of salmonid population. In Atlantic salmon it has been suggested that sea age at maturity is influenced both by freswater and oceanic conditions (Gardner,1976; Dempson et al.,1986; Nicieza et al.,1993). Also, sea age at sexual maturity has been shown to have some genetic basis (Naevdal,1983; Gjerde,1984; Skilbrei,1989). However the identity and relative importance of such factors - genetics and environmental remain undetermined.

In this study we examine the relationships between genetic variability and the age of maturity for Atlantic salmon population from three rivers in Northern Spain. Genetic variability, were determined using the six most polymorphic protein-coding-loci detected in *Salmo salar* in Spain: mMEP-2*; sIDHP-3*; sIDDH-1*; sIDDH-2*; sAAT-4* and sMDH-3,4* (Sánchez et al.,1991,1993).

The null hypothesis tested here is that there are not differences in genetic composition among different age-clases of Atlantic salmon spawners.

Material and methods:

Samples of adult Atlantic salmon were collected from three rivers of northern Spain: Sella (1) and Esva (2) rivers (1988-91), in Asturias, and on Bidasoa (3) river (1991-92) in Navarra.



Age determination for each fish were made from scale analysis. All individuals sampled spent one winter in fresh water and 1 or 2 winters in sea water.

Electrophoresis:Tissue samples of liver and muscle were analyzed by horizontal starch gel electrophoresis and scored for the 6 loci which show polymorphism in Asturias salmon populations: sMDH-3,4*, sIDHP-3*, mMEP-2*, sAAT-3*, sIDDH-1* and sIDDH-2*. The procedures followed those described by Sánchez et al., 1991 and Blanco et al., 1992.

Allele frequencies for each sea-age group were found by direct counting from observed genotype frequencies. Homogeneity of allele and genotype freqecies was tested using G-test with Willians corrections for sample size (Sokal and Rohlf,1981).

As no significant heterogeneity of allele frequencies was found among samples caught in different years, data were therefore pooled to generate sea-age groups.

Results and Discussion

Many data have shown that in nearly impossible to exploit an animal population without altering some of its biological characteristics (Lannan et al.,1989,Thorpe,1993). Reduction in the mean size, weight and sea age at maturity were evidenced in Atlantic salmon in last years (Porter et al.1986). As in other countries, similar reduction in sea age at maturity have also ocurred in Spanish natural salmon populations (Nicieza et al.,1990).

Given that in most trait a correlation exists between phenotypic and genotypic variation (Gjedrem,1983) and that age at maturity show relatively high values of heritability (see Gall 1993) it is necesary to know how change in age structure affect to genetics status of populations.

The allelic frequencies of the most common allele (100) observed and expected heterozygosity at each loci for the different samples investigated are given in Table 1.

For all loci, no significat heterogeneity of alle frequencies was found among age-groups (1SW vs 2SW) within rivers. Deviations from Hardy-Weinberg equilibrium was only significant from genotype distribution at IDDH-1 locus in the grilse group (1SW) sampled in Bidasoa river ($G=15.39; P<0.001$). However different patterns in genetic varibility were found amog age-groups. In all river, salmon groups (2SW) show larger values of mean heterozygosity than grilse groups (H_0 in Table 1) .In all grilse groups, the mean observed heterozygosity is among 2-9% smaller than expected heterozygosity while in salmon groups observed heterozygosity is among 6 to 12 % larger than expected heterozygosity (Table 1).These data suggest that the level of heterozygosity at enzyme loci is associated with age at maturity in adult Atlantic salmon. Individuals having lower levels of heterozygosity have earlier maturation.

Other studies also have shown that heterozygosity is possitively associated with fitness components (Mitton and Grant,1984, Liskaukas and Ferguson,1990,1991; Sánchez et al.,1994). In addition, also particular locus can be directly related with age at maturity in Atlantic salmon.

Thus, Jordan et al. (1990) found an association between earlier maturation and mMEP-2* genotype distribution and suggest that this locus is significant by itself.

In our samples ,grilse group shown larger values of heterozygosity at mMEP-2* locus than salmon group (Table 1). However, in both groups genotype frequencies observed did not differ significantly from those expected in Hardy-Weinberg equilibrium (data do not showns). Although a marginal heterogeneity of genotype frequencies within rivers ($P=0.056$) was found, data of all river were pooled to produce a genotypic frequency distribution for grilse and salmon groups (Table 2). These results shown that there are not differences between allelic frequencies and genotipe distribution ($G=2.97$) but heterozygosity in grilse group is 27% larger that in salmon group.

In Atlantic salmon,it is know that individuals leave their natal streams after to obtain a minimun size and that the size at smolting might be adjusted by selection to local environmental (Nicieza and Braña,1993). In Asturian rivers ,Nicieza and Braña (1993) found a positive relationship between smolt size and maturation as grilse; large smolt tended to mature earlier than small smolts of the same age.

Recent studies provide evidences of an association between mMEP-2* variation and growth in Atlantic salmon (Jordan et al.1990,Pringle et al.1994;Sánchez et al.,1994). Thus , we found in natural populations, that in river age 1+ individuals heterozygous for mMEP-2 have a large mean fork length than homozygotes ones (unpublished data).

These results can provide empirical support for the association between variation at mMEP-2* locus and age at maturity.If heterozygous at mMEP-2* locus growth faster in early life, them, they will return to natal river as grilses.

Also, differences in genetic composition at sMDH-3,4* locus was found between age-groups (Table 1and 2). A significant difference between genotype frequency distribution in salmon and grilse was found (Table 2). Salmon group showed higher frequency of 87 allele (G=3.095;P<0.001), and heterozygosity than grilses group.

From the results of this study, it appears that there are differences in genetic composition between grilses and salmons groups.For these reason changes in age structure in Spanish salmon population may be affect the genetic structure of these population.

The natural salmon populations of Spanish river have distinctive characteristics, such as low level of variability and generally higher frequenciy of the allele 87 at the sMDH-3,4* locus than other European populations (Sánchez et al.1991,1993).

The increasing of grilse in these populations can reduce their genetic variability. It is know that reduction on genetic variability may affect to the capacity of populations to survive and the versatility to adapted to specific environments and habitats, specially in marginal populations (Lewontin,1984) as is the case of Spanish populations.

Obviously, to exploit an animal population without altering its genetic constitution requires that all biological components of that population be harvested in proportion to their relative abundance.

Other implication of change in age-structure is the possible reduction of total biomass catch in Spanish river. In Asturian rivers, grilse range from 7.47 to 8.12% of total catches in 1975 and among 24.4 to 35.14% in 1989 (Nicieza et al. 1990).In contrast there has been a general decline in the proportion of fish which had spent three or more winters in the sea, which represent not more than 2% in last 15 years (Nicieza et al. 1990) (Figure 1). The catches in in Sapnish rivers show wide annual variations, but on average 1,500 fish were caugth per fishing season in last 15 years. If we assume these data , a reduction of 23 % can be expected in the total biomass catch in Spanish fisheries in last 15 years due only to change in age structure (Table 3).

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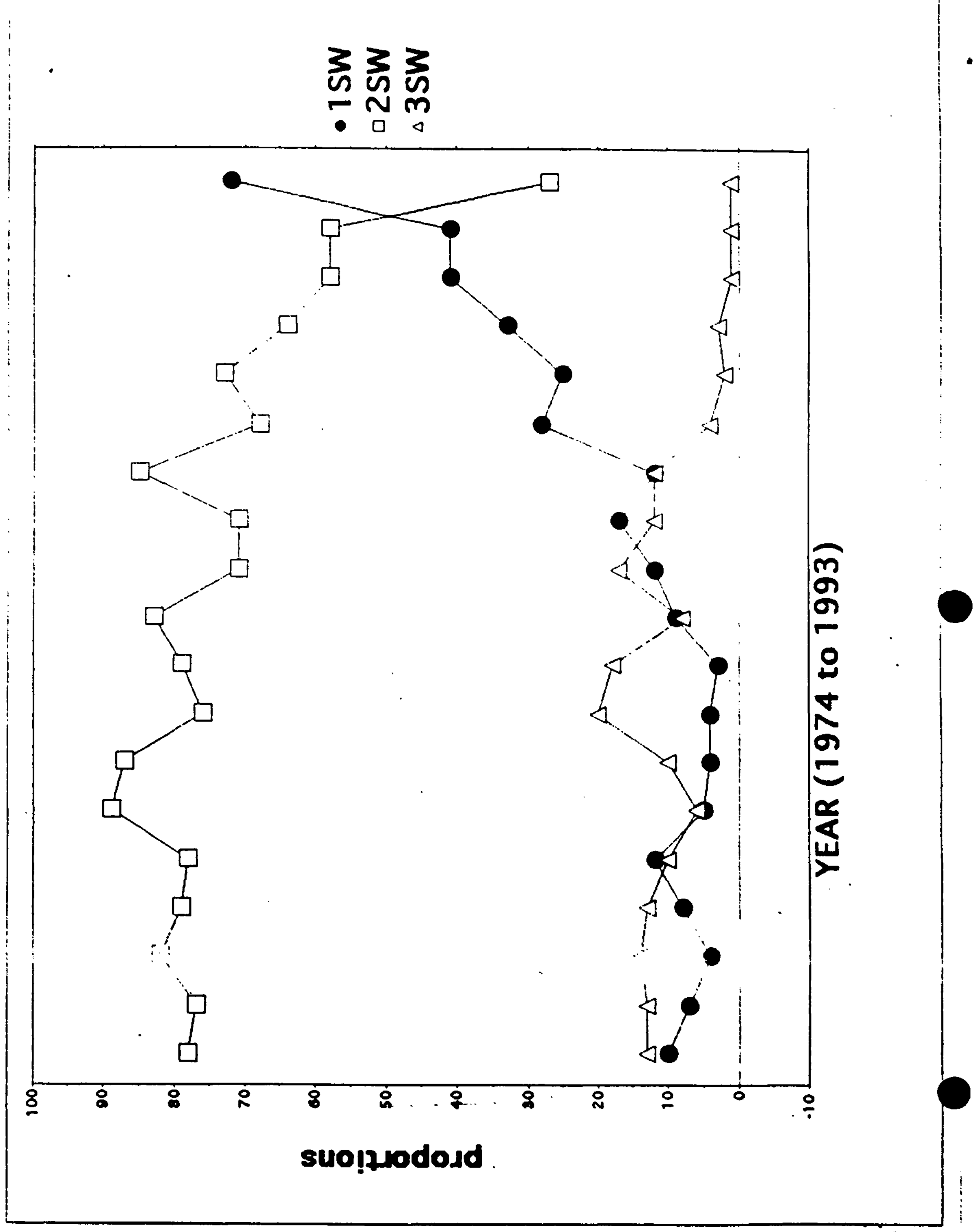

1SW
2SW
3SW
proportions
100
90
80
70
60
50
40
30
20
10
0
-10
YEAR (1974 to 1993)

Figure 1

TABLE 1.Frequency of the most common allele (p) and observed (ho) and expected (he) heterozygosity of the six polymorphic loci in each sample.

		BIDASOA RIVER			ESVA RIVER			SELLA RIVER		
		p	ho	he	p	ho	he	p	ho	he
AAT-4*	1SW	0.643	43.75	45.91	0.700	37.14	42.00	0.750	31.25	37.50
	2SW	0.666	50.00	44.48	0.685	51.42	43.15	0.750	44.44	37.50
IDDH-1*	1SW	0.856	13.75	24.65	0.942	11.42	10.92	0.953	9.37	8.95
	2SW	0.875	25.00	21.87	0.957	8.57	8.23	0.958	8.33	8.04
IDDH-2*	1SW	0.931	11.25	12.84	0.885	17.14	20.35	0.953	9.37	8.95
	2SW	0.895	20.83	18.79	0.928	14.28	13.36	0.944	11.11	10.57
IDHP-3*	1SW	0.976	5.00	4.68	1.000	0.00	0.00	0.968	6.25	6.19
	2SW	0.979	4.16	4.11	1.000	0.00	0.00	0.986	2.77	2.76
MDH-3,4*	1SW	0.912	12.50	16.01	0.957	8.57	8.23	0.890	15.62	19.58
	2SW	0.854	29.16	24.93	0.900	20.00	18.00	0.847	30.55	25.91
m-MEP-2*	1SW	0.700	47.50	42.00	0.828	34.28	28.48	0.828	34.37	28.48
	2SW	0.750	41.66	37.50	0.814	25.71	30.28	0.833	27.77	27.82
mean	1SW		22.29	24.34		18.09	18.33		17.70	18.27
heterozygosity	2SW		28.46	25.28		19.99	18.83		20.82	18.76

TABLE 2.-Genotype frequencies in grilses and salmon groups from m-MEP-2* and MDH-3,4* loci (All rivers pooled).

		GENOTYPE					
		100/100	100/125	125/125	p	ho	he
mMEP-2*	1SW	81	61	5	0.758	41.49	36.38
	2SW	62	29	4	0.805	30.52	31.35
		100/100	100/87	87/87	p	ho	he
MDH-3,4*	1SW	126	18	3	0.918	12.24	14.98
	2SW	70	25	0	0.868	26.31	22.84

p= frequency of 100 allele.
ho=observed heterozygosity
he= expected heterozygosity.

TABLE 3.- Reduction of total biomass catch in Spanish salmon fisheries by changes in age structure

		proportion of each age-classe in total catches	
	mean weight	1975	1991
1SW	2.5 kg	7	43
2SW	4.8kg	80	56
3SW	7.5kg	13	1
total biomass(1)		7485kg	5756kg

(1) On average, annual angling catches inlast 15 years were 1500 fish in spanish rivers.