J. Fish Biol. (1989) **35** (Supplement A), 261–270

Genetic determination of the contribution of stocked and wild Atlantic salmon, *Salmo salar* L., to the angling fisheries in two Spanish rivers

C. GARCIA DE LEÁNIZ, E. VERSPOOR AND A. D. HAWKINS
Department of Agriculture and Fisheries for Scotland, Marine Laboratory, P.O. Box 101, Victoria Road, Aberdeen AB9 8DB, U.K.

From 1983 to 1986 the Rivers Asón and Nansa (northern Spain) were stocked with over 100 000 eyed ova $year^{-1}$ from a Scottish hatchery in an effort to increase angling catches of Atlantic salmon. An inherent genetic marker was used to estimate the contributions of stocked and wild fish from these year-classes to the 1988 rod-and-line fishery. Stocking with foreign ova yielded 0·9 fish per 10 000 ova in the R. Asón and zero fish in the R. Nansa. Natural egg deposition yielded 4·1 and 4·9 fish per 10 000 ova, respectively. Reasons for the difference in performance between stocked and wild fish are examined.

Key words: stocking success; genetic marker; *Salmo salar*; Spain.

I. INTRODUCTION

Rod-and-line catches of Atlantic salmon, *Salmo salar* L., have declined over the last 40 years in many Spanish rivers, and in some the species has disappeared. In an effort to increase angling catches, stocking of eyed ova and juveniles from northern Europe has become commonplace (Garcia de Leániz & Martinez, 1988). However, stocking success is unknown. Stocking may be of limited enhancement value (Withler, 1982; Altukov & Salmenkova, 1987), particularly when stocked fish originate from geographically distant rivers (Ritter, 1975; Reisenbichler, 1988).

Native Spanish populations produce mostly 1- and 2-year-old smolts returning after 2 years at sea (Larios, 1930; Garcia de Leániz & Martinez, 1988; Martin Ventura, 1988). Since 1949 these have been exploited by rod-and-line only, from March to mid-July. Grilse (adult salmon returning after one year at sea) are seldom caught, and were never common (Larios, 1930). In contrast, Atlantic salmon populations in northern Europe consist mostly of older smolts and many return as grilse (Mills, 1989). Spanish salmon populations live at the southern limit of the species distribution and are genetically, as well as geographically, distinct from the northern populations stocked (Verspoor *et al.*, 1988; Garcia-Vazquez *et al.*, 1988). Some of these genetic differences appear to reflect an adaptation to temperature in northern and southern environments (Verspoor & Jordan, 1989).

We report an assessment of the contribution of stocked and wild ova to the 1988 rod-and-line fishery in two Spanish rivers, the Asón and the Nansa in Cantabria. An inherent genetic marker was used (e.g. Murphy *et al.*, 1983; Chilcote *et al.*, 1986; Taggart & Ferguson, 1986). The performance of the wild and stocked ova was determined using estimates of natural egg deposition and known stocking levels.

0022–1112/89/35A261 + 10 $03.00/0

II. MATERIALS AND METHODS

The salmon populations and physical nature of the Rivers Asón and Nansa are described in Garcia de Leániz *et al.* (1987) and Garcia de Leániz & Martinez (1988). Both populations are small: yearly rod-and-line catches for the period 1982–1988 averaged 41 salmon (S.D. = 2) in the Nansa and 123 (S.D. = 97) in the Asón. Stocking was carried out annually during 1983–1986 with eyed ova from a single source—Polly Estates hatchery, Scotland (Table I). Based on age data (Garcia de Leániz & Martinez, 1988; Garcia de Leániz, in prep.), the 1983–86 year-classes were expected to contribute to the 1988 fishery.

TABLE I. Stocking effort with Atlantic salmon eyed ova from Polly Estates hatchery (Scotland) in the Rivers Asón and Nansa during 1983–86

Year	R. Asón	R. Nansa
1983	200 000	100 000
1984	375 000	100 000
1985	100 000	100 000
1986	100 000	100 000

Rod-and-line catches in the Rivers Asón and Nansa during 1988 were 238 and 52 fish, respectively. For nearly all 290 fish, the fork length (cm) and wet weight (g) were recorded, and a sample of scales and white muscle was obtained. Muscle samples were frozen. The Asón sample (242) included three diseased fish and one salmon confiscated from poachers during the fishing season. Fish were aged by two different persons from plastic scale impressions viewed under a Projectina microscope, and the extent of scale erosion was noted (Anon., 1984; Baglinière, 1985). Erosion was scored from zero (none) to six (completely eroded), depending on how many longitudinal sectors of the scale were eroded. Prior to spawning, scale erosion is related to the time spent in fresh water (B. Whyte, pers. comm.).

Salmon redds were counted and mapped during 1984–89, and samples of kelts and spawners were examined, measured and sexed (C. Garcia de Leániz, in prep.). In the R. Nansa, scale and muscle samples from 16 kelts were also obtained during the 1988 spawning season. Redd counts can reliably indicate the number of female spawners (Hay, 1984). Natural egg deposition was calculated from complete redd counts, mean size of female spawners, and predicted average fecundity (Pope *et al.*, 1961). A 1:1 ratio between redd counts and female spawners was assumed for the 1985 year-class.

Salmon were typed for genetic variation at the *Me-2* locus (malic enzyme—E.C. 1.1.1.40—Cross *et al.*, 1979) using starch gel electrophoresis (Verspoor, 1988). The frequency of the common 100 allele ranged from 0·85 to 1·0 in Spanish rivers (Verspoor *et al.*, 1988) but was only 0·337 in the 1986 year-class of the Polly Estates hatchery stock (W. C. Jordan, unpubl. data). The proportions of stocked and wild salmon in the fishery were estimated using the method of Mork *et al.* (1984; also described in Verspoor & Cole, 1989). This assumes that genotype frequencies in each population are in Castle–Hardy–Weinberg (C–H–W) equilibrium, but requires the allele frequency of only one population, in this case the stocked fish. Evidence for recent interbreeding between stocked and wild fish (Verspoor *et al.*, 1988) ruled out other methods which require the allele frequencies of both populations (e.g. Taggart & Ferguson, 1986).

Departures from C–H–W equilibrium and contingency tables were tested by the *G*-test adjusted with Williams correction. This test, the non-parametric Kruskall–Wallis analysis of variance by ranks (*H*), and the Spearman rank correlation (*rs*) are described in Sokal & Rohlf (1981). All probabilities given are two-tailed. F_{IS} represents 1 – (observed/expected) among heterozygotes (Wright, 1931).

TABLE II. Mean size, weight, condition factor ($g \times 100\,cm^{-3}$), and age of adult Atlantic salmon caught by rod and line in the Rivers Asón and Nansa according to their *Me-2* genotype. Standard deviations in parentheses

	Me-2 genotype 100/100		100/125		125/125		*P*	
	Asón	Nansa	Asón	Nansa	Asón	Nansa	Asón	Nansa
n	196	42	21	4	4	0		
Fork × length (cm)	77·7 (4·83)	80·6 (6·16)	77·4 (4·24)	79·8 (4·27)	75·8 (6·56)	—	0·690	0·785
Weight (g)	4538 (845)	5099 (1121)	4477 (805)	5237 (1034)	3988 (1093)	—	0·422	0·813
C.F.	0·96 (0·07)	0·96 (0·07)	0·96 (0·07)	1·02 (0·05)	0·89 (0·06)	—	0·265	0·068
Freshwater age (years)	1·14 (0·35)	1·17 (0·38)	1·24 (0·44)	1·75 (0·50)	1·25 (0·50)	—	0·411	0·007
Sea age (years)	1·94 (0·26)	2·00 (0·38)	1·90 (0·30)	2·00 (0·00)	1·75 (0·50)	—	0·341	—
% grilse	6·7	7·1	9·5	0·0	25·0	—	0·592	1·000

III. RESULTS

Most salmon in the rod catches were *Me-2* (100/100) homozygotes (Table II). Few (100/125) and (125/125) individuals were observed. No significant differences in mean size, weight, condition factor, or sea age were found between genotypes, but some trends were apparent. In both rivers the (100/100) homozygotes smolted at a lower mean age than fish with the other genotypes, but these differences were only significant for the R. Nansa ($t=-2·83$; d.f. = 1,40; $P=0·007$). The proportion of grilse in the Asón was lowest among the (100/100) genotypes (6·7%), intermediate among the (100/125) genotypes (9·5%) and highest among the (125/125) genotypes (25%). Average weight and length decreased also in that order. The Nansa sample contained fewer grilse, more (100/100) genotypes, and the fish were significantly larger ($U=3555$; $P<0·001$) and heavier ($U=3575$; $P<0·001$) than those from the Asón. When salmon with the 125 allele were pooled, no association was found between *Me-2* genotype and month or period of capture (April–May, June–July) (Asón, $G=2·25$, d.f. = 3, $P=0·47$; Nansa, Fisher exact test, $P=1·0$), and rivers did not differ in the proportion of fish caught in each period (Fisher exact test, $P=0·29$). Month of capture, however, may be a poor indicator of month of entry into fresh water, and the delay may vary from fish to fish. None of the four (125/125) fish from the Asón showed any scale erosion, while 46·3% of the (100/100) group did the incidence among the (100/125) group was intermediate at 33·3%. In the Asón, mean scale erosion and the proportion of fish with eroded scales increased significantly with month of capture among the (100/100) homozygotes but not among fish with the 125 allele (Table III); scale erosion was unrelated to fish size in both groups (100/100: $rs=0·09$, d.f. = 191, $P>0·2$; 125

TABLE III. Seasonal differences in mean fork length and degree of scale erosion (0–6) observed among *Me-2* genotypes of Atlantic salmon in the 1988 R. Asón and R. Nansa rod-and-line fishery (four poached and diseased fish from the Asón excluded). Standard error of the pooled mean in parentheses. G-tests adjusted with Williams correction; H is Kruskall–Wallis statistic with 3 d.f.

Me-2 genotype	Month of capture				Pooled	Test	P
	April	May	June	July			
R. Asón							
100/100							
n	39	47	91	15	192		
F.L. (cm)	78·1	78·5	77·7	75·5	77·8 (0·35)	H=1·22	0·748
Erosion	0·08	0·87	1·60	2·67	1·20(0·10)	H=51·0	$<10^{-6}$
% eroded	2·6	36·2	64·8	80·0	46·3	G=61·3	$<10^{-6}$
100/125 125/125							
n	8	5	9	3	25		
F.L. (cm)	79·1	77·8	76·8	72·0	77·2 (0·91)	H=2·66	0·448
Erosion	0·00	0·40	1·67	1·33	0·84(0·29)	H=6·58	0·087
% eroded	0·0	20·0	55·5	33·3	28·0	G=7·29	0·063
R. Nansa							
100/100 100/125							
n	3	20	19	4	46		
F.L. (cm)	84·0	82·1	79·5	75·0	80·5 (0·88)	H=3·94	0·268
Erosion	0·00	0·85	0·74	2·25	0·87(0·19)	H=5·38	0·146
% eroded	0·0	30·0	31·6	75·0	32·6	G=4·83	0·185

allele: rs=0·202, d.f.=24, P>0·2). In contrast, no difference in scale erosion between genotypes was observed in the R. Nansa (Fisher exact test=0·29), nor was there a significant relation between scale erosion and month of capture (Table III).

Most salmon caught in 1988 were from the 1985 year-class (Asón, 88%; Nansa, 63%), and most of the remainder from the 1984 year-class (Table IV). When fish with the 125 allele were pooled, no difference in genotype frequencies was apparent between these year-classes (Asón, G=0·21, d.f.=1, P=0·64; Nansa, G=3·32, d.f.=1, P=0·07). In the Asón the 1985 year-class and the pooled year-classes showed a significant heterozygote deficiency (Table IV), indicative of a mixture of genetically different populations (Wahlund effect, e.g. Hartl, 1980). An estimated 4·3% (8·5 fish) from the 1985 year-class in the Asón, and 0% (no fish) in the Nansa were Polly hatchery fish (Table V); estimates for the overall sample were 3·7% and 0%, respectively. The stocked salmon in the Asón probably included all the (125/125) homozygotes, four of the 18 (100/125) heterozygotes, and one of the 173 (100/100) homozygotes. Thus, the 1988 rod catch in the Asón consisted of 229 wild and 9 stocked salmon, the latter all derived from the 1985 plantings of eyed ova (Table I). The estimated *Me-2* (100) allele frequency for wild fish was identical for both rivers, 0·957, based on the pooled year-classes.

Analysis of kelts and spawners taken outside the fishing season from the R. Nansa in 1988 showed no evidence of the presence of stocked Fish (Table V).

TABLE IV. Atlantic salmon *Me-2* genotype frequencies stratified by year-classes in the 1988 R. Asón and R. Nansa rod-and-line fishery. Departures from Hardy-Weinberg equilibrium tested by the *G*-test with 1 d.f. where appropriate (expected numbers in parentheses)

Year-class	*Me-2* genotype				F_{IS}	*G*
	100 100	100 125	125 125	*Me-2* (100)		
R. Nansa						
1984	10 (10·18)	3 (2·65)	0 (0·17)	0·885	−0·134	0·37
1985	28 (28·02)	1 (0·97)	0 (0·01)	0·983	−0·032	0·02
1986	3 (3)	0 (0)	0 (0)	1·000	—	—
Pooled 1984–86	42† (42·13)	4 (3·79)	0 (0·08)	0·957	−0·057	0·18
R. Asón						
1983	1 (1)	0 (0)	0 (0)	1·000	—	—
1984	17 (17·11)	3 (2·78)	0 (0·11)	0·925	−0·081	0·23
1985	173 (169·86)	18 (24·27)	4 (0·87)	0·933	+0·258	7·78**
1986	4 (4)	0 (0)	0 (0)	1·000	—	—
Pooled 1983–86	196† (192·79)	21 (27·25)	4 (0·96)	0·934	+0·229	6·91**

$^{**}P<0·01$

†Includes one fish with unknown age.

Genotype frequencies among kelts were not significantly different from frequencies among angled fish ($G=0·99$, d.f. = 1, $P=0·32$).

IV. DISCUSSION

Foreign ova planted in Spanish rivers survive to the parr and smolt stages (Verspoor *et al.*, 1988; unpubl. data). This study shows that they also survive to the adult stage, and in the R. Asón contribute to the fishery. However, their contribution is very low and much less than that from natural egg deposition. In the Asón, the yield to the 1988 fishery (number of fish caught per 10 000 ova) from foreign stocking in 1985 is less than 22% of that from natural egg deposition (Table VI). In the Nansa, even if one stocked fish had been caught, the yield from stocked ova would have been less than 3% of that of wild ova. The difference in yield between stocked and wild ova is highly significant in both rivers (Table VI).

The better performance of wild ova could have resulted from underestimation of natural egg deposition. A substantial error seems unlikely (Garcia de Leániz, in prep.), but even had natural egg deposition been twice that calculated, the yield to

TABLE V. Proportions of stocked and wild Atlantic salmon adults in 1988 samples from the Rivers Asón and Nansa estimated by the method of Mork *et al.* (1984) where the *Me-2* (100) frequency of the stocked group is known (0·337)

Group	% of sample	*Me-2* genotype			N_s*	N_c*	*Me-2* (100)
		100 100	100 125	125 125			
R. Asón, rod-and-line fishery							
1985 year-class (sample = 195, catch = 210)							
Stocked	4·3	1·0	3·8	3·7	8·5	(9)	0·337
Wild	95·7	172·0	14·2	0·3	186·5	(201)	0·983
Pooled year-classes (sample = 221, catch = 238)							
Stocked	3·7	0·9	3·7	3·6	8·2	(9)	0·337
Wild	96·3	195·1	17·3	0·4	212·8	(229)	0·957
R. Nansa, rod-and-line fishery							
1985 year-class (sample = 29, catch = 34)							
Stocked	0	0	0	0	0	(0)	0·337
Wild	100	28	1	0	29	(34)	0·983
Pooled year-classes (sample = 46, catch = 52)							
Stocked	0	0	0	0	0	(0)	0·337
Wild	100	42	4	0	46	(52)	0·957
R. Nansa kelts							
Stocked	0	0	0	0	0	—	0·337
Wild	100	13	3	0	16	—	0·906

N_s, estimated number in sample; N_c*, estimated number in catch.

TABLE VI. Estimated contribution of stocked and wild Atlantic salmon ova from the 1985 year-class to adults caught in the 1988 R. Asón and R. Nansa rod-and-line fishery

Group	No. redds	Female size	Mean fecundity	No. ova	No. caught	No. caught per 10 000 ova	*G*
R. Asón							
Wild	76	75·9	6418	488 000	201	4·1	32·5****
Stocked				100 000	9	0·9	
R. Nansa							
Wild	11	75·0	6242	69 000	34	4·9	60·9****
Stocked				100 000	0	0·0	

****$P < 10^{-6}$.

†Estimated from the equation of Pope *et al.* (1961).

the fishery (Asón, 2·1; Nansa, 2·5) would still have significantly exceeded that from stocking (Asón, $G=7\cdot67$; d.f. = 1, $P=0\cdot006$; Nansa, $G=37\cdot06$, d.f. = 1, $P<10^{-6}$). Similarly, underestimation of the *Me-2* (100) frequency for Polly hatchery fish cannot account for the observed differences. Even with an assumed *Me-2* (100) frequency of 0·5, the estimated yield from stocking (Asón, 1·5; Nansa, 0) would have been significantly lower than the yield from natural spawning (Asón, 4·1; Nansa, 4·9).

Lower vulnerability to anglers during the fishing season cannot account for the lower catch of stocked fish. The degree and incidence of scale erosion indicate that stocked fish in the Asón (i.e. 100/125 and 125/125 genotypes, Table III) spent less time, on average, in fresh water before capture than did wild fish. This suggests that stocked fish were more, rather than less, readily caught by anglers, or that they entered the rivers later.

Differences in age composition between stocked and wild salmon alone cannot explain the differences in performance. Eyed ova from the same hatchery were stocked every year from 1983 to 1986 at a level equal to or higher than that of 1985 (Table I). Since stocked fish were absent from all other year-classes (Table IV), they could not have been substantially younger or older and yet return to the fishery in numbers comparable to those of wild salmon. Stocking with foreign ova may be producing fish with an older-than-average smolt age, but this is largely offset by a younger-than-average sea-age (Table II).

This leaves two possibilities: that stocked fish return to the rivers mostly after the fishing season (March to mid-July) or have poorer homing abilities, and that planted ova have lower overall survival rates. Certainly, the differences in scale erosion suggest some differences in timing between wild and stocked fish (Table III). Salmon with the 125 allele, an estimated 36% of which were of stocked origin, may have entered the Asón later on average than (100/100) fish, 99·5% of which were wild. Since the Nansa fish (all of which were wild) showed no such trend, this probably reflects a real difference between wild and stocked populations and not just a difference between genotypes. Analysis of kelts taken outside the fishing season suggests that stocked fish did not return to the R. Nansa in 1988. However, the number of fish (mostly grilse) entering Spanish rivers after the fishing season ends has increased in recent years (Martin Ventura, 1988), and in some rivers this may be related to their stocking history (C. Garcia de Leániz, in prep.). In the Asón, grilse appear more abundant among stocked fish than among wild ones (Table II), as in the R. Nivelle (southern France) where an increase in grilsing rates followed an extensive stocking programme with Scottish fish (Dumas & Casaubon, 1987).

Stocked foreign ova, though clearly surviving to the parr and smolt stages (this study; E. Verspoor *et al.*, 1988, in prep.), may have lower survival rates than wild fish. Poor survival of stocked fish in fresh water has been reported (Bams, 1966; Reisenbichler & McIntyre, 1976; Kelly-Quinn & Bracken, 1989), though lower sea-survival and disrupted homing ability may also have been involved (Ritter, 1975; Reisenbichler, 1988; Standal & Gjerde, 1987). Based on known stocking effort and redd counts, the relative abundance of stocked fish in a small tributary of the Asón was found recently to be considerably lower than that of wild fish 6 months after hatching (C. Garcia de Leániz, unpubl. data).

In the present study, the performance of wild ova did not differ between rivers ($G=0\cdot89$, d.f. = 1, $P=0\cdot34$), but that of planted ova did ($G=11\cdot8$, d.f. = 1,

$P < 0{\cdot}001$). Because stocking during 1985 was carried out in the same way and with the same number and batch of ova in each river, survival at sea was probably the same, but freshwater mortalities must have differed significantly between rivers. This is perhaps not surprising, as the R. Nansa has an impassable hydroelectric dam close to the estuary, and has less juvenile habitat than the Asón (Garcia de Leániz *et al.*, 1987; C. Garcia de Leániz, in prep.).

The lower performance of planted foreign ova may have resulted from poor genetic adaptation (Reisenbichler & McIntyre, 1976; Chilcote *et al.*, 1986; Altukov & Salmenkova, 1987), inadequate stocking methods (Egglishaw *et al.*, 1984), or both. Regardless of the reasons, the enhancement value and long-term benefits of stocking with foreign fish must be questioned. Competition for resources between wild and stocked juveniles may decrease the survival of both (Vincent, 1988; Kelly-Quinn & Bracken, 1989). If foreign fish survive, interbreeding will alter the genetic make-up of wild fish and this may lower population fitness (Altukov & Salmenkova, 1987). Some interbreeding in these rivers has already taken place, not only with wild salmon (E. Verspoor *et al.*, 1988; unpubl. data), but also with wild brown trout, *S. trutta* L. (Garcia de Leániz & Verspoor, 1989). This may affect homing, time of entry and age of return, as these appear to have a genetic component (Gardner, 1976; Nævdal *et al.*, 1978; Altukov & Salmenkova, 1987; McIsaac & Quinn, 1988) and are likely to be adaptive (e.g. Schaffer & Elson, 1975; Power, 1981).

The immediate benefits to anglers must also be questioned, particularly in the R. Nansa. Based on complete age data during 1986–88 (C. Garcia de Leániz, unpubl. data), and known stocking effort (Table I), 100 000 ova in the Nansa, and at the very least 100 000 ova in the Asón, were needed to yield at most 10 stocked fish during 1988 (Asón, 9; Nansa, 1). At a rate of 4 p (U.K.) per imported ovum, the cost of each stocked fish landed in 1988 was at least £800. At an average weight of 4·3 kg per fish, this represents more than £185 per kg of angled fish, excluding costs of transport, hatchery facilities, and manpower.

We thank the Servicio de Montes, Caza y Conservación de la Naturaleza de la Diputación Regional de Cantabria, and especially Juan José Martinez who took care of the logistics of the study, the ' guardas ' of the Rivers Asón and Nansa for collecting much of the data, Bill Jordan for kindly making available his *Me-2* results for Polly hatchery fish, J. Mork for his computer program, and Bryce White for invaluable help with scale reading. This work was supported in part by an Alexander Fleming scholarship to C.G.L. from the Spanish Ministry of Education and Science and by a contract to E.V. from the Department of Fisheries and Oceans, St John's, Newfoundland, Canada.

References

Altukov, Y. P. & Salmenkova, E. A. (1987). Stock transfer relative to natural organization, management, and conservation of fish populations. In *Population Genetics and Fishery Management* (N. Ryman & F. Utter, eds), pp. 333–345. Seattle: University of Washington Press.

Anon. (1984). Atlantic salmon scale reading. ICES Report of the Atlantic salmon scale reading workshop, Aberdeen, Scotland, 23–28 April 1984. 17 pp.

Baglinière, J. L. (1985). La détermination de l'âge par scalimétrie chez le saumon Atlantique (*Salmo salar*) dans son aire de répartition méridionale: utilisation pratique et difficultés de la méthode. *Bull. Fr. Piscic.* **298.** 69 pp.

Bams, R. A. (1966). Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. *J. Fish. Res. Bd Can.* **24,** 1117–1153.

Chilcote, M. W., Leider, S. A. & Loch, J. J. (1986). Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Trans. Am. Fish. Soc.* **115,** 726–735.

Cross, T. F., Ward, R. D. & Abreu-Grobois, A. (1979). Duplicate loci and allelic variation for mitochondrial malic enzyme in the Atlantic salmon, *Salmo salar* L. *Comp. Biochem. Physiol.* **62B,** 403–406.

Dumas, J. & Casaubon, J. (1987). Connaissance et restauration de la population de saumon atlantique (*Salmo salar* L.) de la Nivelle (Pyrénées atlantiques). In *Restauration des Rivières â Saumons* (M. Thibault & R. Billard, eds), pp. 221–230. Paris: INRA.

Egglishaw, H. J., Gardiner, W. R., Shackley, P. E. Struthers, G. (1984). Principles and practice of stocking streams with salmon eggs and fry. Dept Ag. Fish. Scotland, Scot. Fish. Inf. Pamphlet. No. 10, 1984. 22 pp.

Garcia de Leániz, C. & Martinez, J. J. (1988). The Atlantic salmon in the rivers of Spain with particular reference to Cantabria. In *Atlantic Salmon: Planning for the Future (Proceedings of Third International Atlantic Salmon Symposium, Biarritz, 21–23 October 1986)* (D. Mills & D. Piggins, eds), pp. 179–209. London: Croom Helm.

Garcia de Leániz, C. & Verspoor, E. (1989). Natural hybridization between Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in northern Spain. *J. Fish Biol.* **34,** 41–46.

Garcia de Leániz, C., Hawkins, A. D., Hay, D. W. & Martinez, J. J. (1987). *The Atlantic Salmon in Spain.* Pitlochry: The Atlantic Salmon Trust. 28 pp.

Garcia-Vazquez, E., Linde, A. R., Blanco, G., Sánchez, J. A., Vázquez, E. & Rubio, J. (1988). Chromosome polymorphism in farm fry stocks of Atlantic salmon from Asturias. *J. Fish Biol.* **33,** 581–587.

Gardner, M. L. G. (1976). A review of factors which may influence the sea-age and maturation of Atlantic salmon *Salmo salar* L. *J. Fish Biol.* **9,** 289–327.

Hartl, D. (1980). *Principles of Population Genetics.* Sunderland, MA: Sinauer & Associates. 488 pp.

Hay, D. W. (1984). The relationship between redd counts and the numbers of spawning salmon in the Girnock Burn (Scotland). ICES CM 1984/M:22. 4 pp. (mimeo.).

Kelly-Quinn, M. & Bracken, J. J. (1989). Survival of stocked hatchery-reared brown trout, *Salmo trutta* L., fry in relation to the carrying capacity of a trout nursery stream. *Aquacult Fish. Mgmt* **20,** 211–226.

Larios, P. (1930). Rios salmoneros de Asturias (Salmon rivers of Asturias). Reprinted in *Rios Salmoneros de Asturias* (A. Casero, ed., 1987), part I: pp. 9–138. Oviedo: ALSA. (in Spanish).

McIsaac, D. O. & Quinn, T. P. (1988). Evidence for a hereditary component in homing behaviour of chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. aquat. Sci.* **45,** 2201–2205.

Martin Ventura, J. A. (1988). The Atlantic salmon in Asturias, Spain: analysis of catches 1985–86. Inventory of juvenile densities. In *Atlantic Salmon: Planning for the Future (Proceedings of Third International Atlantic Salmon Symposium, Biarritz, 21–23 October 1986)* (D. Mills & D. Piggins, eds), pp. 210–227. London: Croom Helm.

Mills, D. (1989). *Ecology and Management of Atlantic Salmon.* London: Chapman & Hall. 351 pp.

Mork, J., Giskeodegard, R. & Sundnes, G. (1984). Population genetic studies in cod (*Gadus morhua* L.) by means of the haemoglobin polymorphism; observations in a Norwegian coastal population. *FiskDir. Skr. Ser. HavUnders.* **17,** 449–471.

Murphy, B.R., Nielsen, L. A. & Turner, B. J. (1983). Use of genetic tags to evaluate stocking success for reservoir walleyes. *Trans. Am. Fish. Soc.* **112,** 457–463.

Nævdal, G., Holm, M., Ingebrigtsen, I. & Møller, D. (1978). Variation in age at first spawning in Atlantic salmon (*Salmo salar*). *J. Fish. Res. Bd Can.* **35,** 145–147.

Pope, M. A., Mills, D. H. & Shearer, W. M. (1961). The fecundity of Atlantic salmon (*Salmo salar* Linn.). Dept Ag. Fish. Scotland, Freshwat. Salmon Fish. Res. Rep. No. 26. 12 pp.

Power, G. (1981). Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. *Can. J. Fish. aquat. Sci.* **38,** 1601–1611.

Reisenbichler, R. R. (1988). Relation between distance transferred from natal stream and recovery rate for hatchery coho salmon. *N. Am. J. Fish. Mgmt* **8,** 172–174.

Reisenbichler, R. R. & McIntyre, J. D. (1976). Genetic differences in growth and survival of hatchery and wild steelhead trout, *Salmo gairdneri. J. Fish. Res. Bd Can.* **34,** 123–128.

Ritter, J. A. (1975). Lower ocean survival rates for hatchery-reared Atlantic salmon (*Salmo salar*) stocks in rivers other than their native stream. ICES CM 1975/M:26. 10 pp. (mimeo).

Schaffer, W. M. & Elson, P. F. (1975). The adaptive significance of variations in life history among local populations of Atlantic salmon in North America. *Ecology* **56,** 577–590.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry,* 2nd ed. San Francisco: W.H. Freeman. 859 pp.

Standal, M. & Gjerde, B. (1987). Genetic variation in survival of Atlantic salmon during the sea-rearing period. *Aquaculture* **66,** 197–207.

Taggart, J. & Ferguson, A. (1986). Electrophoretic evaluation of a supplemental stocking programme for brown trout, *Salmo trutta* L. *Aquacult. Fish. Mgmt* **17,** 155–162.

Verspoor, E. (1988). Reduced genetic variability in first-generation hatchery populations of Atlantic salmon. *Can. J. Fish. aquat. Sci.* **45,** 1686–1690.

Verspoor, E. & Cole, L. J. (1989). Genetically distinct sympatric populations of resident and anadromous Atlantic salmon *Salmo salar. Can. J. Zool.* **67,** 1453–1461.

Verspoor, E. & Jordan, W. C. (1989). Genetic variation at the *Me-2* locus in the Atlantic salmon within and between rivers: evidence for its selective maintenance. *J. Fish Biol.* **35** Suppl. A, 205–213.

Verspoor, E., Garcia de Leániz, C. & Hawkins, A. D. (1988). A preliminary genetic assessment of stocking on Spanish Atlantic salmon (*Salmo salar*) populations. ICES CM 1988/M:19. 6 pp. (mimeo).

Vincent, E. R. (1988). Effects of stocking catchable-size rainbow trout on two wild trout species in the Madison river and O'Dell creek, Montana. *N. Am. J. Fish. Mgmt* **7,** 91–105.

Withler, F. C. (1982). Transplanting Pacific salmon. *Can. Tech. Rep. Fish. aquat. Sci.* **1079,** 27 pp.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics* **16,** 97–159.