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THEME SESSION (P);
DIADROMOUS FISH EXTINCTION: THREATS ON LOCAL AND GLOBAL SCALES

A comparison between three Atlantic salmon river stocks; using classical population genetics, differences in life history traits and performance in sea ranching.

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Abstract. Characterisation of stocks is essential for fisheries and environmental management in order to conserve genetic diversity. However, classical population genetic methods frequently fail to document stock differences. In this paper we list a number of characters that were used to compare the performance of the offspring of three adjacent river stocks during the freshwater period in culture until release, and their returns as adults. The emphasis will be put on life history traits and their consequences for growth and fishing mortality. We also present data on polymorph isozyme variation between wild fish from the stocks. The overview indicate that it may be necessary to include a number of traits to differentiate between stocks.

INTRODUCTION

The term local stock is often used in litterature on Salmonid species, meaning that the population is genetically and ecologically different from other conspecific populations and thus genetically adapted to its local environment. Such differentiation can be acquired through natural selection given that the migration and exchange of genetic material among populations is restricted, and given that the population is of decent size so that the genetic composition does not fluctuate due to random genetic events or drift. However, only rarely are socalled local populations described in terms of life history traits, probably because studies to describe and compare stocks are expensive and time consuming and also requires holding facilities.

A prerequisite for development of local adaptations through natural selection is a certain degree of geographical isolation from other populations and a restricted migration and gene flow among populations. Immigration above a certain level will override the natural selection and preclude development of local genetically adapted populations (Mork 1991; 1994).

The homing instinct demonstrated in salmonids through studies on marking, migration and straying (Carlin 1969; Raleigh and Chapman 1971; Brannon 1972; Bams 1976; Thorpe and Mitchell 1981; Svärdson and Fagerström 1982; Stabell 1984 (review); Altukhov and Salmenkova 1994 (review) is an important prerequisite for local stocks as this mechanism tends to slow down gene flow among populations. Local stocks are interesting because they encompass the evolutionary forces, in particularly natural selection, and they pose a challenge to management, as a proper management will have to rest on information about the individual stocks. The term is often used in the litterature, although there are a relatively low number of original studies that give clear empirical information about the existence of local stocks (see Taylor 1991 for review). Comparisons of life history traits generally suffers from the fact that such traits are influenced to a large degree of the environment. Thus, lack of strong scientific methodology has to some extent been responsible for the low amount of data on the subject, although there is also the possibility that local stocks are rare in nature. Population genetic studies on variability at single genetic loci, cannot prove that populations are genetically adapted unless the loci examined are influenced by selection. However, studies on neutral loci give information about the extent of exchange of genetic material among populations, and may therefore give additional information and indications about the probability that a given population is locally adapted. Therefore it has sometimes been suggested that studies on genetic differentiation in salmonids should try and combine information from both quantitative traits and single locus variability (Bentsen 1991).

The studies on sea ranching with Atlantic salmon gave an unusual opportunity to compare salmon populations within a geographical region by using a number of quantitative traits as well as variability at single genetic loci as revealed by starch gel electrophoresis.
The aim of the presentation is to try and obtain more information and better understanding of stock differentiation by combining different data sets obtained by studies on quantitative traits, such as growth patterns, sexual maturation with studies on specific genetic loci.

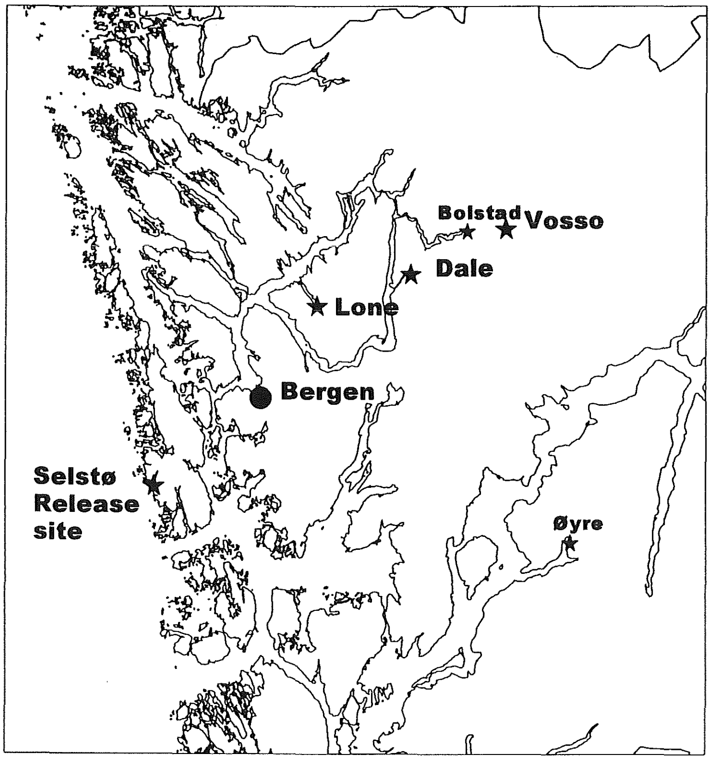


Figure 1: Map showing localisation of the sea ranched river stocks; Lone river, the Dale river, the Vosso river and also the location of the release site in the Selstø Bay. River Øyre and Bolstad (used for genetic analysis) are also shown.

MATERIALS AND METHODS

Broodfish were collected from the spawning grounds in the Loneelv, Dale and the Vosso river during October in 1989, 1990 and 1991. All rivers enters into the same fjord system. The Lone river stock is a typical grilse stock, both sexes usually return after one year. Weights are normally less than 2 kg. River Vosso is one of the largest watercourses on the Norwegian west coast, with a catchment area of 1492 km^2. About 35 km of the river from the Bolstad estuary up to Voss is accessible for salmon and sea trout, *Salmo trutta*. The river stretch includes two lakes, L. Evangervatn and L. Vangsvatn. The R. Vosso salmon is a typical multi-sea winter salmon which often stays 3 years at sea before returning to spawn (Huitfeldt-Kaas 1946), but the variation in sea winter age range from 1 to 5 years, with males more frequently returning as 1 and 2 SW than females. Thus, individuals are large at maturation, and recorded mean weights of spawners are about ten kilos. The male salmon of the Dale river stock most oftenly return as grilse, while most females spend two years in the sea. In 1990 broodfish from the river Onarheim were also included (released 1992). For genetic analysis, the Øyre river and the Bolstad river were included. Bolstad river is in principle the lower part of the Vosso river, only separated by a the lake Evangervatn.

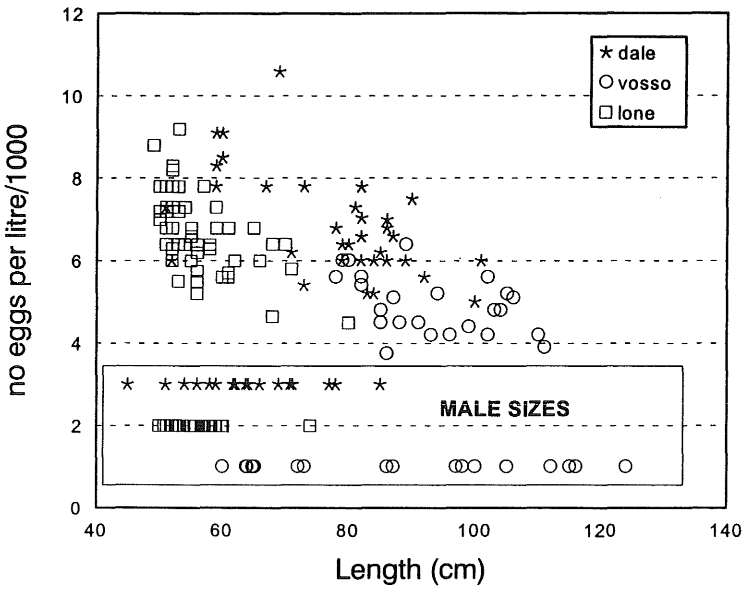


Figure 2: Length of individual female brood fishes versus number of eggs per litre. Male sizes are shown in inserted box.

The eggs from each female were fertilised by one male and kept separately. Each family group were first feed in a 1x1 square tank. During summer the adipose fins of half of the families were clipped to mix 2 and 2 families in larger tanks. Samples from all families were length measured in autumn. After the establishment of bimodal length-frequency distributions (see Skilbrei et al. 1997 for explanation) the potential 2+ smolts were removed. Portions of the 1+ smolts (usually > 12 cm) were individually tagged by either Visible Implant tags (VIT) (1991 and 1992 releases) or Carlin tags (a total 3000 tags in 1992 and 11000 tags prior to the 1993 release) and all groups where mixed in 5m diameter outdoor tanks. Microtags were used to tag approximately 40% of the smolts in 1992 and 1993. Prior to the releases in 1992 the pre-smolts were individually tagged in December-January in 1991. The pre-smolts of the 1993 releases were tagged in October 1992.

The families of the Lone river stock were not kept separately prior to the 1993 release because it was believed that mixing and size-grading would increase their growth rates. The 1991 releases gave very poor returns and are not included in the following text. A total of 41-42.000 smolts were released each of the two years 1992 and 1993. Individually Carlin-tagged 1+smolts were length measured in March/April prior to releases. Details on release methods and release site is given in Skilbrei et al. (1994*a,b*). In 1992 a total of 18.000 smolts of the Lone stock and 16.000 offspring of the Dale stock were tagged by one of the methods mentioned above.

The smolts were either reared at the Selstø hatchery and released in the Selstø Bay, or reared at a commercial hatchery and transferred to Selstø hatchery 1-2 months prior to release.

Mean egg sizes from each female was calculated from measurement of the number of eggs in a row covering 25 cm.

Electrophoresis
The following enzymes were stained for: aspartate aminotransferase (AAT, E.C 2.6.1.1); alcohol isocitrate dehydrogenase (IDHP, E.C. 1.1.1.42); iditol dehydrogenase (IDDH, E.C. 1.1.1.14); malate dehydrogenase (MDH, E.C. 1.1.1.37); malic enzyme (MEP, E.C. 1.1.1.40); glucose-6-phosphate isomerase (GPI, E.C. 5.3.1.9); phosphoglucomutase (PGM, E.C. 5.4.2.2), triose phosphate isomerase (TPI, E.C. 5.3.1.1). Two buffer systems were used (Table 3): I) CAME (modified from Clayton and Tretiak 1972, with EDTA added): 0.0365M Citric acid, 0.00099M EDTA, adjusted to pH 6.8 with N-(3-aminopropyl)-morpholine. Dilute one part in 20 parts H_2O for gels. II) TCB, tris-citrate-borate gel buffer: 0.015M Tris, 0.001M citric acid, 0.003M boric acid, and 0.001M LiOH; electrode buffer: 0.3M boric acid and 0.1M LiOH; both buffers were adjusted to pH 8.6. For staining, a 0.2M Tris buffer with pH 8.0 was used, apart from in IDDH where pH was raised to 8.5, and for AAT where pH was raised to 9.5.

The samples were processed in BIOSYS-1 programme (Swofford and Selander 1981) to calculate allelic frequencies, mean heterozygosity, mean number of alleles per. locus, conformance to Hardy-Weinberg distribution and genetic heterogenity. Genotypic distributions at specific loci of individual samples were compared by a G-test (Sokal and Rohlf 1969).

Samples of juveniles were caught in the rivers listed in Table 2 from 1992 to 1996 to describe polymorph variation.

RESULTS

The length of the Lone river females were roughly between 50-70 cm (Figure 2). All females and females were 1 sea-winter salmon (1SW). The Vosso females were large, from 80-110 cm. Half of them were 2SW and the rest 3SW. Among the males, there were representatives of 1SW, 2SW and 3SW. Most Dale females were 2SW, except for 25% 1SW and one 3SW. All but one male were grilse.

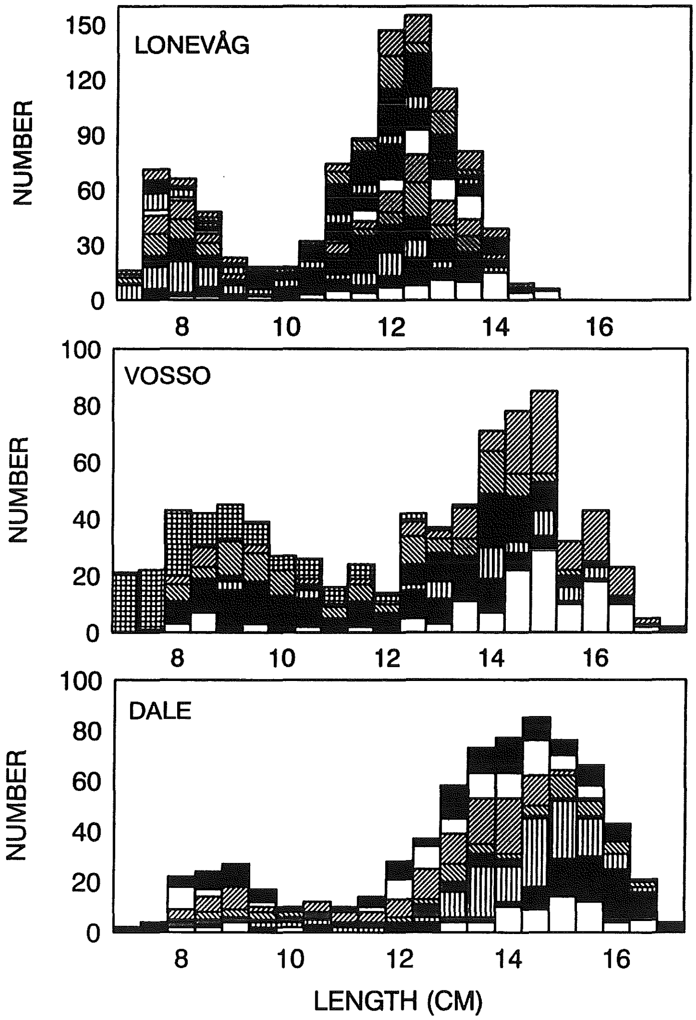


Figure 3. Length-frequency distributions of the three stocks in late autumn 1991 (first fed 1991). Families are shown separately by different shadings and hatchings of the bars. Precocious mature males are excluded from the distributions. One atypical family is shown by hatching.

The egg sizes of the individual females expectedly increased with body length (shown as number of eggs per litre in Figure 2). There was a tendency for the Dale stock to produce smaller eggs than the other stocks when females of comparable sizes are compared. Because of missing overlap in female sizes between the Lone and the Vosso stock it is impossible to statistically compare all three stocks using a multiple-model, but a common regression line for Lone and Vosso stocks is significantly different from that of the Dale stock ($P<0.05$).

A high incidence of repeated spawners were found in the Lone river (32%, 12 out of 37). Only three of these were larger than 2 kg, although 50% of the repeated spawners spawned for the third time. One repeated spawner were found in each of the other rivers.

Growth rates in freshwater varied largely between family groups within each stock. Within each stock the sum of the families produced bimodal distributions (Examplified by the pre-smolt length-distributions of the 1992 releases, Figure 3). Some families produced a high (almost

100%) proportion of 1+ smolting upper mode fish, whereas others contributed very little to the release of one-year smolts as most of the juveniles were of lower mode size. The bimodal distributions for the Dale and the Vosso stocks were similar in appearance. The Lone stock produced smaller fish. This is most easily seen for the upper mode fish in autumn 1991 (Figure 3).

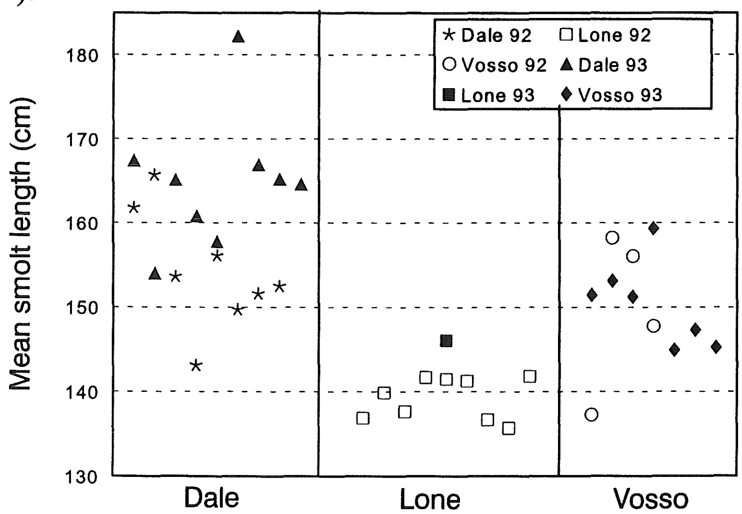


Figure 4. Mean smolt sizes of family groups from the three stocks in March/April 1992 and 1993. Note that Lone 93 is the mean of the stock.

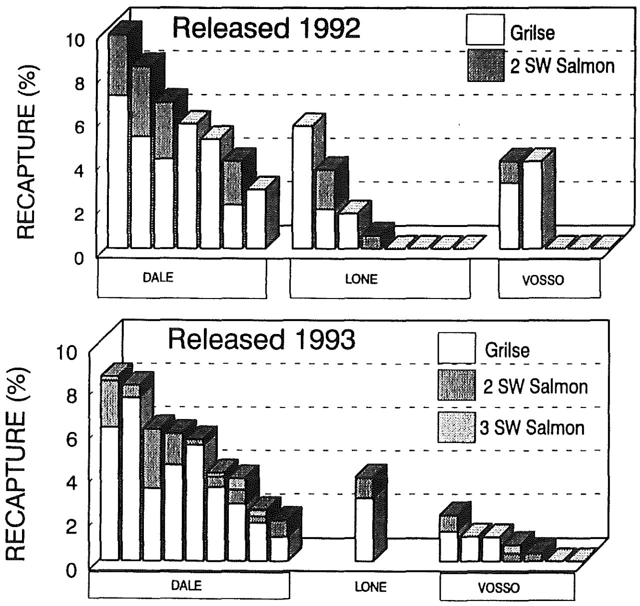


Figure 5. Total recapture (%) of Carlin-tagged smolts from the three stocks released in 1992 and 1993. Single bars are family groups, except the 1993 Lone bar that is the mean for the stock.

These size differences between the stocks were also observed when comparing the family mean smolts lengths in 1992 and 1993 of the Carlin-tagged smolts (Figure 4). The offspring from the Lone river stock is clearly smaller than the other two (families in 1993, mean for the stock in 1993), and the largest smolts are found among the Dale fish for both years.

The poorer growth rate of the Lone stock fish continued during their stay in sea. The Carlin tag data were insufficient for the Lone stock after the 1992 release due to the low returns (Figure 5), but the catch at the release site show that the Lone grilse were small, usually between 0.9 and 1.5 kg (Figure 7). The Dale grilse were evidently larger, most of them between 1.8 and 3 kg. While Carlin-tagged fish of the 1993 releases from the Vosso and Dale stocks obtained a mean grilse size of approximately 2.5 kg, and 2SW sizes of about 5 kg, the Lone grilse were approximately 1.6 kg and the 2SW fish 3 kg when returning from the 1993 release (Table 1).

The Lone stock females returned more frequently as grilse than the Dale females. In 1993 40.1% (37 out of 91) and in 1994 51.3% (40 out of 78) Lone grilse homing to the release site as females. The corresponding numbers for Dale were 1.6% (1 out of 61) and 16.2% (11 out of 68).

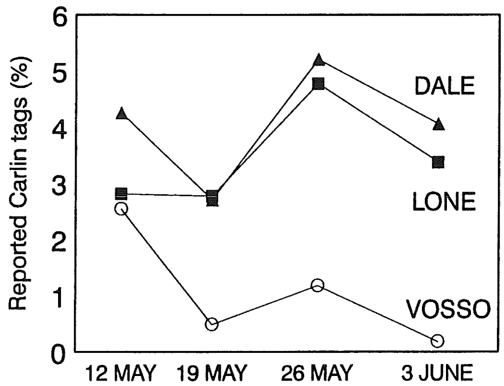


Figure 6. Reported Carlin tags after the 1993 releases shown separately for stocks and release dates.

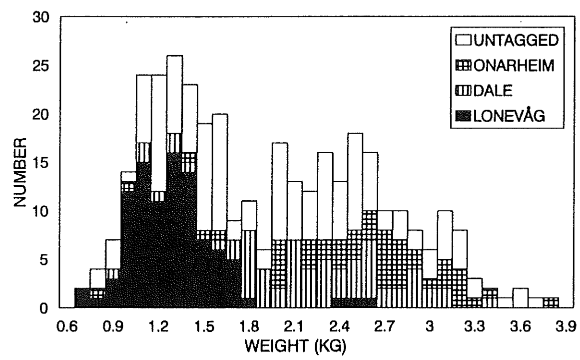


Figure 7. Length-frequency distribution of salmon homing to the release site (Selstø Bay) in 1992. Untagged are adipose fin-clipped while the others are VI-tagged, Carlin-tagged or microtagged. Vosso are excluded because of low numbers.

The total recapture of Carlin tags (release site plus sea-fishery plus strayers) was highest for the Dale stock, 5.3 and 5% after the 1992 and 1993 releases, respectively. The number of Carlin tags from the 1992 releases was only 108 tags. These data are therefore not sufficient to give a good picture of family variation. The tendency of family variation within the stocks is, however, demonstrated for the 1993 releases when 420 tags were reported during the next three years (Figure 5). For both years, the Vosso fish showed poor returns. For the 1993 releases, release date seem to be one reason for this result. The Vosso smolts released in early May show similar return compared to the other stocks, but drops significantly (3 X 4, G-test, P<0.05) during spring for the next releases.

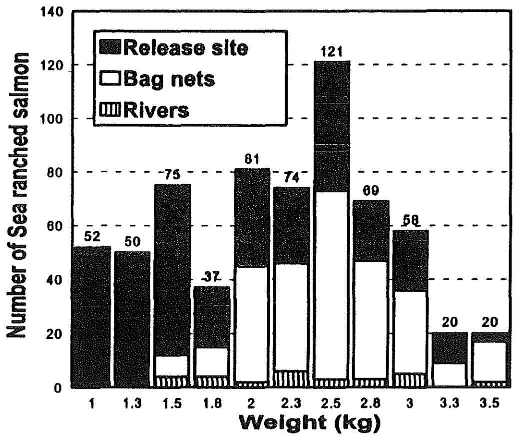


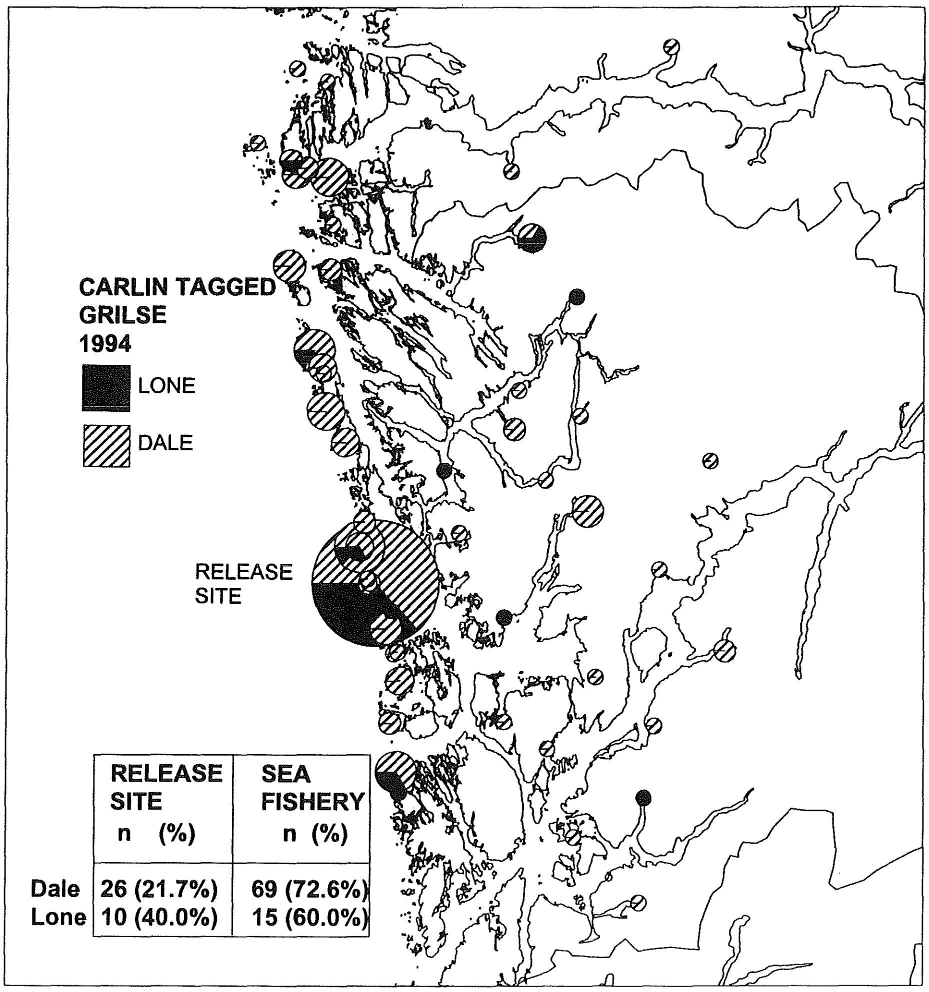
Figure 8. Catch of adipose fin-clipped (plus Carlin-tagged) grilse in Hordaland County, at the release site and in rivers (Carlin tagged only) in 1993.

In 1993 the catch at the release site showed that the Lone grilse were clearly the smallest, usually smaller than 2 kg (Figure 7, and a higher number homed to the release site compared to the Dale grilse (93 vs. 63), that were more frequently larger than 2 kg. A much higher proportion of the grilse below 2 kg was caught in the Selstø Bay, at the release site, compared to the catch in bag nets in Hordaland County (Figure 8). In 1994 there was also the tendency that the Lone grilse homed more successfully to the release site than the Dale grilse (Table 1).

An overview showing the allelic frequencies at 6 polymorph isozyme loci and genetic variability of the three stocks are shown in Table 2. Data from the Øyre river, and from Bolstad river (in principle the lower part of the Vosso river) which are included. Pairwise test between river stocks demonstrated significant diferences between all stock (Table 3). Surprisingly, the fish from Bolstad were significantly different from all other stocks, also the Vosso fish from the upper part of the river system, for all but one locus (Dale-Bolstad). The Lone-Dale comparisons were significantly different in 3 polymorph loci, Vosso-Dale for two, and Lone-Vosso was different in one locus.

DISCUSSION

The three rivers chosen for this study, the Dale, the Lone and the Vosso river stocks, are probably very different when comparing life-history parameters. The data on the brood fish show that the Lone river salmon mostly return as small grilse, the male Dale fish frequently return as grilse while the females stay one extra year in the sea. The Vosso stock i a typical multi-sea-winter stock, reaching large sizes before returning.



	RELEASE SITE n (%)	SEA FISHERY n (%)
Dale	26 (21.7%)	69 (72.6%)
Lone	10 (40.0%)	15 (60.0%)

Figure 9. Map showing sites of reported Carlin tagged grilse from the Lone an Dale stocks in 1994 and summary of tags from the relase site and in bag-nets. Smallest circles refers while one tag, while the largest circle (release site) summarises 41 tags.

The quantitative traits examined under hatchery conditions , bimodality and smolt size, showed large variation in growth rates both within and between stocks. The differences between families in the proportions of lower and upper mode fish indicate that the relative number of 1+smolts was not a trait that differed between the stocks. However, despite the varying contributions from different families the length of the upper mode fish (1+ smolts) were lower for the Lone offspring, and they were smaller during 1+smolt tagging in 1992 and 1993. Although tank effects could not be accounted for during the first part of the rearing period these differences probably reflect a genetic difference resulting from different selective mechanisms, resulting in small smolts from the Lone river stock when reared under similar conditions (mixed in tanks from late autumn).

Table 1: Mean size of 1SW, 2SW and 3SW salmon divided into catch at release site, in sea-fishery or in rivers. Proportions of fish captured in the different fisheries and proportions of 1SW, 2SW and 3SW fish from each stock are added.

	1SW (1994)		2SW (1995)		3SW (1996)	
	Weight (SD) kg	n (%)	Weight (SD) kg	n (%)	Weight (SD) kg	n
LONE RIVER STOCK						
Release site	1.51 (0.37)	15 (23.8)	3.00	1 (4.8)		
Sea	1.76 (0.39)	24 (38.1)	3.20 (0.87)	17 (81.0)	6.50	1
River	1.41 (0.36)	24 (38.1)	2.27 (0.32)	3 (14.3)		
SUM	1.57 (0.40)	63	3.01 (0.85)	21		
Sea age (%)		75%		25%		
DALE RIVER STOCK						
Release site	2.31 (0.52)	27 (11.2)	3.96 (1.22)	5 (7.7)		
Sea	2.54 (0.62)	146 (60.3)	5.14 (1.48)	42 (64.6)	9.35 (2.62)	6
River	2.40 (0.66)	68 (28.1)	5.44 (1.59)	18 (27.7)	8.70 (1.70)	6
SUM	2.49 (0.63)	242	5.14 (1.52)	65	9.04 (2.17)	12
Sea age (%)		76%		20%		4%
VOSSO RIVER STOCK						
Release site	2.65	2	5.65	2		
Sea	2.52 (0.42)	10	4.72 (1.88)	6	?	1
River	2.5	5	5.50	1		
SUM	2.60 (0.40)	17	5.01 (1.60)	9	?	1
Sea age (%)		63%		33%		4%

The lower growth rate of the offspring of the Lone stock continued during the stay in sea. The Lone grilse reached sizes comparable to their parents. However, unlike the brood fish, a portion returned as 2-sea-winter salmon. These older fish were clearly smaller than the 2SW from the other two stocks. The sea-ranched offspring from the Dale stock returned as 1SW, 2Sw and 3SW, and were of a similar size range as their parents, while the Vosso fish returned from the sea at least one year earlier than their parents.

The Vosso offspring seemed to higher sea mortality than the other stocks, especially when compared to the Dale stock from which the highest returns was observed. The reasons for this are unknown. Data is missing on stock specific migration routes (if there are any), and also if the open sea mortality differs geographically. The higher return for Vosso smolts released early in spring and the following decline when postponing release date, may result from such differences. Alternatively, the smoltification process may have reached its optimal level at an earlier date for the Vosso smolts. Despite the lack of explanation, the Vosso offspring consequently performed poorer after release.

Table 2. Allelic frequencies at polymrphic isozyme loci and genetic variability in sea ranched stocks in Hordaland.

Locus **Alleles**	**Dale**	**Bolstad**	**Vosso**	**Lone**	**Øyre**
AAT-4*					
(N)	137	97	107	154	51
*25	.080	.124	.126	.094	.176
*50	.128	.134	.033	.023	.000
*100	.792	.742	.841	.883	.824
IDDH-2*					
(N)	137	110	102	154	106
*-100	.365	.682	.441	.594	.495
*28	.033	.050	.088	.029	.033
*100	.062	.268	.471	.377	.472
IDHP-3*					
(N)	137	110	102	154	106
*100	.905	.991	.986	.996	.952
*116	.095	.009	.014	.004	.048
MDH-3,4*					
(N)	137	110	107	181	115
*85	.033	.105	.028	.022	.017
*100	.967	.895	.972	.978	.983
MEP-2*					
(N)	137	109	103	181	109
*100	.387	.564	.364	.398	.317
*125	.613	.436	.636	.602	.683
TPI-3*					
(N)	137	63	108	180	115
*100	.836	.540	.699	.694	.704
*103	.164	.460	.301	.306	.296
# Allel/locus	2.3	2.3	2.3	2.3	2.2
	(0.2)	(0.2)	(0.2)	(0.2)	(0.2)
Heterozygoti	0.319	0.342	0.30	0.250	0.271
	(0.074)	(0.082)	(0.096)	(0.088)	(0.070)

Table 3: Significance values (p-values) in pairwise comparisons (G-test) of distributions of genotypes and of alleles at four polymorphic loci in the ranched salmon stocks in Hordaland.

COMPARISON	*AAT-4**	*IDDH-2**	*MEP-2**	*TPI-3**
Bolstad-Vosso	***	***	***	***
Bolstad-Lone	***	*	***	***
Bolstad-Dale	ns	***	***	***
Lone-Dale	***	***	ns	***
Vosso-Lone	ns	***	ns	ns
Vosso-Dale	***	ns	ns	***

*:<0.05
**:<0.01
***:<0.001

The low return of Lone Carlin-tagged grilse in 1993 after the 1992 release may partly result from their small smolt sizes, increasing tag loss and tag mortality. This is supported by the relatively high number of VI-tagged and microtagged Lone grilse at the release site in 1993 compared to the Dale stock. This may also explain the higher returns of Lone salmon after the 1993 release, as family groups were mixed and size-graded at the hatchery to increase smolt size.

If there is a size-selective commercial sea-fishery for salmon, its effect upon the numbers of returning spawners and the sea age and size at maturity should be taken into account. The higher probability of 1SW Lone salmon to reach the release site compared to the Dale fish that were more frequently caught in bag nets imply that the numbers of brood fish of a slow growing grilse stock will be higher than for faster growing stocks. Vice versa, the number of brood fish may be critical for stock conservation, and if the number of brood fish is supposedly low, there may be needs for special protection of stocks growing rapidly in the sea phase. The Vosso river stock is regarded as a stock of special interest in Norway because of its historical catches of large sized salmon, but the stock has dropped to a very low size during the last decade. The Carlin data results for this stock may examplify the situation in several multi-sea-winter salmon rivers in Norway at the moment. One reasom may be low survival of multi-sea-winter in the North Atlantic Ocean (see also discussion below). The effects of raising the smolts in a hatchery, and also removing the potential 2+ smolts, is however, unknown in the present study.

The present listing of different quantitative traits, related to growth rates and size and age at maturity, clearly indicate important differences in life-history strategies between the three stocks. These traits are selectable, and may result as a response to size of river, density of fish, conditions for growth and spawning grounds. We therefore assume that the differences reflect genetic differences between the stocks. However, because of environmental influence, the expression of genetic differences under cultured conditions does not necessarily imply that the fish develop similarly to the natal fish in the river. For example, 25% of the Lone returned as 2SW but all parents were 1SW (or had been prior to repeated spawning) and the sea ranched Vosso adults returned returned earlier than their parents did. Such differences may also result from the hatchery rearing. According to Kallio-Nyberg and Koljonen (1997), when they compared sea-ranched with reared and wild parents, selective factors during rearing can have genetic influence of life-history traits.

The two different methods, measurement of quantitative characters and the use of variability in polymorphic isozyme loci, both demonstrated stock differences. However, the quantitive measurements showed very large differences in life-history traits between River Lone offspring and the other stocks, probably most when compared to Vosso if sea survival is included, but the polymorph variation was smallest between these two stocks. The clear differences between the Bolstad fish and the Vosso fish from the upper part of the river was surprising. In what way, or to what degree differences in life-history strategies should be supposed to be found when examining polymorphic isozyme variation is not known. Such problems may arise from using different methods that study traits that are under selection or not. Significant qualitative variation may develop between stocks, but lack of or low qualitative variation does not imply that the stocks in question are indifferent. The present study was an attempt to study stocks from different point of views. Although such comparisons are troublesome, the study imply that it is beneficial to consider a number of traits in order to satisfactorily describe and differentiate between stocks, both quantitative and qualitative measurements should be applied to improve management of river stocks.

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