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VARIATION IN GROWTH RATE AND AGE AT SEXUAL MATURITY IN ATLANTIC SALMON.

By

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INTRODUCTION

In a previous paper (Nævdal et al. 1975) an account of an experiment on selective breeding of salmon in Norway was given, and some preliminary results on variation in growth rate were presented. In the present report further results concerning variation in growth rate and age at first maturity are presented, and discussed in relation to control by genetic factors and consequencies for first farming and management of natural salmon populations.

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MATERIAL AND METHODS

An account of the material used and the rearing methods was given in a previous report (Nævdal et al. 1975). In the present report only the year class hatched in 1972 is concerned. It consists of 47 sib groups. The parent fishes were collected from 12 Norwegian, two Canadian and one Swedish river besides one Norwegian fish farm (Eros Laks, Bjordal). Normally two fishes of each sex from each river were used. The egg portion of each female was divided into two parts, and each part was fertilized with milt from one of the males. In this way four groups of full sibs from each river were obtained. The specimens within each group were paternal half sibs to the specimens in one other group, maternal half sibs to the specimens in another group, and unrelated to the specimens in the third group. At Eros Laks eggs from 12 groups were collected following the same mating pattern.

For various reasons, mostly because of vibriosis, some groups died or were so reduced during the egg and fry stages that too few specimens were left for allowing statistical calculations based on data from these groups.

Two years old, most of the fishes reached smolt size in spring 1974. In some groups there were still some parr after two years. For practical reasons all fish were handled as smolt and transferred to sea water in spring 1974.

About 20 specimens of each surviving sib group were individually tagged with Carlin tags (Carlin 1955) in spring 1974 and transferred to a fish farm, Svanøy Stiftelse, Svanøybukt, where they were kept in a 100 m^3 floating pen (batch I). The rest of the smolt were kept at another fish farm, Risnefisk, Brekke, in 50 m^3 floating pens for one year. Four to seven sib groups, marked with combinations of fin removal, were kept in each pen. In spring 1975 maximum 100 fish of each of these groups were individually tagged with numbered FT-4 "lock-on tags" (Floy Tag & Manufacturing, Inc., Seattle) and transported to Svanøy Stiftelse where they were kept in 500 m^3 floating pens (batch II). The surplus fish were also tagged with Floy tags (maximum 50 ind. per group) and left at

Risnefisk (batch III). In September 1975 batch I was transferred into the same pens as batch II at Svanøy Stiftelse.

Lengths were measured twice a year (in spring and autumn). During autumn maturing fish were recorded. Individual weights were recorded for batch II and III in spring 1975 (36 months old), and for batch I and II in autumn 1975 and spring 1976.

In the present report, mainly the data from autumn 1975 are concerned as the data of the 1976 measurements have not yet been worked up.

Due to fouling with mussels and sea weeds, loss of the FT-4 Tags was heavy, and the results therefore are based on considerably lower numbers within groups than planned. Especially in batch III the tag loss was heavy.

Standard methods of calculating regression and correlation coefficients, means etc. were used. Calculations of heritability factors were based on analysis of variance, and methods described by Becker (1967) were used. Per cent data were transformed to arc sin $\sqrt{\%}$ before calculations.

RESULTS AND DISCUSSION

Growth rate

Mean lengths (l) at 30 months of age, mean lengths, weights (w) and condition factors ($k = \frac{w(g)}{l^3(cm)} \cdot 10^2$) at 36 and 42 months of age for all sib groups represented in batch II are shown in Table 1. The 41 months data are given separately for maturing and immature fishes.

The means varied considerably between groups at all ages. Within the groups mean lengths and weights in September were found to be approximately the same for immature as for maturing fishes, implying that whether a fish shall mature in its second year in the sea seems to be unrelated to individual size within groups. No correlation was found between mean length at 36 months of age and proportion of fish maturing the following autumn. But a negative correlation ($r = -0.49$, $P < 0.01$) was found between mean lengths in September (42 mths.) and proportions

Table 1. Mean lengths, weights and condition factors for sib groups of salmon. $\bar{l}$: mean lengths, $\bar{w}$: mean weights, $\bar{k}$: mean condition factors, n: number of fish

Gr.		30 months		36 months				42 months maturing				42 months immature			
nr.	Origin	$\bar{l}$	n	$\bar{l}$	$\bar{w}$	$\bar{k}$	n	$\bar{l}$	$\bar{w}$	$\bar{k}$	n	$\bar{l}$	$\bar{w}$	$\bar{k}$	n
01	Målselv	35.2	101	45.9	0.85	0.82	97	58.7	1.84	0.90	21	55.8	1.62	0.91	60
04	"	33.5	107	44.5	0.78	0.78	95	54.3	1.54	0.92	7	55.7	1.57	0.88	73
05	Lakselv	31.3	13	40.5	0.51	0.76	8	-	-	-	0	47.0	0.90	0.85	6
19	Lonevåg	36.0	34	46.7	1.04	1.01	31	53.2	1.41	0.92	24	53.0	1.27	0.85	2
21	Lærdal	34.9	37	45.8	0.88	0.90	53	54.0	1.56	0.99	1	56.3	1.66	0.92	44
22	"	36.4	104	47.5	1.01	0.93	108	-	-	-	0	58.7	1.88	0.92	96
23	"	36.1	66	47.3	0.98	0.92	67	-	-	-	0	58.2	1.82	0.92	59
24	Rauma	37.4	79	51.3	1.11	0.81	76	49.2	1.89	0.92	57	61.5	2.05	0.86	6
28	Etneelva	34.6	101	44.1	0.78	0.87	100	59.0	1.84	0.90	1	57.7	1.81	0.91	86
30	"	32.8	104	42.2	0.64	0.81	100	51.0	1.35	1.02	2	53.8	1.44	0.89	84
31	"	33.5	102	42.4	0.67	0.84	99	56.7	1.67	0.91	3	53.8	1.43	0.89	80
32	Tengselva	35.2	46	46.7	0.88	0.85	49	56.0	1.81	1.03	3	56.1	1.68	0.93	38
33	"	35.9	34	46.6	0.88	0.83	37	57.0	1.88	0.98	8	55.7	1.62	0.89	19
34	"	36.3	69	48.1	0.95	0.82	65	58.9	1.98	0.96	18	56.7	1.66	0.89	38
37	Gaula	31.6	108	40.6	0.62	0.88	100	51.0	1.24	0.93	1	53.3	1.45	0.93	79
38	"	32.3	114	42.2	0.68	0.88	100	52.0	1.30	0.92	1	54.4	1.52	0.93	79
39	"	32.2	104	40.9	0.62	0.94	100	60.0	1.94	0.90	1	52.6	1.34	0.90	86
40	Opo	34.0	101	43.1	0.65	0.81	104	-	-	-	0	55.0	1.52	0.90	85
41	"	34.1	51	43.4	0.69	0.84	46	-	-	-	0	57.7	1.75	0.90	39
43	Eio	33.2	100	42.6	0.66	0.83	100	54.0	1.58	1.00	6	54.9	1.56	0.93	76
46	Vosso	31.2	102	39.5	0.50	0.81	103	-	-	-	0	52.4	1.23	0.83	67
47	"	32.0	98	41.4	0.63	0.87	90	-	-	-	0	53.8	1.36	0.86	72
48	"	30.3	103	41.1	0.57	0.80	116	-	-	-	0	55.8	1.53	0.86	94
49	"	31.3	100	41.7	0.66	0.87	98	56.5	1.87	1.02	2	56.4	1.63	0.89	76
52	Eros Laks	36.9	100	47.4	1.06	0.98	100	57.0	2.02	1.09	1	58.2	1.83	0.92	78
55	" "	29.3	114	39.3	0.53	0.85	80	52.0	1.45	1.00	13	51.1	1.27	0.93	61
57	" "	36.6	85	47.7	1.12	1.02	84	-	-	-	0	59.1	1.94	0.92	63
59	" "	28.8	110	39.2	0.53	0.86	100	51.0	1.34	1.01	1	52.2	1.35	0.93	87
60	" "	30.4	46	34.0	0.55	0.84	48	54.8	1.57	0.95	4	52.7	1.39	0.94	39
61	" "	27.4	64	38.8	0.55	0.85	52	55.8	1.71	0.98	5	52.8	1.46	0.94	34
62	" "	31.9	110	41.5	0.69	0.89	100	57.7	2.06	1.06	6	55.0	1.67	0.97	78
63	Skelläfteälv,	28.4	103	39.0	0.57	0.94	99	46.4	1.07	1.05	36	49.6	1.26	1.00	41
64	Sverige	27.1	106	35.3	0.41	0.87	100	44.1	0.87	0.98	34	46.7	1.08	1.01	31
65	" "	28.2	95	38.0	0.50	0.83	80	47.1	1.05	0.98	27	50.6	1.35	1.00	38
66	" "	26.8	100	37.6	0.50	0.87	55	47.2	1.08	0.99	16	50.1	1.35	1.00	25
67	Maria Pond,	33.4	15	41.8	0.79	0.86	8	-	-	-	0	55.8	1.90	0.98	5
68	Canada	40.0	96	49.1	0.95	0.80	96	57.0	1.66	0.90	1	58.1	1.87	0.92	76
69	" "	40.1	14	47.2	0.90	0.83	13	-	-	-	0	56.7	1.85	0.98	11
72	MacDonald	28.6	30	41.0	0.83	0.97	19	57.0	1.96	1.05	9	49.0	1.64	1.09	1
73	River,Canada	32.6	20	40.7	0.76	0.92	22	56.1	2.00	1.11	8	52.3	2.14	0.96	8

of maturing fishes. This implies that on an average there is no differences in growth rate for "grilse" and other salmon until maturity retards growth rate.

In the previous report (Nævdal et al. 1975) correlation and regression coefficients between mean lengths for the same groups at different ages were calculated. In Table 2 corresponding calculations also including the data at 36 and 42 months of age are presented. The new calculations confirm the conclusion from the previous report that selection for high growth rate cannot be based on growth rate at early ages. Because maturity also retards growth rate, early maturing and late maturing fishes cannot be compared. Selection for high growth rate therefore should be based on lengths of salmon at normal time for slaughter, that is, after about two sea years according to usual Norwegian fish farming practice.

The effect of selection is greatly influenced by degree of control by additive genetic factors of the observed variations. Although not conclusive, calculations of heritability factors based on length variations of parr and smolt, imply that additive genetic factors control a considerable part of the observed variations (Nævdal et al. 1975). In Table 3 calculated heritability factors for length, weight and condition factor at 42 months of age are shown. In these calculations data both from batch I and II were used because the measurements were taken at the same time and the means were approximately the same. A nested design (Becker 1967) based on paternal and maternal half sib groups, and of full sib groups within half sib groups were used. Generally the estimates were high (Table 3), and similar to earlier estimates based on presmolt growth rate. With one exception estimates based on full sibs were lower than estimates based on half sibs. Because estimates based on full sibs contain part of the non-additive genetic variance (Becker 1967), the observations imply that non-additive genetic factors are of no importance for the actual traits. However, for these calculations one pair of half sib groups from each river was used, and each pair was also kept in the same floating pen until spring 1975. The higher estimates based on half sib correlations therefore represent both variation between populations and possible effects of systematic environmental variation. The estimates based of full sibs within groups of half sibs represent the heritability on the individual level, possibly also effect of non-additive genetic factors.

Table 2. Correlation coefficients (above diagonal) and coefficients of regression (below diagonal) of mean length of sib groups of salmon measured at seven different ages.

Age months	6	12	18	24	30	36	42
6	-	0.76	0.27	0.004	0.01	0.05	-0.03
12	1.27	-	0.49	0.32	0.20	0.18	0.10
18	0.51	0.56	-	0.60	0.49	0.48	0.19
24	0.01	0.48	0.70	-	0.69	0.64	0.50
30	0.03	0.87	1.72	2.04	-	0.93	0.72
36	0.39	0.88	1.87	2.15	1.00	-	0.76
42	0.17	0.43	0.63	1.39	0.65	0.64	-

Table 3. Heritability factors for growth of salmon after 18 months in the sea (total age 42 months). Letters S, D and A indicate that the factors are calculated from paternal half sibs, maternal half sibs and full sib groups respectively.

Trait	Paternal half sib groups		Maternal half sib groups	
	h^2_S	h^2_A	h^2_D	h^2_A
Length	0.76	0.21	0.84	0.16
Weight	0.34	0.13	0.34	0.52
Condition factor	0.71	0.04	0.81	0.08

In any case the heritability seems to be high enough both for length, weight and body shape to expect genetic improvement by selection. Selection for these trait will be started in autumn 1976, and will be carried out both within and between populations.

Age at first sexual maturation

Table 4 shows the proportions of mature fish in the batches. The proportions of mature fish (grilse) in the second sea year varied greatly. Generally the results for the same group in the different batches, were similar but in some groups (i.e. no. 18, 23, 47, 49, 62, 65) the proportions of mature fishes were considerably higher in batch I than in the other batches. But as the numbers in batch I were low and variation by chance might have occurred. The results so far indicate that age of first maturation in controlled by heredity, but on the other hand the differences between the batches also indicate that environmental factors may play some part. Influence of heredity on age at first maturation was indicated also by Elson (1971) and Ritter (1972).

Between groups of the same origin only small variations could be observed. But as the parent material from each river population was small, no conclusions can be drawn concerning variation within populations. Some variations were observed between the groups originating from the fish farm Eros Laks. This, however, could be expected because the salmon at Eros Laks originate from salmon caught in the sea thus probably representing several different river populations.

By and large the variations between the river populations correlated well with the life histories of the different river populations. From "grilse" rivers such as Lonevågselva and the Canadian MacDonald River, 60 - 100% of the salmon matured during their second sea year, while in groups originating from rivers with mainly large salmon (a.o. Altaelva, Lærdalselva, Etneelva, Opo, Vosso) few or no mature fish were found.

Considerably more males than females were found among the mature fishes in most groups (Table 4). But also here the variation was great and in some groups the females even were in majority. The significance of these findings is still uncertain, and the relationship between sex and age at maturity will be more closely dealt with when the rest of the fish reach maturity.

Table 4. Proportion of mature salmon during second sea year.
See text for further explanation.

Group no.	River or fish farm	Batch I		Batch II		Batch III		Proportion of males %
		Numbers	Mature %	Numbers	Mature %	Numbers	Mature %	
60001	Målselv	14	57.1	81	25.9	15	46.7	82.6
04	"	7	42.9	80	8.8	-	-	81.5
05	Lakselv	15	20.0	6	0	-	-	33.3
06	"	8	0	-	-	-	-	-
09	Altaelva	2	0	-	-	-	-	-
10	"	7	0	-	-	-	-	-
15	Lonevåg	16	100	-	-	-	-	68.8
17	"	8	100	-	-	-	-	75.0
18	"	7	100	-	-	-	-	71.4
19	"	10	100	26	92.3	-	-	61.8
21	Lærdal	13	23.1	45	2.2	-	-	100
22	"	16	0	96	0	10	0	-
23	"	16	12.5	59	0	-	-	66.7
24	Rauma	9	88.9	63	90.5	-	-	60.0
27	"	11	81.8	-	-	-	-	55.6
28	Etneelva	14	0	87	1.1	10	0	100
30	"	15	13.3	86	2.4	-	-	25.0
31	"	15	20.0	83	3.6	12	8.3	42.6
32	Tengselva	17	35.3	41	7.3	-	-	66.7
33	"	14	42.9	27	29.6	-	-	71.4
34	"	11	45.5	56	32.1	-	-	90.9
37	Gaula	10	10.0	80	1.3	10	0	50.0
38	"	10	0	80	1.3	8	0	100
39	"	14	7.1	87	1.1	11	0	100
40	Opo	13	0	85	0	5	0	-
41	"	11	0	39	0	-	-	-
43	Eio	15	40.0	82	7.3	13	15.4	78.6
46	Vosso	10	0	67	0	-	p	-
47	"	9	66.7	72	0	-	-	50.0
48	"	10	10.0	94	0	5	0	100
49	"	9	33.3	78	2.5	13	23.1	66.7
52	Eros Laks	8	0	79	1.9	13	0	100
55	" "	12	50.0	74	17.6	-	-	81.3
57	" "	8	0	63	0	-	-	-
59	" "	7	0	88	1.1	14	7.1	100
60	" "	10	20.0	43	9.3	-	-	83.3
61	" "	14	0	39	12.8	-	-	100
62	" "	10	30.0	84	7.1	21	0	100
63	Skelläfteälv,	9	33.3	77	46.8	16	56.3	95.8
64	Sverige	10	60.0	65	52.3	11	36.4	100
65	" "	13	76.9	65	41.5	-	-	94.6
66	" "	8	62.5	41	39.0	-	-	100
67	Maria Pond,	15	6.6	5	0	-	-	100
68	Canada	12	0	77	1.3	-	-	0
69	" "	15	20.0	11	0	-	-	50.0
72	MacDonald	13	46.2	10	90.0	-	-	37.5
73	River, Canada	12	66.7	16	50.0	-	-	31.3

To reveal the mode of inheritance of the observed variations, heritability factors were calculated based on paternal and maternal half sib groups and on full sib groups within pair of half sibs. Based on half sibs high values were found ($h_S^2 \sim 1.00$, $h_D^2 = 0.67$), implying that this trait is controlled by additive genetic factors. But because each pair of half sib groups represent one river population, calculated values therefore represent the differences between populations. Variation within populations was low in the present material, and this is also reflected by the low values calculated for heritability factors based on full sib groups within pair of half sibs ($h^2 = 0.05$ and 0.10 respectively). Selection of populations therefore should be expected to give genetic improvement, but selection of individuals within populations seems less promising.

However, the present results both concerning age at first maturity, growth and body shape, show that the different river populations are characterised by heritable differences which make them more or less suitable for fish farming, and thus the economic yield for the fish farms to a great extent depends on the genotype of the fish used. We do not know the reason for the differences in genotypes within and between populations, but it is reasonable to assume that each population is adapted to the special environmental condition in each river. For management of natural populations this implies that each river population should be treated separately, and one should be careful with transferring fish from one river to another for artificial stocking.

CONCLUSIONS

1. Growth rate of salmon varies among sib groups both in the fresh water and sea water stages.
2. Additive genetic factors seems to control at least part of the variation.
3. The ratio of salmon maturing during the second sea year, vary between sib groups of different river populations. Variation between groups from the same origin was moderate.
4. Genetic factors seems to control the age of first maturity; although some influence by environmental factors cannot be ignored.

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