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INDIVIDUAL GROWTH RATE AND AGE AT FIRST SEXUAL MATURITY IN ATLANTIC SALMON

by

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INTRODUCTION

In two previous reports (Nævdal *et al*. 1975, 1976) tentative results from experiments with selective breeding of Atlantic salmon, *Salmo salar*, in Norway have been dealt with. The experiments started in autumn 1971 when fertilized eggs from several river populations and one fish farm were collected. Since then new material has been collected each year, although gradually more emphasis has been laid upon selected parent fishes from the first two year classes.

The first year classes were used to study the variability in traits of economical importance for fish farming, especially growth rate and age at first sexual maturity. The influence of genetic factors on these traits were estimated from full sib and half sib correlations.

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The fish of the first year class of these experiments were individually tagged, which enables more detailed studies on correlation of growth rates at different ages and the possible connection between growth rate and age at sexual maturation. The aim of the present report is to analyse the data on the individually tagged fish in order to throw light on the topics mentioned above.

MATERIAL AND METHODS

The material used and the rearing methods are described in the previous reports (Nævdal et al. 1975, 1976).

The parent fish for the first year class (1972) were collected from the following Norwegian rivers: Målselv, Lakselv, Lonevågselva, Lærdalselva, Rauma, Etneelva, Tengselva, Gaula (Sunnfjord), Opo, Eio and Vosso. Material from one Swedish (Skellefteälv) and two Canadian rivers (MacDonald River and Maria Pond) were also included as well as eggs of farmed salmon from one fish farm (Eros Laks, Bjordal). Eggs from two to ten (usually four) sib groups from each locality were collected, but some groups died or were drastically reduced during early rearing, mostly because of vibriosis.

Two year old most of the fish 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 smolts, totally about 1000, of each surviving group were tagged with Carlin tags (Carlin 1955) in May 1974 and transferred to a fish farm, Svanøy Stiftelse, Svanøybukt, where they were kept in a 100 m^3 floating pen. The rest of the smolts were transferred to another fish farm, Risnefisk, Brekke, where they were kept 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 April 1975 maximum 100 fish of each sib group were tagged with numbered FT-4 "Lock on tags" (Floy Tag and Manufacturing, Inc., Seattle) and transferred to Svanøy Stiftelse farm where they were kept in 500 m^3 floating pens. In September the same year the Carlin tagged fish were transferred into the same pens as the Floy tagged fish.

Total lengths were measured each spring and autumn for fish of this year class, except that the Carlin tagged fish were measured one month earlier than the others in autumn 1974 and not measured at all in spring 1975. In 1976 the fish were measured in late June only. Individual weights were recorded for the tagged fish except for at the first measurement. Data on sex and of state of maturity were recorded when possible by external observation and at slaughtering in August 1976.

Due to fouling with mussels and sea weed, loss of the FT-4 tags was heavy, and the results therefore are based on considerably lower numbers within groups than planned. Tag loss by the Carlin method was insignificant, but about one third of the tagged fish were lost during the first summer. The results of the tagging experiments have been described in a separate report (Nævdal, Holm and Knutsson 1977).

Standard methods of calculating correlation and regression coefficients, means, standard deviations etc. were used, (cf. Sokal and Rohlf 1969). The calculations of correlations of individual growth rate at different ages were made using deviation from the mean of all fish from the same locality measured in standard deviations. To reveal causes of variations, standard methods of analyses of variance were used (Bonnier and Tedin 1940).

RESULTS

Variation in growth rate and age at first maturity.

Data on mean lengths and weights of the different sib groups were given in previous reports (Nævdal *et al*. 1975, 1976).

Variations in growth rate (measured as length or as weight) were great at all ages. Especially the variations between localities were pronounced, although some variations between sib groups within localities also were noted. The variation is illustrated in Fig. 1 which shows mean weights in June 1976 (25 months in the sea) for the groups pooled for river origin.

Estimates of heritability factors have been made (Nævdal et al. 1976) and usually high values were obtained. The use of the heritability concept is, however, somewhat dubious in this particular case, since the high values mainly reflect variation between populations.

Incidences of maturing fish in the first (mainly small males resembling precocious parr), the second and the third sea year varied considerably. In Fig. 2, percentages of mature fish during the second (1975) and third (1976) sea year respectively are illustrated. Fish mature in 1975 were regarded as mature in 1976 regardless of whether their gonads were ripening or not in 1976.

Also for this trait the variations were most pronounced between localities, but variations were also noted between sib groups within localities (not shown in Fig. 2). Calculations of heritability factors gave high estimates, but a great part of the variation is assumed to be caused by additive gene effect, reflecting variation between populations.

Individual growth rate at different ages.

In the previous reports (Nævdal et al. 1975, 1976) correlation analysis of mean length of the same sib groups at different ages was performed. Correlation coefficients were low between mean lengths at the presmolt stages but fairly high between measurements from the smolt stage and onwards. Omitting the presmolt stages and supplying with data from June 1976 (25 months in the sea) the data matrix of Table 1, was obtained.

Table 1. Correlation coefficients (above diagonal) and coefficients or regression (below diagonal) of mean length of sib groups of salmon measured at five different ages.

Month in the sea	0	5	11	16	25
0	-	0,69	0,64	0,50	0,59
5	2,04	-	0,93	0,72	0,62
11	1,72	2,04	-	0,76	0,56
16	1,87	2,15	1,00	-	0,85
25	2,59	0,85	0,65	1,21	-

To analyse correlation between individual size at different age the lengths of the individually tagged fish at the different measurements were compared. To eliminate the variation between populations (caused by genetic factors or by possible systematic environmental variation), individual deviations from the group means measured in standard deviations, were used instead of absolute lengths. By using both Carlin tagged and Floy tagged fish, the correlation coeffisients in Table 3 were found.

Table 2. Correlation coefficients of length (deviation from group means measured in standard deviations) of salmon at four different ages.

Months in the sea	0	4	16	25
0	-	0,69	0,53	0,37
4		-	0,71	0,63
11			0,84	0,67
16			-	0,87
25				-

The correlation coefficients are in the same order of magnitude for individuals within populations as for means of sib groups. After the smolt stage both individual growth rate and mean growth rate of the sib groups are rather highly correlated with size at later ages.

Relationship of age at first sexual maturity with growth rate.

The Carlin tagged smolt were separated according to population, sex and fish maturing the second year in the sea, the third year in the sea or later. To see if there was any connection between smolt size (length) and some of the mentioned factors, an analysis of variance, Table 3, was performed.

Table 3. Analysis of variance of smolt size distributed on sex, population and age at first maturation.

Source of variation	d.f.	Sum of squares	Mean squares
Between sex	1	0,80	0,80
Within sex	375	1175,42	19,15
Between river	26	498,13	
Within river	349	677,29	
Between age at first maturity	44	119,10	2,64
Within age	305	559,19	1,83
Sum	376	1176,22	

Kvotients: Influence of sex: $\frac{0,80}{19,15} = 0,04, \quad p > 0,2$

Influence of population: $\frac{19,15}{2,64} = 7,25, \quad p < 0,001$

Influence of age of maturation: $\frac{2,64}{1,83} = 1,44, \quad p \sim 0,05$

At this stage influence of sex seems to be insignificant. As expected the influence of populations is highly significant representing variation caused by genetic factors and possibly systematic environmental variations. Influence of age of maturation is possibly significant, and from the data it is seen that within some of the populations the fish maturing as grilse tend to be slightly bigger as smolt than the later maturing fishes.

In table 4, a corresponding analysis of lengths after one summer in the sea (for Carlin tagged fishes that means about 4 months) is shown.

Table 4. Analysis of variance of length at one sea summer distributed on sex, population and age at first maturation.

Source of variation	d.f.	Sum of squares	Mean squares
Between sex	1	1,23	1,23
Within sex	366	3214,77	
Between locality	26	973,20	37,43
Within locality	340	2241,57	
Between age at first maturity	45	429,83	9,55
Within age	295	1811,74	6,14
Sum	367	3216,00	

Kvotients: Influence of sex: $\frac{1,23}{37,43} = 0,03$, $p > 0,2$

Influence of population: $\frac{37,43}{9,75} = 3,92$, $p < 0,001$

Influence of age of maturation: $\frac{9,55}{6,14} = 1,56$ $p \sim 0,05$

Also here the influence of sex is insignificant, and influence of populations highly significant. Influence of age at first maturation is possibly significant but it is impossible to see a general trend when comparing the mean lengths.

A corresponding analysis is shown in Table 5, but the data used are lengths after 11 months in the sea, i.e. half a year before maturation of the grilse. Only Floy tagged fish could be used.

Table 5. Analysis of variance of length of salmon after one year in the sea.

Source of variation	d.f.	Sum of squares	Mean squares
Between sex	1	10,4	10,4
Within sex	1143	36099,6	
Between locality	24	14242,1	593,4
Within locality	1119	21757,5	
Between age at maturation	43	1183,5	27,4
Within age	1076	20572,0	19,1
Sum	1145	36110,0	

Kvotients: Influence of sex: $\frac{10,4}{593,4} = 0,02, \quad p > 0,2$

Influence of locality: $\frac{593,4}{27,4} = 21,66, \quad p < 0,001$

Influence of age of maturation: $\frac{27,4}{19,1} = 1,44 \quad p \sim 0,05$

The conclusion will here be the same as in the former analysis; the length of the salmon after one year in the sea is not influenced by sex, greatly influenced by locality of origin and possibly influenced by the age of which the fish are destined to mature.

However, by eliminating first the influence of locality, then possible influence of age of maturation, the results in Table 6 were obtained.

Influence of locality is still strong, but influence of age of maturation cannot be found by this method of analysis. However influence of sex is probably significant when eliminating first the influence of locality. The reason for this is probably that influence of sex is more pronounced in some populations than in others. From the data it is evident that even at this stage the males are significantly smaller than the females within one of the localities, which might explain why the analysis of variance showed significant differences when testing influence of sex within localities, but not when testing it on the total material.

Table 6. Analysis of variance of length of salmon after one year in the sea.

Source of variation	d.f.	Sum of squares	Mean squares
Between locality	12	13551,3	1129,2
Within locality	1133	22558,7	
Between age at maturation	24	1003,7	41,8
Within age	1108	21554,3	
Between sex	27	881,0	32,6
Within sex	1076	20673,3	19,2
Sum	1145	36110,0	

Kvotients: Influence of locality: $\frac{1129,2}{41,8} = 27,0 \quad p < 0,001$

Influence of age of maturation: $\frac{41,8}{32,6} = 1,28 > p \quad 0,2$

Influence of sex: $\frac{32,6}{19,2} = 1,70 \quad p < 0,05$

Survival and growth rate of mature salmon.

Survival and growth rate (weight gain) during the spawning season of fish maturing as grilse compared to immature fish are shown in Table 7. Because of a rather heavy tag loss during the actual period survival of mature fish is given in per cent surviving compared to immature fish, assuming that tag loss was the same for mature and immature fishes. All females were stripped for eggs. It can be seen in the table that survival of females after spawning (stripping) is about the same as of immature fish while there is somewhat higher death rate of males. However, weight gain of females is less than the half compared to immature fishes, while it is still lower for males. The individual data also showed that there was great variation especially for the males, probably reflecting the observation that some mature fish start to eat soon after spawning, while others start again later or not at all. Of the grilse 68,4% were found to mature again the next spawning season. This figure was practically the same for both sexes.

Table 7. Survival and growth rate of immature and mature salmon (September 1975 to June 1976). The groups are pooled for each river. Survival of mature salmon in per cent of surviving immature, and mean weight increase in kg.

Locality no.	Immature	Females		Males	
	mean weight	survival	mean weight	survival	mean weight
1	1,72	-	-	100	0,65
2	2,42	100	1,24	100	0,89
3	2,22	100	1,21	100	0,77
4	2,31	0	-	100	0,80
5	2,33	100	2,10	100	1,14
6	2,12	88	0,30	100	1,36
7	-	100	0,85	94	0,60
8	2,61	97	0,65	100	0,53
9	2,78	-	-	-	-
10	2,69	98	0,43	82	0,92
11	3,19	88	1,14	90	1,00
12	1,61	100	1,60	76	0,73
13	2,47	89	0,80	100	1,00
14	2,15	100	1,33	100	0,87
15	2,95	100	0,74	100	0,99

DISCUSSION

The great variation in growth rate and age at first maturity among populations and sib groups seems to have a genetic base, although some of the variation may be caused by systematic environmental variation because the populations usually were kept in separate floating pens until the fish were individually tagged. Great variances probably with a genetic base have also been found in later year classes in the same experimental series (unpublished). It therefore seems clear that salmon used for fish farming purposes in Norway is of varying value concerning their ability of growth and especially concerning their age at first maturation. Selection of populations, probably also of individuals within populations seems promising, and is now under way.

The importance of late maturation in fish used for fish farming is clearly shown by the differences in weight gain by the salmon maturing as grilse and the salmon not maturing during their second year. Although the death rates for mature and immature fish were not so different as expected and as claimed by the fish farmer the weight gain during the spawning season and until next summer was less than the half of mature fish compared to the immature ones. Surprisingly, both the weight gain and survival rate were higher for mature females than for males.

The growth differences between males and females were not very pronounced until maturation and could not be seen when looking at the total material. Within populations, however, such differences seemed to excist, and the populations probably behave differently in this trait. Especially in the groups from one of the localities the males were significantly smaller than the females half a year before maturation.

The analysis of variance performed to investigate any possible connection between growth rate and age of maturation gave no clear answers. There seemed to be some variation in growth rate which could be connected with the fish's maturation later on, e.g. the smolt size of the grilse seemed to be somewhat greater than the smolt size of larger salmon, and a similar tendency was found concerning size after one year in the sea, although not very pronounced.

Ritter (1975) reports that within groups of hatchery reared smolt the larger smolts produce proportionally fewer grilse than did the smaller ones. In the present study it is not possible to find such a tendency within groups, on the contrary, in the total material and within some populations there seems to be tendency to a somewhat higher mean for smolt size of the grilse than of the larger salmon. A similar tendency has been found for coho salmon by Hager and Noble (1976).

Correlations of growth rates were found to be in the same order of magnitude for sib group means as well as for individual deviations from population mean. The correlation coefficients were all significant, and even smolt size correlated well with the size of the fish at later ages. However, low correlation was found between presmolt growth rate and the growth rate in the sea (Nævdal et al. 1976).

The rather high correlations which were found are of some importance for making selection for higher growth rate. High correlations imply that selection both of sib groups and of individuals within sib groups can be made earlier than at normal slaughtering age, thus reducing the cost of rearing of experimental fish. However, more data on this is needed, and it is also evident that the residual (error) variance is rather great implying that other factors than size at a given time may have considerable influence on the size at slaughtering.

CONCLUSIONS

1. Growth rates and possible connection between growth rate and age at maturation were studied on individually tagged salmon originating from different river populations.

2. Great variations in growth rate and in age at first maturity were found among sibgroups of salmon originating from different populations (localities). Although much less pronounced, variations in these traits were also noted among groups within the localitites.

3. When separating the individuals into groups according to age at first maturity, small variations were found within populations for smolt size, size after one summer in the sea. The correlation between age at maturation and earlier growth rate thus seems to be rather small.

4. Significant correlations were found between size (length) at different times after the smolt stage both concerning the group means and the individual deviations from the means.

5. Mature female grilse stripped for eggs survived at about the same rate as immature fish during the spawning season while the survival rate of male grilse was considerably lower. Weight gain for immature fish during the same period was about two and a half time that of mature females and three times that of mature males.

REFERENCES

BONNIER, G. and O. TEDIN, 1940. Biologisk variationsanalys. Stockholm. 325 pp.

CARLIN, B. 1955. Tagging of salmon smolt in the river Lagan. Inst.Freshwater Res., Drottningholm. Annual Rep. 1954: 57-74.

HAGER, R.C. and R.E. NOBLE 1976. Relation of size at release of hatchery-reared coho salmon to age, size and sex composition of returning adults. Progr.Fish.Cult. 38: 144-147.

NÆVDAL, G, M. HOLM and S. KNUTSSON, 1977. Erfaring med bruk av ytre merker på oppdrettsfisk. Fisken og Havet, Ser. B, 1977 (1). 19 pp.

NÆVDAL, G. M. HOLM, D. MØLLER and O.D. ØSTHUS 1975. Experiments with selective breeding of Atlantic salmon. ICES, C.M. 1975 (M 22): 1-10.

\- 1976. Variation in growth rate and age at sexual maturity in Atlantic salmon. ICES, C.M. 1976 (E 40): 1-10.

RITTER, J.A. 1975. Retationship of smolt size and age with age at first maturity in Atlantic salmon. Environment Canada. Fisheries and Marine Service. Tech.Rep.Ser. MAR/T-75-5: 1-7.

SOKAL, R.R. and F.J. ROHLF. 1969. Biometry. San Francisco. 776 pp.

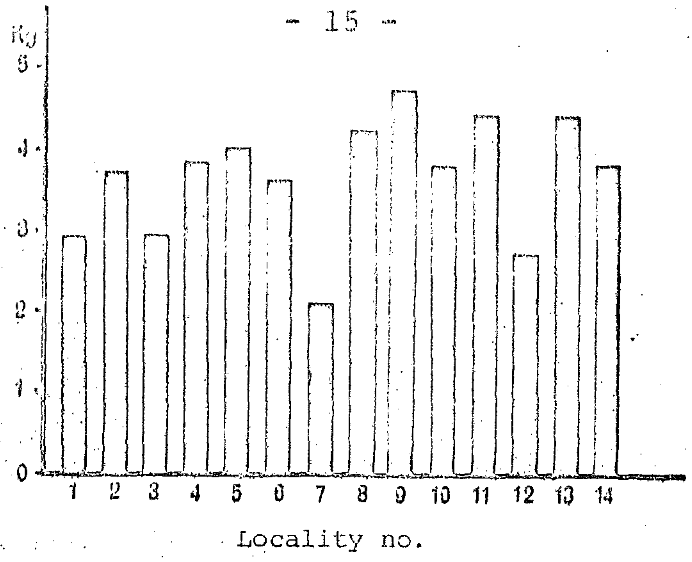

Fig. 1. Mean weights of salmon from different river localities after 25 months in the sea. Each locality represents from two to four sib groups.

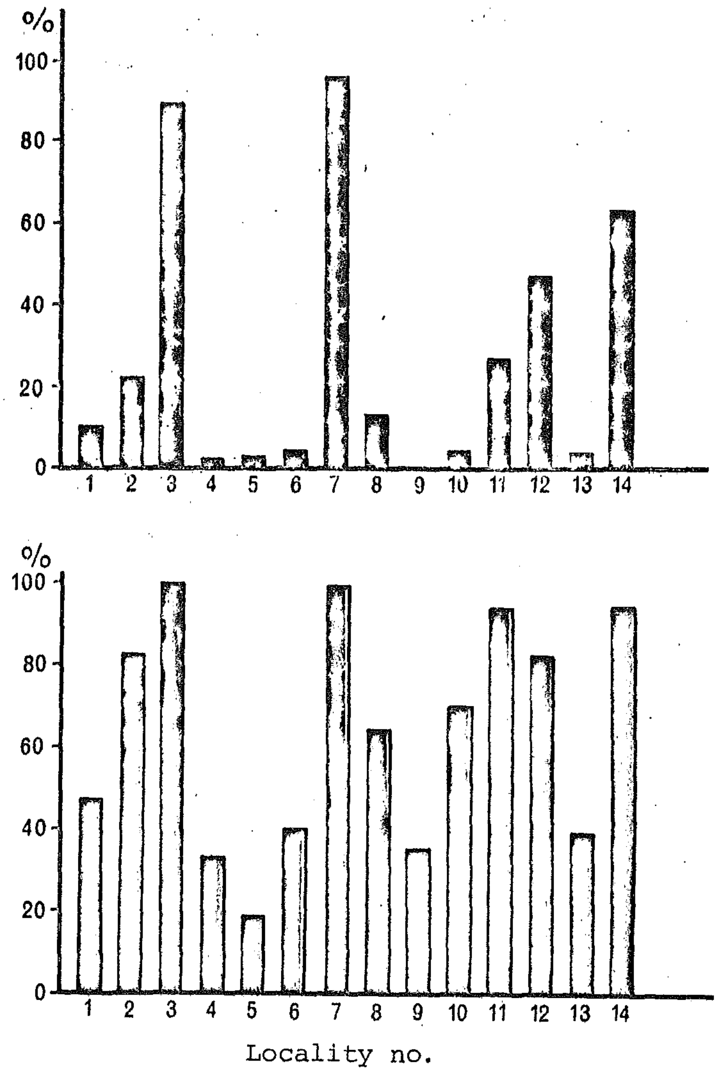

Fig. 2. Per cent mature fish the second (A) and third (B) sea year of salmon originating from different rivers reared under fish farming conditions.