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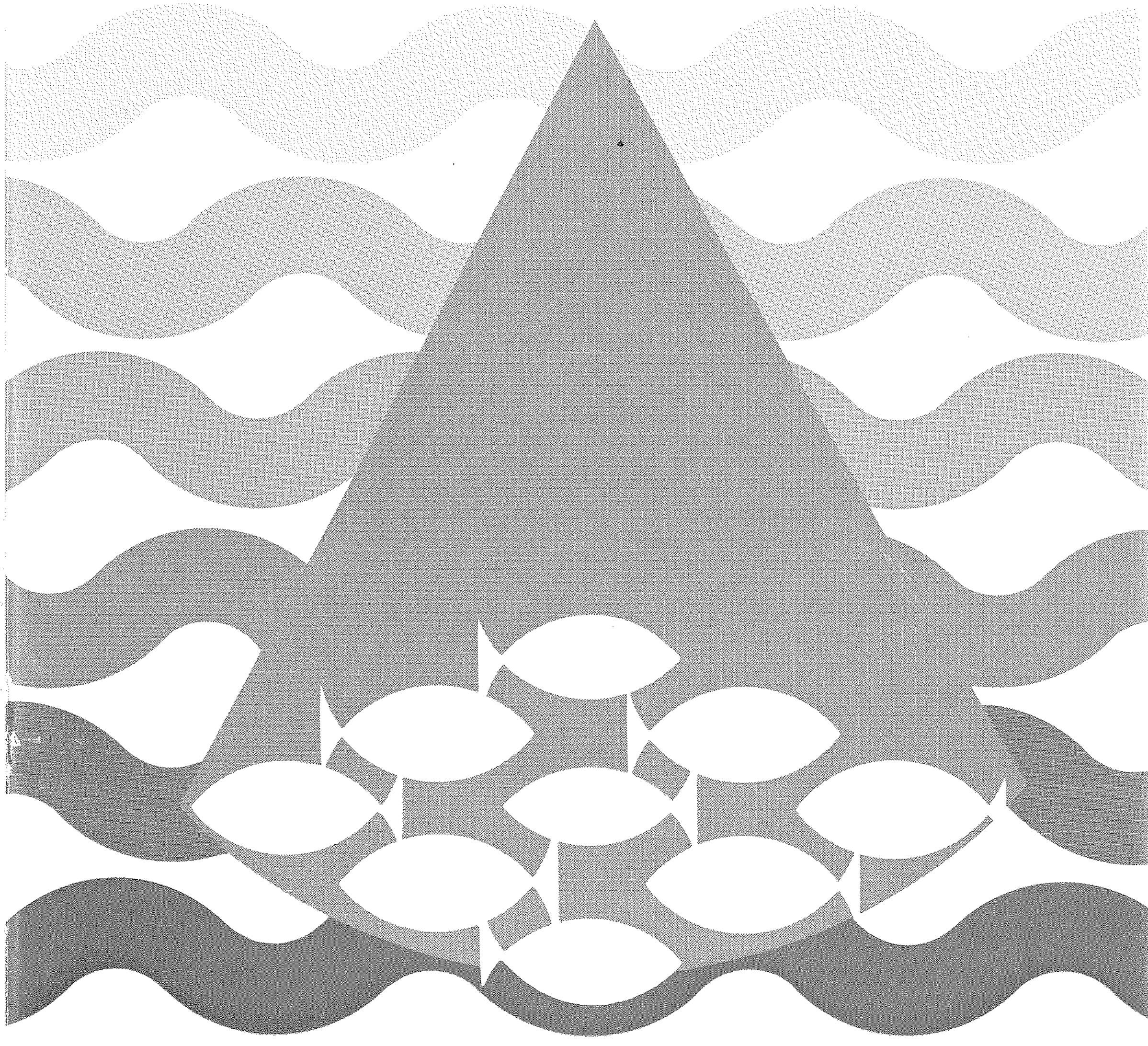

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GROWTH AND SURVIVAL STUDIES ON 0-GROUP PLAICE (*PLEURONECTES PLATESSA* L.) IN A SMALL BASIN WITH A CLOSED ECOSYSTEM

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ABSTRACT

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A growth and survival experiment on 0-group plaice was carried out in a small basin during the summer of 1976. The volume of the basin was about 25 m^3, and the seawater was left stagnant during the summer. Of the initial 200 metamorphosed fry released, 154 survived, and a mean daily length increment of 0.28 mm was observed for a period of 105 days. The temperature was about 20 °C for half of the experimental period.

The main energy flow is supposed to have followed this simplified route: phytoplankton → *Mytilus edulis* produced faeces → detritus-eating crustaceae → plaice fry. Calculations of food intake and gross growth efficiency have been carried out, applying the metabolic values earlier reported (Edwards, Finlayson and Steele 1969), and the present data have been compared with their results. The basin appeared to be an ecosystem with a high production, giving better survival and growth than previous tank experiments.

In spite of the extreme temperature during midsummer, the growth was comparable to that observed under natural conditions (Loch Ewe), but the survival was far better due to lack of predators in the basin.

INTRODUCTION

In the middle of the 1960's studies on the ecology of 0-group plaice (*Pleuronectes platessa* L.) was carried out in Loch Ewe, Scotland (Edwards and Steele 1968, Steele and Edwards 1970). In order to interpret the observations, a number of experiments with 0-group plaice and their main prey organism, *Tellina tenuis* (L.), in the lake was undertaken at Aberdeen in laboratory tanks (Edwards, Finlayson and

STEELE 1969, EDWARDS, STEELE and TREVALLION 1970), in large outdoor tanks (EDWARDS *et al.* 1970) and in underwater tanks (STEELE 1966).

They made estimates of the metabolism and the Q_{10}, which were used to calculate the carrying capacity of Loch Ewe and to explain the observed fish growth in relation to the feeding conditions.

The main conclusions drawn from their field and laboratory investigations were:

1. Predation was the main controlling factor for the size of the population of 0-group plaice, permitting better growth of the surviving fry due to lesser competition.
2. There seemed to be a maximum gross growth efficiency of 40%.
3. The metabolism was modified by the food supply.

The experiment on 0-group plaice described in this paper was carried out to study growth and survival in a stagnant outdoor basin where the growth of the fish was limited by the carrying capacity and the high temperature of the basin water.

The experiment was carried out at Statens Biologiske Stasjon Flødevigen, Arendal, in southern Norway.

MATERIAL AND METHODS

On 2 March a large number of plaice eggs were fertilized and incubated in a laboratory tank. The larvae hatched about 20 March and were fed on newly hatched *Artemia salina.* The temperature increased slowly from 7 °C in March to 11 °C on 17 June when 226 metamorphosed fry were sampled randomly from the dense and slow growing population in the tank. Of these larvae, 200 were transferred to an outdoor basin while the remaining 26 were length measured.

The basin had a surface area of 18.5 m^2 and a depth of 1.3 m, giving a volume of 24 m^3. The walls were made of concrete, and the bottom consisted of equal parts of bedrock, sand and mud.

During most of the experimental period a phytoplankton bloom was in progress in the basin. The warm summer in southern Norway in 1976 resulted in an increase in both bottom and surface daytime temperatures from 17 °C on 17 June to about 23 °C two weeks later. From the end of August the temperature decreased to 13 °C at the bottom in late September. Three linear temperature functions are used in the later calculations: a linear increase from 17 °C to 20 °C (day 0—20), a steady temperature of 20 °C (day 21—60), and a linear decrease from 20 °C to 13 °C (day 61—105). Due to evaporation the salinity increased from about 34‰ to about 37‰ during the experimental period.

Previous to the initiation of this experiment the basin had just been drained after an experiment on herring larvae. It was refilled with sea water on 16 June and left stagnant for the following months until drainage on 28 September when the experiment was terminated.

In addition to the plaice fry, about 200 adult *Mytilus edulis* L. were transferred to the basin, most of them hanging in a basket at a depth of 3/4 m, but some clusters were also placed on the bottom. The *M. edulis* were intended to harvest the phytoplankton production, and their faeces would serve as food for the detritus-eating crustaceae in the basin. Two small *Carcinus maenas* (Pennant) were also released to clean the basin.

The equations used in the calculations of metabolism, growth rate, food demands and food intake are mainly taken from EDWARDS *et al.* (1969, 1970) and from WARE (1975). The different concepts are reviewed in the Appendix.

RESULTS

The length distributions of the larvae for the day of transfer, 17 June, a sample from 7 July and the fry surviving on 28 September are given in Fig. 1. The mean lengths on the three days were 14 mm, 23 mm and 43 mm respectively.

The intervals between the measurements were 20 and 85 days respectively, giving a daily increment of 0.49 mm for the first period, 0.23 mm for the second and 0.28 mm for the total 105 day period.

The mean weight of the fry was 23 mg on 17 June, increasing to 112 mg on 7 July, and at the end of the experiment it was 742 mg. This gives a specific daily growth rate based upon wet weight of 7.9% for the first 20 days, 2.2% for the next 85 days and 3.3% for the whole experimental period.

On 28 September a total of 154 fry had survived, giving a survival of 77% and a daily mortality rate of 0.0025.

The density of fry in the basin decreased from 11/m^2 to 8/m^2. The diet consisted mainly of harpacticoid copepods, juvenile amphipods and

Table 1. The gut contents of five plaice fry caught on 28 September ($\bar{l}$ = 3.8 cm).

Prey organisms	Occurence	Mean number per gut	Mean length of prey organisms
Amphipod juveniles	0– 20	7	3 mm
Chironomid larvae	1– 22	10	2 mm
Harpacticoid copepods (small) ...	15– 35	20	0.5 mm
Harpacticoid copepods (large) ...	135–300	210	1.3 mm

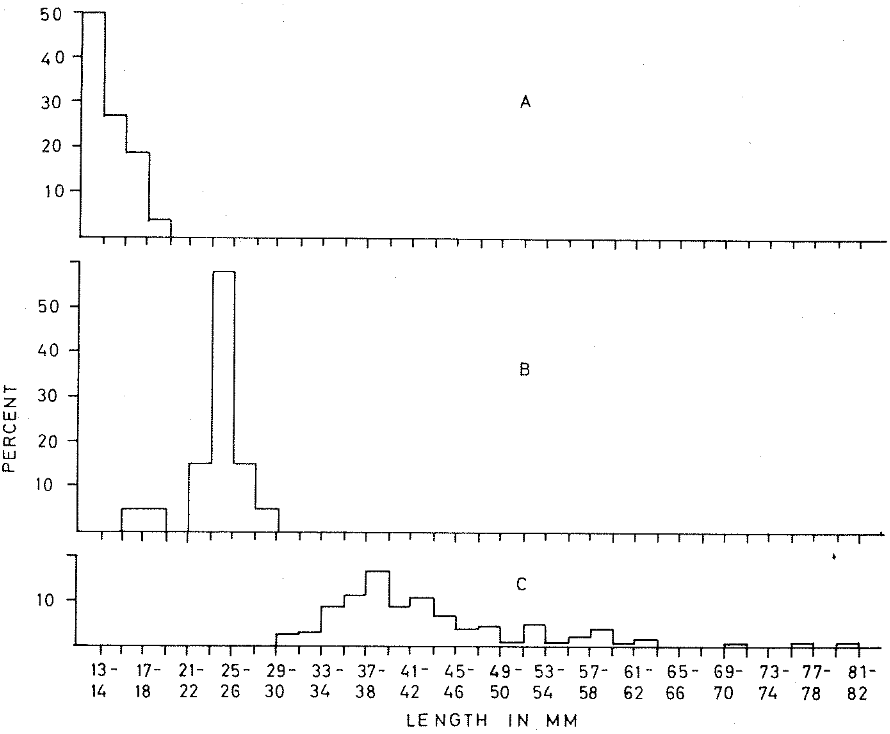


Fig. 1. Length distribution of plaice fry in the basin.
A: 17 June, B: 7 July, C: 28 September.

chironomid larvae (Table 1). The calorific value of the stomach contents on 28 September based on five fry ranged from 5 to 15 cal with a mean of 10 cal.

DISCUSSION

Steele and Edwards (1970) stated that predation was the main reason for the reduction of the standing stock of fry in Loch Ewe. They observed that mortality was negligible among fry exposed to a controlled environment without any predation compared to heavy mortality in the loch (Table 2) (Steele 1966, Edwards *et al.* 1970, Steele and Edwards 1970). The same effect was clearly demonstrated in the Flødevigen basin experiment, leading to a high survival rate.

The density of fry in Loch Ewe decreased from about 1/m^2 in late June to about 0.1/m^2 in late September. The densities were considerably higher in the tanks on land and in the underwater tanks (up to 15/m^2) and were in most cases only reduced to half the initial values (Table 2).

Table 2. A comparison between different growth and survival studies on plaice fry.

	Daily mortality rate	Daily growth rate (mm)	Density/m²		Duration in days
			June	September	
Loch Ewe 1965	0.025	0.37	1.0	0.1	105*
1966	0.023	0.30	0.3	0.03	105*
1967	0.008	0.20	—	—	105*
1968	0.016	0.32	—	—	105*
Tank experiments	0.01 —0.0016	0.16—0.25	15—1.5	4.1—0.9	130**
Underwater tanks	0.01 —0.005	0.05—0.25	15—1.5	7.2—0.8	105***
Flødevigen experiment	0.0025	0.28	11	8	105

* Calculated for the period 17 June—28 September, data from STEELE *et al.* (1970).

** Calculated for the period 5 May—15 September (the actual experimental period), data from EDWARDS *et al.* (1970).

*** Calculated for the period 17 June—28 September, data from STEELE (1966).

The initial density in the basin experiment at Flødevigen was comparable with that of the tank experiments at Aberdeen, but the reduction in number per m² was considerably less.

STEELE (1966) concluded that a density above 1.5 fry/m² would permit survival, but would lead to a reduced growth rate compared with the natural conditions.

The growth rate in the basin experiment was 0.28 mm/day during the 105 day period at a density between 11—8 fry/m². During midsummer the growth rate might have been low due to the high temperature. Therefore, the main growth probably occurred during the first and last part of the experiment as indicated by the high growth rate observed during the first 20 day period when the temperature was more favourable.

Nevertheless, the observed mean daily growth rate at Flødevigen was much higher than the observed length increment in most of the underwater tanks and even higher than in the tank with the lowest density (Table 2). The basin growth rate is, however, comparable with the growth rate under natural conditions in Loch Ewe for the same period. This was the case even though the temperature was near the lethal limit (EDWARDS *et al.* 1969, EDWARDS and STEELE 1970, DANIELSSEN and IVERSEN 1976), the density considerably higher, and the growth completely dependent upon production within the small basin.

The use of an enclosed system gives an opportunity to calculate the production within the system. The survival of the bottomliving animals, *M. edulis*, *C. maenas* and the plaice fry in this shallow basin, indicate that the oxygen supply was sufficient during the whole period, probably due

Table 3. Survival, growth, resting metabolism and temperature and the resulting values of daily food intake (I), gross growth efficiency (K), food intake as a percentage of body weight and the accumulated food intake for the total population and for individual fry according to the hypothesis suggested by EDWARDS *et al.* (1969).

Days since transfer (17 June)	Number of fry N	Mean wet weight (mg) W	Daily growth (mg wet weight) G	Population biomass (gram wet weight)	Resting metab. cal/day Q	Temp. °C t	First hypothesis: $E = 2Q$*					Second hypothesis: $E \sim Q$***				
							I_1 cal	K in %	$\frac{I_1 100}{W'^{**}}$ (%)	$\Sigma I_1 N$ kcal	ΣI_1 kcal	I_2 cal	K in %	$\frac{I_2 100}{W'^{**}}$ (%)	$\Sigma I_2 N$ kcal	ΣI_2 kcal
0	200	23	—	4.6	5.7	17.0	—	—	—	—	—	—	—	—	—	—
10	195	76	4.3	14.8	18.2	18.5	58	7.3	77	100	0.5	33	12.9	44	72	0.4
20	190	122	4.9	23.2	30.2	20.0	93	5.2	77	248	1.3	49	10.0	40	152	0.8
30	185	174	5.8	32.3	39.0	20.0	119	4.6	69	450	2.4	61	9.5	35	256	1.3
40	181	232	6.1	42.0	48.0	20.0	145	4.2	63	694	3.7	73	8.4	31	379	2.0
50	176	296	6.8	52.2	57.2	20.0	173	3.9	59	981	5.3	85	7.9	29	520	2.8
70	168	442	7.9	74.2	64.5	18.4	195	4.0	44	1,647	9.2	97	8.1	22	845	4.7
90	159	612	9.1	97.8	51.5	15.3	160	5.7	26	2,236	12.8	85	10.7	14	1,146	6.5
105	154	742	6.9	114.3	41.3	13.0	127	5.4	17	2,575	14.9	67	10.3	9	1,330	7.7

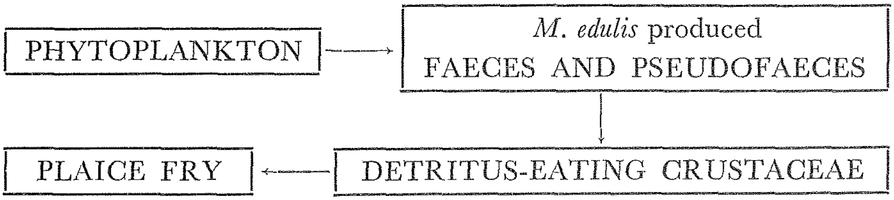
* EDWARDS *et al.* (1969).

** W′: wet weight converted to cal.

*** Second hypothesis: metabolism is a function of food intake rate (EDWARDS *et al.* 1970); in the Flødevigen experiment being close to Q.

to the high phytoplankton production previously mentioned. The temperature condition was uncontrolled, but appeared to be within the survival limits of the organisms.

The main energy flow in the basin is supposed to have followed this simplified route:



The studies on metabolism carried out by Edwards *et al.* (1969, 1970) give an opportunity to backcalculate the food intake in the basin, based on the observed growth and information about the temperature conditions. Although rather sporadic observations on growth and temperature, such calculations have been carried out according to the two hypothesis of Edwards *et al.* (1970).

1. Metabolism = 2Q
2. Metabolism is a function of food intake rate (see Appendix).

The two sets of calculated values are given in Table 3.

The table shows that the gross growth efficiency, K, according to the first hypothesis, is 4—6% most of the time. The daily food intake is high compared with the body weight and decreased from about 80% ($I_1 \times 100/W'$) in the beginning of the experiment to 20% at the end. The accumulated food intake per fish fry for 105 days was about 15 kcal, giving a mean gross growth efficiency of 5.4% for the whole growth period. The fry population consumed food of about 3 600 g wet weight, being equivalent to 2 600 kcal.

The second hypothesis gives a metabolism practically equal to resting metabolism, Q. Consequently the food intake, I_2, was half of the above calculations. The gross growth efficiency was 8—11% most of the time (Table 3), and the food intake as a percentage of the body weight reached a value of 10% in late September although it was 20—40% most of the time. The accumulated food intake per fry was about 8 kcal, giving a mean gross growth efficiency of 10%. The total food consumption by the population was about 1 800 g wet weight, being equivalent to 1 300 kcal.

EDWARDS *et al.* (1969) observed a reduction in active metabolism with increasing temperatures above 10 °C. Further they observed that the active metabolism at 20 °C was nearly the same as the resting metabolism at that temperature. Due to this EDWARDS *et al.* (1969) suggest that 20 °C might be a possible upper limit for survival. The fish in the basin survived for a long period at this supposed critical temperature and had a high daily food consumption (Table 3). The critical temperature might therefore be higher than the suggested 20 °C, implying a laboratory artifact in their experiments. Further the resting metabolism might have been considerably lower than the active metabolism permitting the fry to hunt for food and digest it. The high resting metabolism might be due to laboratory stress as suggested by EDWARDS *et al.* (1969). After all, it seems reasonable to assume that the active metabolism, E, of the fry in the basin was equal to the observed $\underset{\sim}{Q}$, but in this case $\underset{\sim}{Q}$ represent the active metabolism under the actual feeding and temperature regime.

The stomach contents on 28 September give support to this view as the mean calorific contents of the five investigated guts at 1200 hours was calculated to be 10 cal. Assuming a steady food intake for 16 hours and that the gut contents at 1200 hours represented the food eaten since 0800 hours, the plaice fry consumed 40 cal until 2000 hours. This is more in agreement with the calculated food intake of 67 cal according to the second hypothesis than to 127 cal according to the first hypothesis (Table 3). As a metabolism of $E = \underset{\sim}{Q}$ seems to be a more reliable estimate in the basin experiment, this will be used in the following calculations.

According to both hypothesis, the density of food close to the bottom needed to be rather high. A newly metamorphosed plaice can effectively search 3 litres/day with a 16 hour feeding time (BLAXTER and STAINES 1971); therefore, at the start of the experiment the fish must have captured 10 cal/litre to obtain 30 cal (Table 3). The food density had to be even higher as some of the water was searched several times by several fry, and also there had to be prey animals surviving to ensure production in the future. Calculation of the calorific content per litre can be carried out according to WARE (1975):

$$I = \frac{v\gamma\varrho}{1 + \gamma v h \varrho}$$

A food intake of 3 cal/hour (I), a search volume of 0.2 litre/hour (γv) and consumption time of 0.04 hour/cal (h), using the value from IVLEV (1960) for bleak (*Alburnus alburnus*), gives a density, ϱ, of 17 cal/litre as an estimate for organisms living close to the bottom. THIJSSEN, LEVER and LEVER (1974), studying the feeding intensity of 0-group plaice, observed a food intake of 18 cal from 0500 hours to 0800 hours which gives 0.10 hour/cal. As those plaice were bigger than these in this experiment, it is more likely that the consumption speed in the basin was somewhat slower, and assuming a search time of 0.20 hour/cal, the density of food close to the bottom had to be 38 cal/litre. The actual minimum production rate of prey animals in the basin had to be 13 kcal per days as a mean value, being equivalent to about 10 g wet weight. With an assumed mean gross growth efficiency of 15% at the ambient temperature (GAUDY 1974), the consumption of detritus by the evertebrates was probably about 60 g wet weight per day.

With an assumed growth rate of 10% (CHANG and PARSONS 1975), the standing stock of prey organisms must have been at least 100 g wet weight, giving 2.9 cal/litre. This density seems to be rather low, but as the main prey organisms were semipelagic, being distributed close to the bottom, an assumed distribution within a 10 cm range over the bottom gives about 40 cal/litre as a close to the bottom value which is in agreement with the earlier calculations.

The discrepancy in growth and survival between this basin experiment and the tank experiments referred to, seem to originate from the character of the ecosystem into which the fry were introduced. The key to the applied system, which gave a comparatively high growth rate and survival of the plaice fry at high stocking density and at unfavourable temperature conditions, seems to be the harvesting of phytoplankton by *M. edulis*. The faeces gave a high food supply to the detritus-eating crustacea which in turn served as food for the plaice.

REFERENCES

BLAXTER, J. H. S. and STAINES, M. 1971. Food searching potential in marine fish larvae. P. 467–485 in CRISP, D. J. ed. *IV European Marine Biology Symposium.* Cambridge University Press, Cambridge.

CHANG, B. D. and PARSONS, T. R. 1975. Metabolic studies on the amphipod *Anisogammarus pugettensis* in relation to its trophic position in the food web of young salmonids. *J. Fish. Res. Bd Can., 32*: 243–247.

COMITA, G. W. and SCHINDLER, D. W. 1963. Calorific values of micro crustacea. *Science, N. Y., 140*: 1394–1396.

DANIELSSEN, D. S. and IVERSEN, S. A. 1976. Innvirkning av små overtemperaturer på dødelighet og vekst hos I-gruppe rødspette (*Pleuronectes platessa* L.). *Fisken og Havet Ser. B, 1976* (4): 1–18.

EDWARDS, R. R. C., FINLAYSON, D. M. and STEELE, J. H. 1969. The ecology of 0-group plaice in Loch Ewe. II. Experimental studies of metabolism. *J. exp. mar. Biol. and Ecol., 3*: 1–17.

EDWARDS, R. R. C. and STEELE, J. H. 1968. The ecology of 0-group plaice and common dabs in Loch Ewe. I. Population and food. *J. exp. mar. Biol. and Ecol., 2*: 215–238.

EDWARDS, R. R. C., STEELE, J. H. and TREVALLION, A. 1970. The ecology of plaice and common dabs in Loch Ewe. III. Preypredator experiments with plaice. *J. exp. mar. Biol. and Ecol.*, *4*: 156—173.

GAUDY, R. 1974. Feeding four species of pelagic copepods under experimental conditions. *Mar. Biol. 25*: 125—141.

IVLEV, V. S. 1960. On the utilization of food by planktophage fishes. *Bull. math. Biophys.*, *22*: 371—389.

SHELBOURNE, J. E., BRETT, J. and SHIRAHATA, S. 1973. Effects of temperature and feeding regime on the specific growth rate of sockeye salmon fry (*Oncorhynchus nerka*), with a consideration of size effect. *J. Fish. Res. Bd Can.*, *30*: 1191—1194.

STEELE, J. H. 1966. Experiments on 0-group plaice in underwater tanks. *Coun. Meet. int. Coun. Explor. Sea*, *1966* (C:9): 1—4. 8 fig. [Mimeo.]

STEELE, J. H. and EDWARDS, R. R. C. 1970. The ecology of 0-group plaice and common dabs in Loch Ewe. IV. Dynamics of the plaice and dab populations. *J. exp. mar. Biol. and Ecol.*, *4*: 174—187.

THIJSSEN, R., LEVER, A. J. and LEVER, J. 1974. Food composition and feeding periodicity of 0-group plaice (*Pleuronectes platessa*) in the tidal area of a sandy beach. *Neth. J. Sea Res.*, *8*: 369—377.

WARE, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. *J. Fish. Res. Bd Can.*, *32*: 33—41.

APPENDIX

The resting metabolism expressed in cal/day is (EDWARDS *et al.* 1969, 1970):

$$Q = 0.214 \times 4.8 \times 24 \times W^{0.721}(1 + 0.1\, Q_{10}(t-10)) \text{ where}$$

W is gram wet weight derived from $W = 0.00805\ 1^3$,

4.8 is the oxycalorific coefficient

Q_{10} is in the temperature range 10—15 °C 3.6 and
in the temperature range 15—20 °C 5.6

The calorific value of young plaice is in the range of 4.8—5.2 kcal/g dry weight. Applying a mean value of 5 kcal/g dry weight and a conversion factor of 5:1 for live to dry weight, 1 g wet weight becomes equivalent to 1 kcal.

The daily food intake, I, is:

$$I = \frac{G' + E}{\tau} \text{ modified from WARE (1975)}$$

where G' is the growth expressed in cal/day and
E the metabolism in cal/day including standard metabolism and swimming cost.

$$\tau = p - s$$

where p is the assimilation factor and
s the specific dynamic effect of food (SDA) and loss of chemical energy in the urine. The suggested value of τ is $0.86 - 0.16 = 0.70$ (WARE 1975).

The first hypothesis of EDWARDS *et al.* (1970) suggest that $E = 2Q$. Therefore, according to the above suggested value 0.7 for food efficiency, the daily food intake will be:

$$I_1 = \frac{G' + 2Q}{0.7}$$

According to the second hypothesis of EDWARDS *et al.* (1970), metabolism is a function of the food intake rate. In EDWARDS *et al.* (1970) an average curve for food intake, I_2, is suggested and is indicated on their Fig. 9, page 169. In the present paper an equation for this curve has been calculated to be:

$$Y = 0.8\,X + 0.4 - \frac{4.4 - \sqrt{4.4^2 - 4\,X^2}}{2}$$

where $Y = \frac{I_2}{I_1}$ and

$$X = \frac{G'}{Q}$$

giving $$I_2 = I_1 \left(\frac{0.8\,G'}{Q} + 0.4 - \frac{4.4 - \sqrt{4.4^2 - 4\left(\frac{G'}{Q}\right)^2}}{2}\right)$$

The relationship between food intake and concentration of food is:

$$I = \frac{v\gamma\varrho}{1 + \gamma v h \varrho} \quad \text{(WARE 1975)}$$

where γv is the water volume effectively searched through by the fry,
ϱ is calories of food/litre and
h is the time required to capture and consume one calorie of food.

The calorific value of the food organisms was taken as 5.6 kcal/g dry weight (COMITA and SCHINDLER 1963) and 1 g wet weight became equivalent to 0.72 kcal (IVLEV 1960).

The specific daily growth rate (SHELBOURNE, BRETT and SHIRAHATA 1973) is:

$$\mathrm{SDG} = \frac{(\ln W_1 - \ln W_0)100}{T_1 - T_0}$$

where T is time in days.

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

By

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ABSTRACT

NÆVDAL, G., HOLM, M., LERØY, R. and MØLLER, D. 1978. Individual growth rate and age at first sexual maturity in Atlantic salmon. *FiskDir.Skr.Ser.HavUnders., 16*: 519—529.

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

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

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 and size after one year in the sea. The correlation between age at maturation and earlier growth rate thus seems to be rather small.

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.

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.

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.

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 for 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 *vibrosis.*

Two years 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, (Svanøy foundation) 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 analysis of variance were used (BONNIER and TEDIN 1940).

RESULTS

VARIATIONS 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 presented. Fish mature in 1975 were

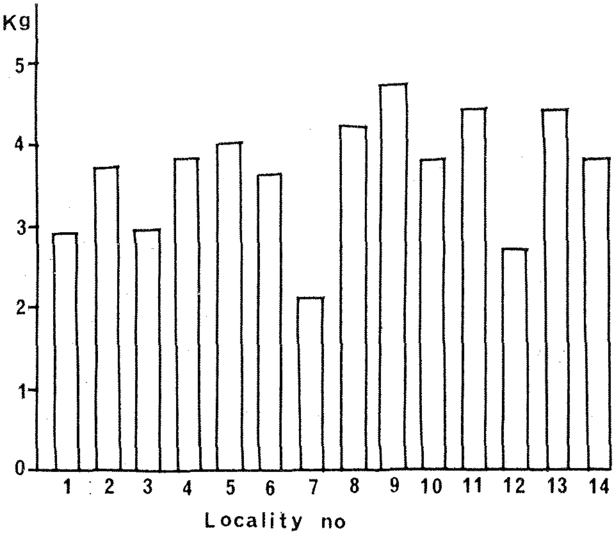

Fig. 1. Mean weights of salmon from different river localities after 25 months in the sea. Each locality represents from two to four sib groups.

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.

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),

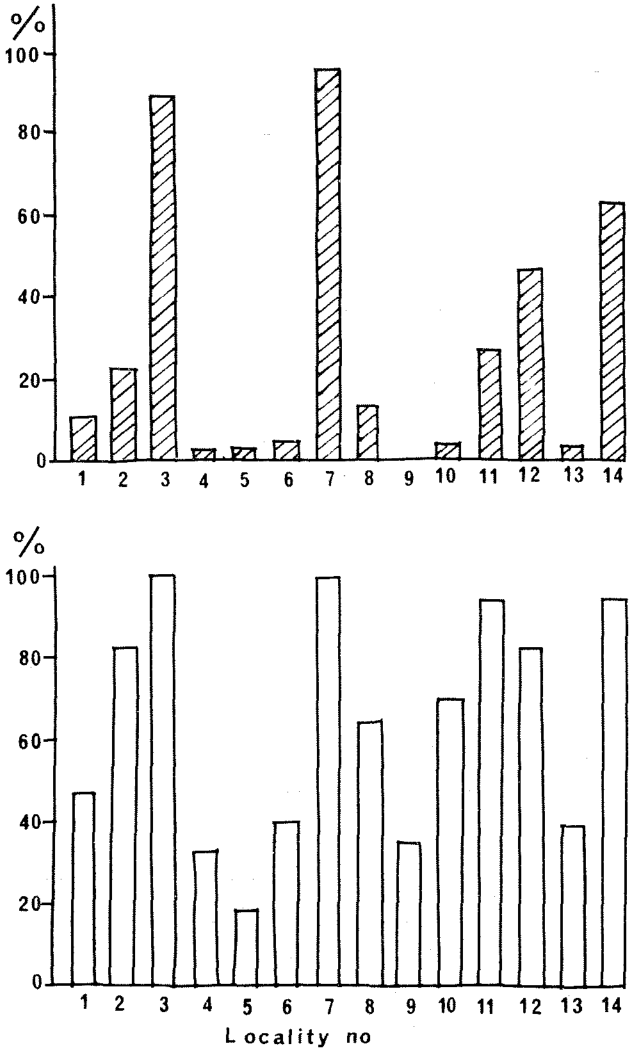

Fig. 2. Per cent mature fish the second (top) and third (below) sea year of salmon originating from different rivers reared under fish farming conditions.

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 coefficients in Table 2 were found.

The correlation coefficients are in the same order of magnitude for individuals within populations as for means of sib groups. After the smolt

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.

Months 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	—

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				—

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 seperated 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.

At smolt 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. Also

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

Source of variation	d. f.	Mean squares	P
Between sex . . .	1	0.80	> 0,2
Within sex	375		
Between river .	26	19.15	< 0,001
Within river . .	349		
Between age at first maturity . .	44	2.64	~ 0,05
Within age	305	1.83	

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.	Mean squares	P
Between sex . . .	1	1.23	> 0,2
Within sex	366		
Between locality	26	37.43	< 0,001
Within locality	340		
Between age at first maturation	45	9.55	~ 0,05
Within age	295	6.14	

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. The conclusion will here

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

Source of variation	d. f.	Mean squares	P
Between sex . . .	1	10.4	> 0,2
Within sex	1143		
Between locality	24	593.4	< 0,001
Within locality	1119		
Between age at maturation	43	27.4	~ 0,05
Within age	1076	19.1	

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 age of which the fish are destined to mature.

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

Source of variation	d. f.	Mean squares	P
Between locality	12	1129.2	< 0,001
Within locality.	1133		
Between age at maturation	24	41.8	> 0,2
Within age	1108		
Between sex ...	27	32.6	~ 0,05
Within sex	1076	19.2	

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 maturation age 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. This 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.

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. The table shows 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

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	Immature	Females		Males	
No.	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

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.

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 variations, 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 are different concerning 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.

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REFERENCES

BONNIER, G. and TEDIN O. 1940. *Biologisk variationsanalys.* Svenska Bokförlaget, Albert Bonnier, Stockholm. 325 p.

CARLIN, B. 1955. Tagging of salmon smolt in the river Lagan. *Rep. Inst. Freshwat. Res. Drottningholm, 36*: 57—74.

HAGER, R. C. and NOBLE R. E. 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., HOLM, M. and KNUTSSON, S. 1977. Erfaring med bruk av ytre merker på oppdrettsfisk. *Fisken og Havet Ser. B, 1977* (1): 1—19.

NÆVDAL, G., HOLM, M., MØLLER, D. and ØSTHUS, O. D. 1975. Experiments with selective breeding of Atlantic salmon. *Coun.Meet.int.Coun.Explor.Sea, 1975* (M 22): 1—10. [Mimeo.]

— , HOLM, M., MØLLER, D. and ØSTHUS, O. D. 1976. Variation in growth rate and age at sexual maturity in Atlantic salmon. *Coun.Meet.int.Coun.Explor.Sea,* 1976 (E 40): 1—10. [Mimeo.]

RITTER, J. A. 1975. Relationship 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 ROHLF, F. J. 1969. *Biometry. The Principles and Practise of Statistics in Biological Research.* W. H. Freemann and Co. San Francisco. 776 p.

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