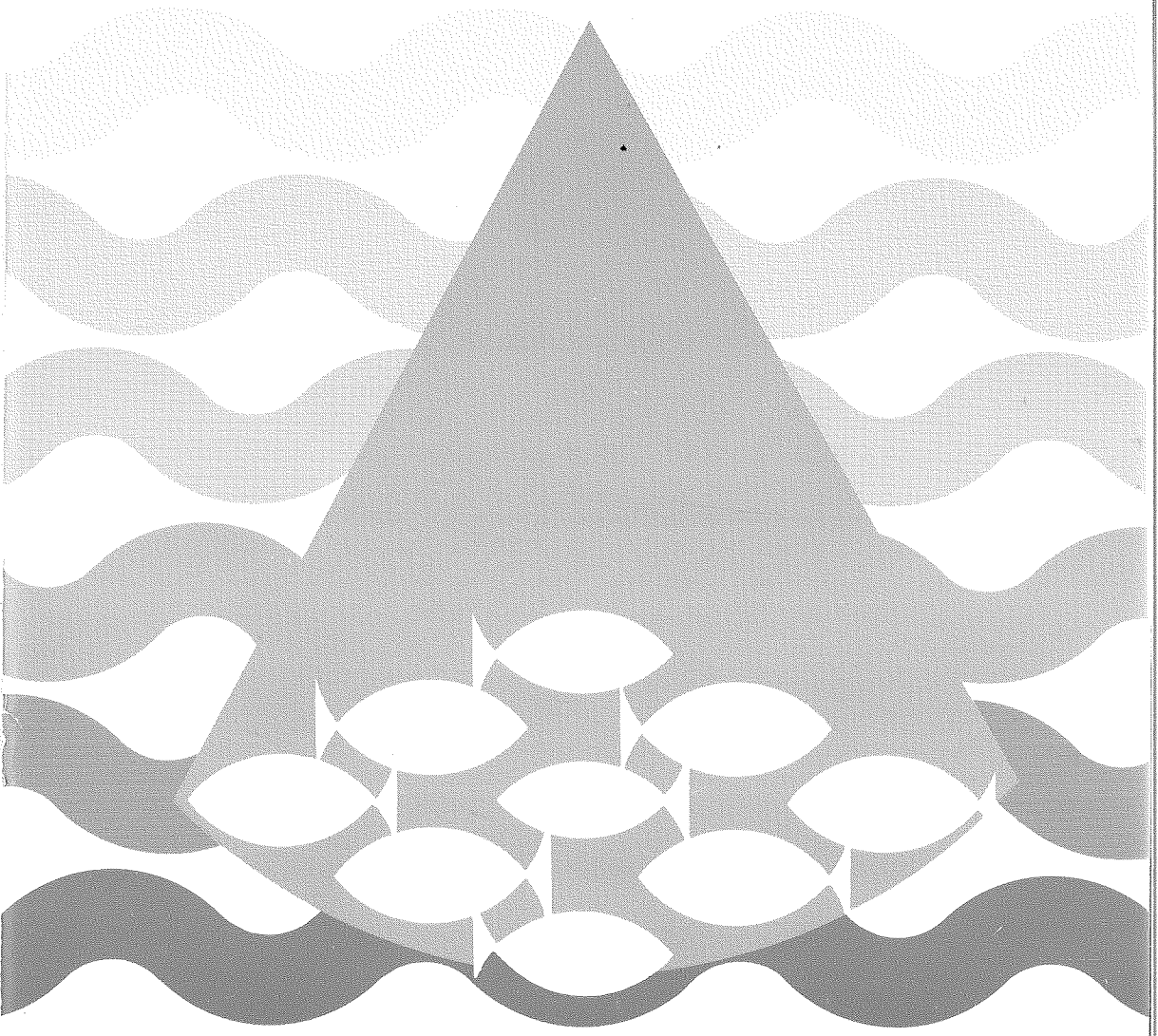
FISKERIDIREKTORATETS SKRIFTER
SERIE HAVUNDERSØKELSER

VOL. 17, No. 9



DIRECTORATE OF FISHERIES, BERGEN, NORWAY
1983

FiskDir. Skr. Ser. HavUnders., *17*: 347–357.

DIGESTION RATE OF FOOD PARTICLES IN THE GUT OF LARVAL HERRING (*Clupea harengus* L.)

By
PETTER FOSSUM
Institute of Marine Research, Bergen, Norway

ABSTRACT

FOSSUM, P. 1983. Digestion rate of food particles in the gut of larval herring. (*Clupea harengus* L). *FiskDir. Skr. Ser. HavUnders.*, *17*: 347–357.

Laboratory experiments with herring larvae (*Clupea harengus* L.) from the local stock in Lindåspollene, north of Bergen, Norway, were performed in the spring of 1978 and 1979. Digestion rates of copepod nauplii and polychaet larvae less than 1.5 hours were found both in first-feeding (8 days post-hatching) and in more advanced (22 days post-hatching) larvae. Bivalve larvae passed undigested through the gut. The rate of passage through the gut varied between 12.5 and 22.5 hours, depending on the type of food organisms. The light conditions in the laboratory seemed to be the most important cause of the observed food selection.

INTRODUCTION

Several studies have been carried out to measure the rate of food passage through the gut of fish larvae. BHATTACHARYYA (1957) dissected the gut of herring larvae during night-time in *in situ* investigations. LAURENCE (1971) fed the larvae coloured microzooplankton. A visual inspection of the continuously feeding larvae gave information of the rate of passage through the larval gut. BLAXTER and HEMPEL (1961) measured the time from the end of feeding to the gut being transparent, and defined this as the rate of passage through the gut of the larvae. WERNER and BLAXTER (1981), using Laurence's method, concluded that the rate of passage is strongly affected by the prey density. Another parameter of importance is the digestion rate of food particles in the gut. If the larvae are continuously feeding, this parameter is dependent on the prey density. WERNER and BLAXTER (1981) observed that some *Artemia* nauplii were still alive after passage through the larval gut, when preyed upon at high prey densities. At lower densities all of the nauplii were digested.

The present experiments were carried out in the spring of 1978 and 1979 in order to measure the digestion rate in the gut of first-feeding (8 days post-hatching) and more advanced (22 days post-hatching) larvae. The rate of food passage and the eventual preference for certain prey organisms were also studied.

MATERIALS AND METHODS

Naturally spawned herring eggs were collected at the spawning grounds of the local herring stock in Lindåspollene (Fig. 1). Eggs were incubated in 8.8 l black glass aquaria with 90 µm mesh size plankton net bottoms. The temperature was kept constant at 9°C. The salinity was a constant 34.5‰, and the light conditions were measured as 10–100 lux during the 1978 experiment, which was performed at the Aquarium in Bergen. After hatching, the yolk sac

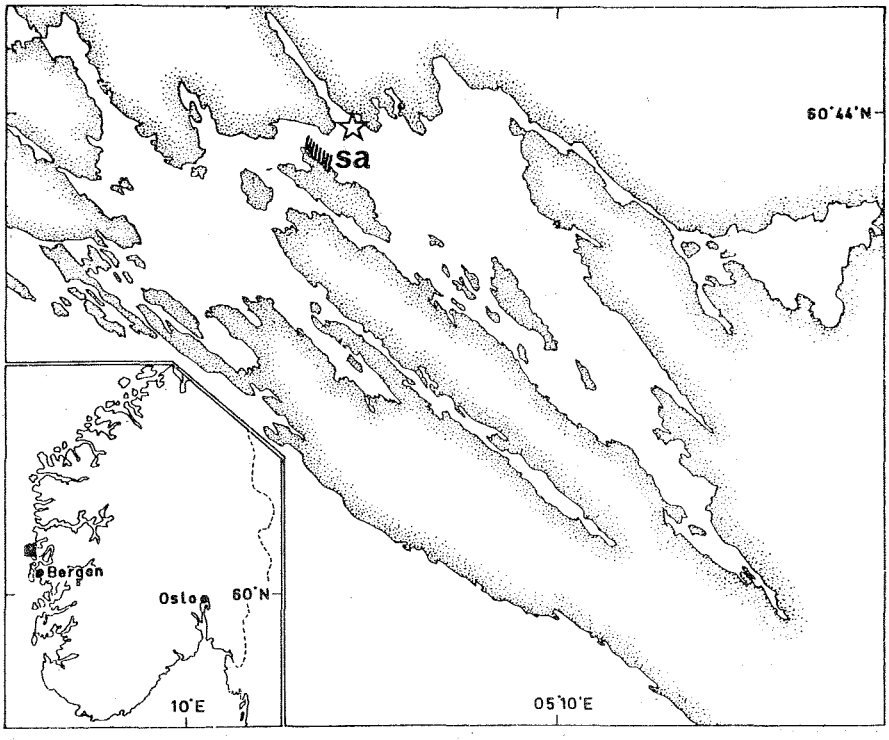


Fig. 1. The location of Lindåspollene with laboratory raft (☆) and spawning area (sa) of the local herring stock.

larvae were put into stock aquaria and fed natural zooplankton to excess from day four after hatching. The larvae were put into the experimental aquaria (Fig. 2) 24 hour prior to the experiment.

In 1979 the experiments were performed on a lab raft at Lindåspollene. The light conditions were the same, while the temperature and salinity, respectively 6°C and 30‰, were lower than in 1978. After hatching, the yolk sac larvae were put into a 400 l stock plastic pen together with natural microzooplankton. To avoid mortality caused by handling, samples of herring larvae in the stock pen were caught with a plastic box during night-time. All the larvae were distributed in the upper 10 cm layer in the plastic pen. They were located with an underwater light. When the plastic box was lowered into the water, the larvae were sucked into it and could be transferred to the

experiment aquarium without being exposed to air or plankton nets. The adaptation time was 14 hours.

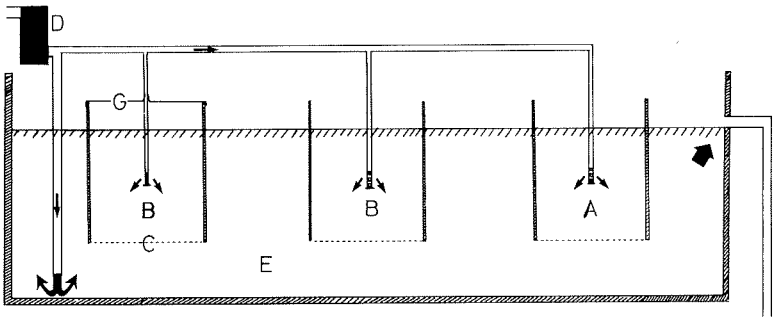


Fig. 2. Experimental equipment. A) Feeding aquarium 8.8 l, B) Digesting aquaria 8.8 l, C) Plankton net bottom, D) Fulflo filter 7 µm, E) Waterbath, G) Black plastic sheet.

During the feeding part of the experiments, the herring larvae were fed copepod eggs and nauplii, copepodites, bivalve larvae and polychaet larvae. The larvae were allowed to feed for one hour. The concentration of microzooplankton was 4–5 per ml both years. After feeding the larvae were transferred to an aquarium with filtered sea water. Ten larvae were preserved each hour, their guts dissected and the digestion rate of the gut content identified (Fig. 3). To avoid the effect of gut clearance, only larvae preserved within 3.5 hours after the end of feeding were used in the feeding incidence (FI%) and selection studies (Prey selection after BERG 1979). The microzooplankton used in the 1978 experiments were collected from 15 meters depth in the Byfjord close to the Institute of Marine Research, Bergen, by the automatic plankton sampler system described in TILSETH, SOLBERG and WESTRHEIM (1981). In 1979 the microzooplankton were collected with the pumping and filtering system shown in Fig. 4.

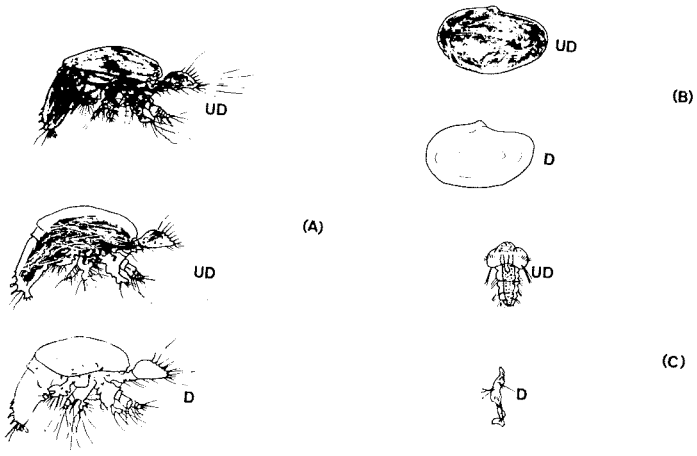


Fig. 3. Rate of digestion: UD) undigested, D) digested. A) Copepod nauplii, B) Bivalve larvae and C) Polychaet larvae.

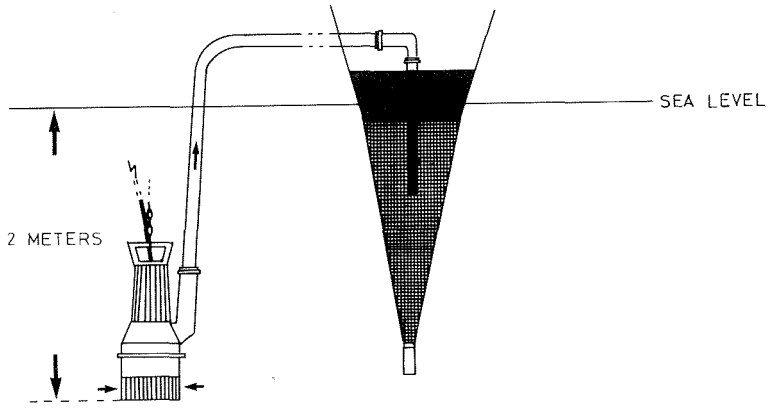


Fig. 4. Pumping and sieving system used in Lindåspollene in 1979. 90 µm plankton net.

RESULTS

The first-feeding larvae reached a standard length of 10.5 mm in 1978 and 10.7 mm in 1979. They weighed 99 and 95 µg, respectively. The more advanced larvae were 12.0 mm long, implying a mean daily growth rate of 0.11 mm from day 8 to day 22 after hatching (Table 1). The gut contents of the larvae preserved before any of the gut content was eliminated, are shown in Table 2. Several food items were found in the guts in 1978. As many as 6 bivalves or 3 copepod nauplii were found in one larvae. The feeding incidence was 63 and 92% in 8 and 22 days old larvae. In 1979 only 9% of the larvae had prey organisms in their guts.

Table 1. Some parameters of the larvae used in the experiments.

Larval age (days after hatching)	Standard length (mm)	Standard deviation (mm)	Dry weight (µg)	Standard deviation (µg)	Numbers of larvae
9 (1979)	10.7	0.60	95	21	160
8 (1978)	10.5	0.45	99	21	152
22 (1978)	12.0	1.06	135	57	130

Table 2. The gut contents of the larvae.

Year	Age (days)	Numbers of larvae	FI (%)	Copepod nauplii			Bivalve larvae			Poly-chaet larvae	Others
				1	2–3	>3	1	2–3	>3		
1978 ...	8	43	63	14	2	0	2	3	7	1	5
1978 ...	22	38	92	15	4	0	6	7	0	13	3
1979 ...	9	80	9	4	3	0	0	0	0	0	0

The percent distribution of different microzooplankton organisms offered to the larvae in the stock aquaria and in the feeding experiments are shown in Table 3. During the first-feeding period (5–9 days post-hatching) the larvae were given 30–40% copepod eggs, 10–30% copepod nauplii, 20% bivalve larvae and 10–30% polychaet larvae. After the experiment with the first-feeding larvae, the larvae were given an increasing amount of copepod eggs (20–60%), 15–30% copepod nauplii, a decreasing amount of bivalve larvae (20–10%) and variable amounts of polychaet larvae.

Table 3. Frequency of different microzooplankton organisms offered to the larvae (1978).

Days after hatching	4	5	6	7	8	9	10	11	12	13	14	15	16	18	19	20	21	22
Copepod eggs . .	.35	.43	.29	.34	.34	.28	.31	.26	.21	.25	.38	.28	.29	.67	.56	.55	.59	.36
Copepod nauplii	.21	.12	.24	.21	.10	.32	.28	.35	.24	.16	.35	.31	.31	.18	.15	.15	.19	.13
Copepodites . . .	.12	.03	.12	.13	.11	.08	.10	.13	.10	.13	.14	.11	.24	.02	.06	.15	.10	.07
Bivalve larvae . .	.23	.22	.02	.23	.20	.23	.13	.17	.12	.20	.08	.24	.10	.11	.13	.10	.02	.14
Polychaet larvae	.08	.08	.32	.09	.25	.06	.14	.07	.33	.24	.05	.04	.04	.01	.09	.04	.09	.28
Others	.01	.01	.01			.03	.04	.02		.02		.02	.02	.01	.01		.01	.02

First-feeding larvae digested 50% of the copepod nauplii in 0.5 hours (Fig. 5) in 1978. Of the nauplii, 80% were digested after 1.5 hours. The 1979 results strengthened the impression of a fast dissolution rate in the first feeding

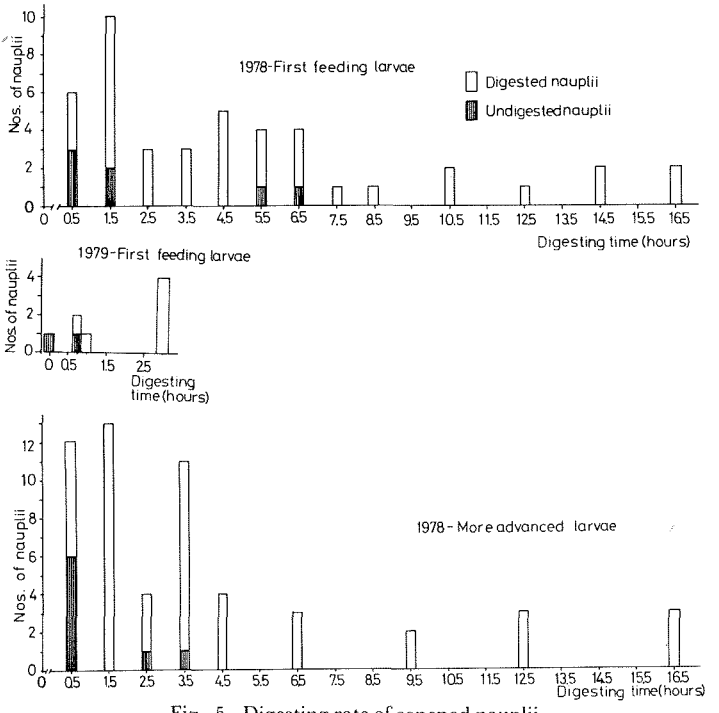


Fig. 5. Digesting rate of copepod nauplii.

larvae in spite of rather scarce material. One undigested copepod nauplii was found in the middle of the feeding period. One out of two nauplii were digested 45 minutes later. At a later time, all of the copepod nauplii were digested.

At 0.5 hours digesting time, 50% of the nauplii in the gut of the more advanced larvae were digested. One hour later all of the copepod nauplii were digested. Still later, two undigested copepod nauplii were found. These were found in guts which contained bivalve larvae.

Most of the bivalve larvae passed undigested through the gut (Fig. 6). A few empty bivalve shells were found after 3–4 hours digesting time in both first-feeding and more advanced larvae in 1978. Polychaet larvae were always found as remains in the larvae gut (Fig. 7).

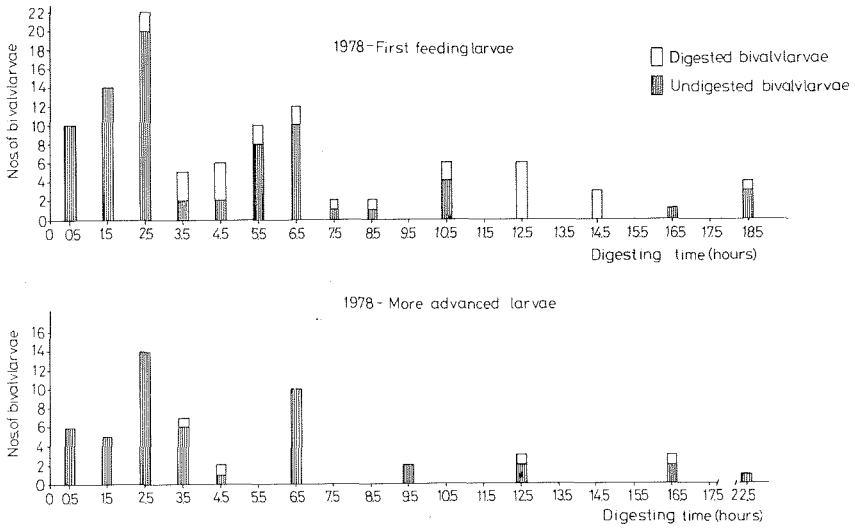


Fig. 6. Digesting rate of bivalve larvae.

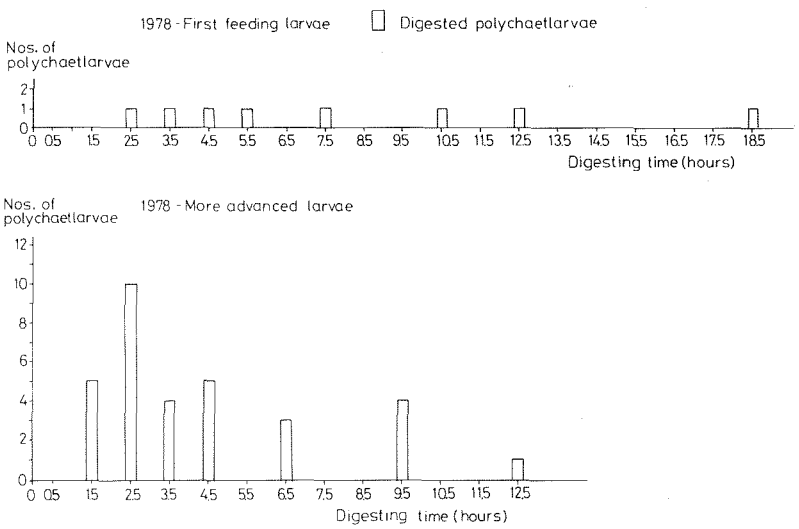


Fig. 7. Digesting rate of polychaet larvae.

The larvae showed a positive selection for copepod nauplii and bivalve larvae. But they avoided copepod eggs and copepodites (Figs. 8 and 9). The first-feeding larvae took just small amounts of polychaet larvae, while the more advanced larvae had the same frequency of polychaet larvae in the gut as were present in the food.

The time of passage through the gut was 16.5 hours for copepod nauplii, 22.5 hours for bivalve larvae and 12.5 hours for polychaet larvae. However, most of these particles pass faster through the gut as indicated by the drop in the number of food particles in the gut after 2.5–4.5 hours (Figs. 5, 6 and 7).

DISCUSSION

The larval period is one of fast growth and high mortality. Prey availability is generally considered as the most important regulator of recruitment (CUSHING 1976). Reduced food availability would most probably result in starvation and concequently prolong the larval period during which the larvae are most vulnerable to predation. Copepod nauplii dominate the diet of most fish larvae (HUNTER 1980), so also in herring larvae, but they feed on many other organisms (BLAXTER 1965), and the composition of the diet is another regulatory mechanism. The present material shows that herring larvae have a low digestibility of bivalve larvae. Then high concentrations of this food item can be dangerous or even fatal to the larvae, resulting in starvation or a prolonged larval period.

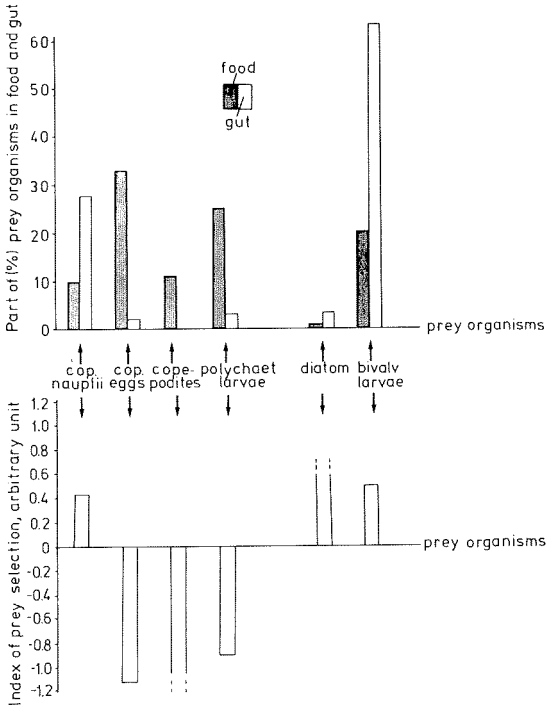


Fig. 8. Prey selection in first-feeding larvae (8 days post-hatching).

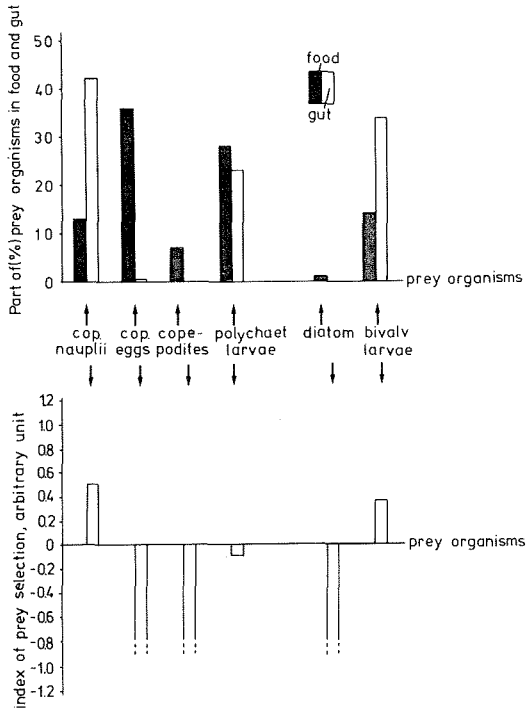


Fig. 9. Prey selection in more advanced larvae (22 days post-hatching).

The fast digestion rate of copepod nauplii in the gut of herring larvae corresponds with results of TILSETH (pers. comm.) on first-feeding cod larvae. TILSETH stresses that copepod nauplii are completely digested in 0.5 hours. In my material the more advanced larvae digested the copepod nauplii in one hour. The results from the experiments with first-feeding larvae are not as clear, but the 1979 experiment strengthened the impression that also the first-feeding larvae are able to digest the nauplii in one hour.

Polychaet larvae are dissolved in a short time and can be an important food organism of herring larvae from an age of two to three weeks after hatching.

The difference in time of passage through the digestive tract between the present results and results reported by other authors are shown in Table 4.

Table 4. Time of passage of food particles through the digestive tract of two different fish larvae.

Source	Year	Fish	Temperature (°C)	Time (hours)
Kurata	1959	Herring	9	12–20
Blaxter & Hempel	1961	Herring	8–13	4–6
Rosenthal & Hempel	1969	Herring	10	4–10
Werner & Blaxter	1981	Herring	9	3
Present results	1981	Herring	9	12.5–22.5
Laurence	1977	Winter flounder	8	6

The present experiment was primarily designed to measure the digestion rate of food particles in the gut of herring larvae, not the time of passage. The reasons for the extended time of passage observed in the present experiment, compared to others, can be the high impact of bivalve larvae, which are almost indigestible, and the fact that no new food items were ingested during the digesting period. Probably the best method to study the larval gut clearence rate is the one described by LAURENCE (1971). In continuously feeding larvae, newly taken food items can press digested ones out of the gut. This will have a great effect on the passing time. Visual investigations of the gut (BLAXTER and HEMPEL 1961) do not show the empty shells of the prey organisms, and an underestimation of the passing time will be the result.

Herring larvae are generalists, and a wide sprecter of microzooplankton organisms are found in their guts (BLAXTER 1965). The larvae do, however, prefer special food items, illustrated by the positive selection for copepod nauplii and bivalve larvae in the present experiment (Figs. 8 and 9).

The mouth size of the larvae will determine the size of the prey organisms the larvae can take (WIBORG 1948, BLAXTER 1965). In the present experiment the light condition in the laboratory can be the underlying cause of the observed food selection. Although the light conditions are well above the light threshold for feeding of herring larvae, 0.1 lux (BLAXTER 1966), small and transparent plankters like copepod eggs are neglected. ELLERTSEN *et al.* (1980) observed the highest feeding incidence of cod larvae on *Peridinium trochoideum* at 1000 lux, while the highest feeding incidence on easily detectable *Artemia* nauplii was 1.4 lux. SCHNACK (1972) observed a preference for certain size groups, and plankters which showed a contrast against the background. WERNER and BLAXTER (1979) state that herring larvae prefer easily detectable *Artemia* to transparent natural plankton. Mobile food organisms such as copepodites and copepod nauplii could probably be able to avoid the larvae in good light conditions, but not under lower light intensities. Under such conditions, for example, in the laboratory or at dusk conditions *in situ,* the larvae with its relatively well developed vision (BLAXTER and HOLLIDAY 1963) will search for easily visible particles, nauplii or coloured bivalve larvae. Under improved light conditions the larvae will take immobile transparent plankters and prey organisms of smaller size and lesser mobility.

Observations of the food selection abilities of herring larvae *in situ* (BJØRKE 1978) indicate a positive selection for copepod eggs, while the present results show the opposite. The reason might be different light conditions in the field and laboratory investigations.

Of the first-feeding 67% and 92% of the more advanced larvae had food particles in the gut after a one-hour feeding time in high prey concentrations (1978). In 1979 only 9% of the first-feeding larvae had food particles in the gut. The difference in feeding incidence the two subsequent years can be due to the different life history of the two larval cohorts. In 1978 the larvae were stored in

a similar aquarium as the experimental ones. In 1979 the larvae were stored in a plastic pen. They were captured 14 hours before the start of the experiment. There were no signs of capture or handling mortality, but the transfer to a new environment could have stressed the larvae and resulted in a low feeding incidence.

The feeding incidence of 67 and 92% observed in the 1978 experiment is high compared to the maximum of 40% in first-feeding larvae from field investigations at Lindåspollene in the same year (FOSSUM and JOHANNESSEN 1979). ØIESTAD and MOKSNESS (1979) found 63% feeding incidence in 17 days old larvae in a concrete enclosure experiment, and 97% in 24 days old larvae in a plastic pen experiment. The present experiment agrees more closely with these results. Herring larvae may partially or completely void their digestive tract when captured or preserved (ROSENTHAL 1969, HAY 1979). In field studies the larvae are often captured in nets. When the larvae are exposed to the hauling equipment for a long time, they will void their digestive tracts. This will happen to a greater extent in field investigations than in plastic pen and laboratory experiments due to different sampling methods.

The digestion rate in the gut of fish larvae can easily be measured with the present experimental design. The design of the experiment was less satisfying in measuring the time of passage through the gut. Continued feeding will give the most reliable estimates of the gut clearence rate. Food selection abilities can be studied, but the selection is easily influenced by variations in abiotic factors as the light conditions in the laboratory. Additional work where the larvae are fed coloured microzooplankton (LAURENCE 1971) at different food densities and where the gut is dissected according to the present method, can give more informtion about the digestive process in first-feeding larvae.

REFERENCES

BERG, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Mar. Biol., 50*: 263–273.

BHATTACHARYYA, R. N. 1957. The food and feeding habits of larval and postlarval herring in the northern North Sea. *Mar. Res. Scot., 3*: 1–14.

BJØRKE, H. 1978. Food and feeding of young herring larvae of Norwegian spring spawners. *FiskDir. Skr. Ser. HavUnders., 16*: 405–421.

BLAXTER, J. H. S. 1965. The feeding of herring larvae and their ecology in relation to feeding. *Rep. Calif. coop. oceanic. Fish Invest., 10*: 79–88.

– 1966. The effect of light intensity on the feeding ecology of herring. P. 393–409 in BAINBRIDGE, R., EVANS, G. C. and RACKHAM, O. ed. *Light as an ecological factor*. Blacwell Sc. Publ., Oxford.

BLAXTER, J. H. S. and HEMPEL, G. 1961. Biologische Beobachtungen bei der Aufzucht von Heringsbrut. *Helgoländer wiss. Meeresunters., 7*: 260–283.

BLAXTER, J. H. S. and HOLLIDAY, F. G. T. 1963. The behaviour and physiology of the herring and other clupeoids. *Adv. mar. Biol. 1*: 261–393.

CUSHING, D. H. 1976. Biology of fishes in the pelagic community. P. 317–340 in CUSHING, D. H. and WALSH, J. J. *The ecology of the seas*. W. B. Saunders Co., Philadelphia.

ELLERTSEN, B., SOLEMDAL, P., STRØMME, T., TILSETH, S., WESTGÅRD, T., MOKSNESS, E. and ØIESTAD, V. 1980. Some biological aspects of cod larvae (*Gadus morhua* L.). *FiskDir. Skr. Ser. HavUnders., 17*: 29–47.

FOSSUM, P. and JOHANNESSEN, A. 1979. Field and laboratory studies of herring larvae (*Clupea harengus* L.). *Coun. Meet. int. coun. Explor. Sea, 1979* H:28): 1–17. [Mimeo.]

HAY, D. E. 1979. The effect of capture and fixation on gut contents and body size on Pacific herring larvae. *Int. Coun. Explor. Sea Symp. The Early Life History of Fish, 1979* (PE: Poster 6).

HUNTER, J. 1980. The feeding behaviour and ecology of marine fish larvae. *International Center for Living Aquatic Resources Management Conference Proceedings, 5*: 287–330.

KURATA, H. 1959. Preliminary report on the rearing of herring larvae. *Bull. Hokkaido reg. Fish. Res. Lab., 20*: 117–138.

LAURENCE, G. C. 1971. Digestion rate of larval largemouth bass. *N.Y. Fish game J. 18* (1): 52–56.

— 1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder. *Pseudopleuronectes americanus,* larvae during the period from hatching to metamorphosis. *Fishery Bull. Fish Wildl. Serv. U.S. 75*: 529–546.

ROSENTHAL, H. 1969. Verdauungsgeschwindigkeit, Nahrungswahl und Nahrungsbedarf bei den Larven des Herings (*Clupea harengus* L.). *Ber. dt. wiss. Kommn. Meeresforsch., 20* (1): 60–69.

SCHNACK, D. 1972. Nahrungsøkologische Untersuchungen an Heringslarven. *Ber. dt. wiss. Kommn. Meeresforsch., 22* (3): 273–343.

TILSETH, S., SOLBERG, T. S. and WESTRHEIM, K. 1981. Sublethal effects of the water-soluble fraction of Ekofisk crude on the early larval strages of cod (*Gadus morhua* L.). *Coun. Meet. int. Coun. Explor. Sea, 1981* (E:52): 1–21. [Mimeo.]

WERNER, R. G. and BLAXTER, J. H. S. 1979. The effect of prey density on mortality, growth and food consumption in larval herring (*Clupea harengus* L.). *Int. Coun. Explor. Sea Symp. The Early Life History of Fish, 1979* (FM:4): 1–11. 6 tab, 4 fig. [Mimeo.]

— 1981. The effect of prey density on mortality, growth and food consumption in larval herring (*Clupea harengus* L.). *Rapp. P.-v. Réun coun. int. Explor. Mer, 178*: 405–408.

WIBORG, K. F. 1948. Investigations on Cod Larvae in Coastal Waters of Nothern Norway. *FiskDir. Skr. Ser. HavUnders., 9* (3): 1–27.

ØIESTAD, V. and MOKSNESS, E. 1979. Study of growth and survival of herring larvae (*Clupea harngus* L.) using plastic bag and concrete enclosure methods combined. *Int. coun. Explor. Sea Symp. The Early Life History of Fish, 1979* I:2): 1–26. [Mimeo.]

Received 14 September 1982
Printed 15 June 1983

FiskDir. Skr. Ser. HavUnders., *17*: 359–366.

SOURCES OF VARIATION IN WEIGHT AND LENGTH OF ATLANTIC SALMON

By
GUNNAR NÆVDAL, RITA LERØY and DAG MØLLER
Institute of Marine Research, Bergen, Norway

ABSTRACT

NÆVDAL, G., LERØY, R. and MØLLER, D. 1983. Sources of variation in weight and length of Atlantic salmon. *FiskDir. Skr. Ser. HavUnders.*, *17*: 359–366.

Variances of weight and total length of four year classes of farmed Atlantic salmon after two years in the sea were distributed on strain, family, maturing/immature (after two winters) and sex. Highly significant variations between families were found. Also significant variations due to sex and stage of maturity were evident. On an average males were heavier and longer than females, and maturing fish on an average were heavier and showed higher condition than immature within most groups. Differences in length between maturing and immature fish were not obvious. The higher condition factors of mature than immature fish were not caused by higher gonad weights.

INTRODUCTION

For genetic improvement of salmonids for fish farming, the traits of growth rate and age at first maturity are of special interest. Concerning age at first maturity, it is important to omit from the broad stock salmon (*Salmo salar*) maturing after one sea-winter (grilse) and rainbow trout (*Salmo gairdneri*) maturing during their second year of life. It is widely discussed within the fish farming industry whether it is desirable to select for still higher age at first maturity, i.e., for salmon maturing after three sea-winters or later. The advantages are that large fish (15–20–25 kgs) may be reared, if wanted, and that the slaughtering may be conducted independently of the breeding season, hence is better adapted to the market situation. The main drawback will be production and handling of the brood stock, because in commercial fish farming it seems that the maturing process is more irregular for old spawners, and the egg quality is lower and more variable. Fish mortality due to handling of large fish is also a problem.

In rainbow trout it was found that fish maturing at 2+ were on average significantly larger than their immature sibs, and this difference could be traced back one year on individually tagged fish (NÆVDAL *et al.* 1979 b and unpublished). In a limited material of individually tagged salmon a similar, but not very obvious, tendency was observed (NÆVDAL *et al.* 1978). Earlier reports have suggested different growth rate between males and females.

In the present report interdependence of growth rate, sex and age at first maturity is studied on four year classes of sib groups of salmon. The study is part of a more extensive study on genetic variation in quantitative traits of salmonids. Observations from commercial production of salmon are also included.

MATERIALS AND METHODS

The present study is based on year classes of salmon hatched in the years 1972, 1973, 1974 and 1975. The rearing methods are described in earlier reports (NÆVDAL *et al.* 1978, 1979 a) where the year classes 1972 and 1974 were described. The 1973 and 1975 year classes were made up in a similar way, except that the 1975 year class contained more sib groups from reared parents, while the other year classes mostly were based on brood stocks caught in rivers. Growth rates were recorded by length measurements during the rearing periods of half year or one year intervals. Maturing fish were recorded during the second sea-year. After two years in the sea the fish was slaughtered, except about 20 fish which were selected as brood stock from each sib group of the 1972 and 1973 year class. Lengths, weights, sex and stage of maturity were recorded for killed fish. The sex of immature fish could not be determined on the live broodstock fish. As the live fish were selected for size, no grouping according to sex was made on the first two year classes, because such data would have been biased. In the two last year classes all fish were killed because they were infected by IPN-virus and could not be used as broodstock. In the present analyses weight and total length were used as representing size. In order to confirm the results from the experimental fish, two groups of commercially reared salmon (A/S Bolaks, Eikelandsosen) were sampled. These fish were killed so early in the year (March) that the difference between immature and maturing fish could not be detected by visual inspection, but they gave, however, very good data for studying the relationship between sex and size. Standard analysis of variance were used for the analyses.

RESULTS

COMMERCIALLY REARED SALMON

Mean length and weights for the two groups of commercially reared fish are shown in Table 1. In both groups the males are on an average 0.8–1 kg heavier than the females. The difference between the two groups is probably due to their different origin. Group A was sorted out for high presmolt growth rate and B was the smaller ones when grading after one summer. This may also explain the difference in the proportions of grilse and sex ratio as higher presmolt growth rate for males than females is indicated and thus will give sex

ratio deviating from 1:1 proportions. The grilse were mainly males, and higher proportions of grilse may in this connection only indicate higher proportions of presmolt fast growing males. However, also the later maturing males showed significantly higher growth rate than the females.

Table 1. Observations from two groups of commercially reared salmon in the same plant after about 21 months in the sea. The grilse were omitted when the means were calculated.

Group	Mean lengths (cm)		Mean weights (kg)		Grilse %	Sex ratio
	♂	♀	♂	♀		♂ : ♀
A	78.1	73.9	6.0	5.0	~ 10	61:39
B	80.9	76.4	6.4	5.6	< 1	47:53

EXPERIMENTAL FISH

Weights

The weight data showed extensive variations in the total material. To reveal the sources of variation, the data were analysed by nested analyses of variance. The analyses are shown in Table 2.

In the three first year classes there is a significant influence of locality or sib groups within localities. This represents the genetic variation of the total experimental populations. The variation between sib groups within localities may be used for calculating heritability factors. In the present analyses reliable estimates cannot be made because the material includes both sib groups and groups of half sibs. Evidently there is much genetic variation which may be utilized for selective breeding. However, the main purpose of the present report is to study the influence of sex and age of maturation on growth rate. In order to eliminate the genetic effect on growth rate, the analysis of variance was made on a within-sib-groups-basis.

Significant differences were found between those fish maturing during their third year in the sea and those maturing later. From the calculated means it was clear that the maturing fish were on average the greater, although immature fish were also found among the greatest individuals. Similarly, there was a significant difference between the two sexes. On an average both among the maturing as well as among the immature fishes the males were the biggest.

The results correspond to the results of the commercially reared salmon, although the effects of sex were not so evident in the experimental fish.

However, some exceptions to the overall rules were observed. In some groups, especially from some river populations, there were very small differences between males and females, and occasionally females were on average the greatest. Concerning age at maturity, also some exceptions were observed.

Table 2. Analysis of variance of salmon weights distributed on localities, sib groups and mature/immature after two winter in the sea.

Source of variation	1972 year class			1973 year class			1974 year class			1975 year class		
	d.f.	Mean square	P	d.f.	Mean square	P	d.f.	Mean square	P	d.f.	Mean square	P
Between locality	10	37,9	<0.05	5	39.4	>0.05	10	86.0	<0.01	4	227.9	>0.05
Between sibgroups	21	9.9	>0.05	10	30.0	<0.01	29	4.2	>0.2	29	84.6	>0.05
Between mature/ immature.....	32	9.0	<0.01	16	5.3	~0.05	39	29.3	<0.01	31	42.8	<0.01
Between sex.....							76	4.3	<0.01	68	4.9	<0.01
Residual.....	1 198	1.6		695	2.7		1 762	1.1		2 922	1.8	

Table 3. Analysis of variance of salmon lengths distributed on localities, sibgroups and mature/immature after two winters in the sea.

Source of variation	1972 year class			1973 year class			1974 year class			1975 year class		
	d.f.	Mean square	P	d.f.	Mean square	P	d.f.	Mean square	P	d.f.	Mean square	P
Between locality	10	16029	<0.01	5	294.4	>0.2	10	1877.0	<0.01	4	3926.3	>0.05
Between sibgroups	21	225.0	>0.05	10	504.6	~0.01	29	301.1	<0.01	29	736.0	<0.01
Between mature/ immature.....	32	123.3	<0.05	16	112.6	<0.05	39	102.5	>0.2	31	176.0	>0.05
Between sex.....							76	118.1	<0.01	60	171.3	<0.01
Residual.....	1 198	72.8		695	50.4		1 762	37.4		2 922	30.2	

Lengths and conditions

Similar analysis of variance concerning total length were also carried out (Table 3). The effects of locality or family within locality were significant in all year classes. However, the effect of maturation was much less evident on lengths than on weights, as significant differences ($P < 0.05$) were found only for two year classes. This probably reflect the fact that in nearly all groups the calculated condition factors were higher for maturing than for immature fish of both sexes. No special gonad weights were recorded, but the differences cannot be due to gonad weight at this stage because the gonads were just starting to develop when the samples were taken, and they were negligible compared to the total weights of the fish. The differences in condition thus reflect real differences in body proportions between maturing and immature fish. According to lengths there was a significant sexual difference.

Co-variations within families

The relationship between mean size of males and females, respectively maturing/immature fish within sib groups were also studied by calculating correlation and regression coeffisients between mean lengths and weights. The results are summarized in Table 4. In all but one case, high and very significant correlations were found showing that in spite of the clear difference between maturing and immature fish and males and females respectively, the sib groups possessed inherent growth characteristics.

Table 4. Correlation coeffisients (above diagonal) and regression coeffisients (below diagonal) between mature and immature males and females within salmon sib groups. Left:mean weights, right: mean lengths.

Sex and stage of maturity	Immature			Maturing		
	♂	♀	Sum	♂	♀	Sum
Immature ♂		0.93/0.93		0.77/0.19		
♀	0.64/0.62				0.81/0.80	
Sum						0.75/0.81
Maturing ♀	0.80/0.0				0.82/0.87	
♀		0.78/0.85		0.66/0.73		
Sum			0,87/0,96			

DISCUSSION

This paper mostly deals with variation in growth rate in farmed Atlantic salmon not directly genetically controlled. The main purpose of the study is to reveal genetic variation to be utilized for selective breeding, but information on non genetic variation also are important for understanding the variations observed.

In a previous paper NÆVDAL *et al.* (1978) found small, although statistically significant, variations in growth rate related to age at first maturity on a limited number of individually tagged fish (partly in the same material as the 1972 year class on the present study). However, in that study also grilse were included and found responsible for the main part of the variation. Effect of sex was not clear.

In a comparative study of subsequent growth rate of one and two year smolt of the same sib groups (NÆVDAL *et al.* 1979) the incidences of grilse were highest among the one year smolt (the fast growing individuals at the pre-smolt stage), but in contrast to the results from the commercially reared salmon in the present study, no surplus of males could be found among the faster growing fish on the pre-smolt stage. DALZIEL and SHILLINGTON (1966), however, found surplus of males among one year smolt of Atlantic salmon, and HAGER and NOBLE (1976) observed the same tendency in coho salmon, *Onchorynchus kisutch*. In three year old fish, however, the same authors found nearly the same mean lengths for males and females, but there was a significant higher variance for males than for females as both the biggest and smallest fish usually were males. Corresponding weight data showed slightly higher mean weight for females than for males.

KATO (1975) found that the mean body length of maturing rainbow trout was larger than for the immatures before the spawning season, and NÆVDAL *et al.* (1979 b) and NÆVDAL, LERØY and MØLLER (1981) found the same both in weight and length on individually tagged fish. Fish maturing at 2+ (about 31 months) were bigger than those maturing later even at 18 months of age. The effect of sex on growth rate was not very clear. It could, however, be revealed when variations due to other known sources were excluded.

However, the results of the present report contradict several investigations on growth of wild salmon. By backcalculating of growth zones in the scale of Scottish and Canadian salmon, COLDERWOOD (1925) and MENZIES (1925) found that the earliest maturing fish showed lower growth rate during the first seayears than the later maturing fish, i.e. salmon maturing as two-winters fish were shorter than salmon maturing as three-winters fish at the end of their second winter in the sea. Also ALLEN, SAUNDERS and ELSON (1972) found that the length of two-winters spawners were on an average less than the corresponding length of three-winters or older spawners after two years at sea, because the growth rate of the spawners already had slowed down at that time. Similarly, SCHAFFER and ELSON (1975) found a positive correlation between mean age at first spawning and marine growth rate after the grilse stage on a large material of wild Canadian salmon, i.e. high growth rate subsequent to the grilse stage is assosiated with delayed reproduction.

This discrepancies of the results of observation of wild salmon growth rate and the main results in the present study, may reflect differences between natural and fish farming conditions. Reared fish are usually given food in excess, and the fish are prevented from migration, and thus probably the

growth patterns are influenced. Differences in growth patterns between strains may also be an explanation, and this is indicated in the present study.

The obvious variation between strains or sib groups is in accordance with results of GUNNES and GJEDREM (1978) who found great variations in weights and lengths between strains from Norway, and also quite high heritability factors for these traits on a within-strain-basis.

ACKNOWLEDGEMENT

The authors are grateful to the staff of the research station at Matre, to the Svanøy Foundation for keeping the fish during the rearing periode, and to several river owners and commercial fish farms for providing the material.

REFERENCES

ALLAN, K. R., SAUNDERS, R. L. and ELSON, P. F. 1972. Marine growth of Atlantic salmon (*Salmo salar*) in the Northwest Atlantic. *J.Fish.Res.Bd Can., 29*: 1979–1980.

CALDERWOOD, W. L. 1925. The relation of sea growth and spawning frequency in *Salmo salar*. *Proc.R.Soc.Edinb. 44*: 143–148.

DALZIEL, J. A. and SHILLINGTON, K. G. 1961. Development of a fastgrowing strain of Atlantic salmon (*Salmon salar*). *Can.Fish Cult., 30*: 57–60.

GUNNES, K. and GJEDREM, T. 1978. Selection experiments with salmon. IV. Growth of Atlantic salmon during two years in the sea. *Aquaculture, 15*: 19–33.

HAYER, 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. *ProgveFish Cult. 38*: 144–146.

KATO, T. 1975. The relation between the growth and reproductive characters of rainbow trout, *Salmo gairdneri*. *Bull.Freshwat. Fish.Res.lab., Tokyo, 25* (2): 83–115.

MENZIES, W. J. M. 1925. Salmon (*Salmo salar*) of the river Moisie (Eastern Canada). *Proc.R.Soc. Edinb., 44*: 334–345.

NÆVDAL, G., BJERK, Ø., HOLM, M., LERØY, R. and MØLLER, D. 1979 a. Growth rate and age at sexual maturity of Atlantic salmon smoltifying aged one and two years. *FiskDir.Skr. Ser. HavUnders., 17*: 11–17.

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.

NÆVDAL, G., HOLM, M., LERØY, R. and MØLLER, D. 1979 b. Individual growth rate and age at sexual maturity in rainbow trout. *FiskDir. Skr. Ser. HavUnders., 17*: 1–10.

NÆVDAL, G., LERØY, R. and MØLLER, D. 1981. Variation in growth rate and age at first maturation in rainbow trout. *FiskDir. Skr. Ser. HavUnders., 17*: 71–78.

SCHAFFER, W. M. and ELSON, P. F. 1975. The adaptive significance of variation in life history among local populations of Atlantic salmon in North America. *Ecology, 56*: 577–590.

Received 14 September 1982
Printed 15 June 1983