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International Council for the Exploration of the Sea

C.M. 1975/M:20
Anadromous and Catadromous Fish Committee
Ref: Fisheries Improvement

SEAWATER ADAPTATION IN ATLANTIC SALMON (SALMO SALAR) AT DIFFERENT EXPERIMENTAL TEMPERATURES AND PHOTOPERIODS

BY

Sten Knutsson and Torfinn Grav[x)]

INTRODUCTION

The freshwater life of a young salmon ends after a variable number of years in the seaward migration of the smolt. Among the most obvious changes occuring in the smoltifying salmon are the apperance of a silvery colour and a modification of body shape. The period of smoltification normally occurs in the spring.

The existence of marked difference in salinity tolerance of the parr and the smolt has been observed many times since the second half of the previous century (Bert, 1871) and has been abundantly confirmed since that time (KOCH 1968).

PARRY (1960) concluded from his experiment with Atlantic salmon, that osmoregulation and survival were better in the larger fishes. However, to consider that salinity resistance and the osmoregulatory capacity of the young salmon is dependent on a single correlation with size would be an over-simplification. There are considerable seasonal fluctuations in the absolute value of the degree of resistance which effect all sizes simultaneously. All other conditions being equal, the mineral regulation capacities, and therefore the seawater tolerance of young salmon, are far more developed in the spring (KOCH 1968).

HOAR (1965) suggests that photoperiod has a regulatory effect on the smoltification process in salmonid fishes. Experiments with

x) Institute of Marine Research
Directorate of Fisheries
Bergen, Norway.

Atlantic salmon (SAUNDERS and HENDERSON 1970) and Steelhead trout (WAGNER 1974) show that photoperiod manipulation exerts a regulatory effect on parr-smolt transformation.

This laboratory study was carried out to investigate the effect of gradually increasing day length at different temperatures on the smolting process and on growth rate of Atlantic salmon during smolting.

MATERIALS AND METHODS

Experimental fish

Hatchery-reared yearling salmon from the research station, Fisk og Forsøk, N-5198 Matredal, belonging to the Institute of Marine Research, Bergen, were brought to the laboratory on September 21 in 1974 and held in fresh water at about 12°C and in natural photoperiod. The fishes were hatched on March 18, 1974 and descended from fish, that were caught in the river Suldalslågen on the west-coast of Norway inside Haugesund. In their natural environment fish from this population starts to migrate to sea in the beginning of May and migration continue till about the middle of June. The migration starts at a water temperature of 4-5°C and the migrators are usually 13 to 15 cm long and about 3 years old.

Fish-Holdinh Conditions

In September 1975 salmon-parr were placed in growth tanks, that were modified versions of a model developed by BRETT et.al. 1971. Each tank had a volume of 175 l and the water depth was about 40 cm. Flow rates of freshwater were maintained at about 5 liters/min. The oxygen saturation of the water varied between 90 and 100 per cent and pH was held at about 6.7. The tanks were self-cleaning through a pipe-system in the center. The water supply maintained a currant that elicited a positive rheotactic response by the salmon and improved feeding conditions by dispersal of the fish throughout the tank and by imparting movement to the food.

Fish were fed a commercially prepared dry pellet through automats. The automats were switched on at the same time as the light. Fish were generally fed to repletion.

Each tank were equipped with glass-fiber hoods, where illumination was provided by a daylight-type tube rated at 20 w, and placed behind a dim plexiglass disc centered about 6 cm over the water surface of each tank. Lights were controlled by manual adjustments of timers to produce an increment every 3 days. Lights went on or off suddenly; no attempt was made to simulate dawn or dusk conditions. Light intensity at the water surface was 800 lux, 19 cm above the bottom 430 lux and at 10 cm above the bottom 250 lux.

The tanks were secured against any light coming from outside into the tanks through black paint on the outsides of the tanks, rubber lists between tank and hood and a light-proof black plastic sheet over the whole tank.

The tanks' ability not to let light in were tested by placing each tank in a completely dark room, thereafter a 100 w bulb was placed in the tank and if a human eye could not detect any light coming out through the tank, the tank was said to be light-proof.

Experiment

Fig. 1 shows the photoperiod for Bergen from June 1974 to June 1975 and the three experimental photoperiods L_1, L_2 and L_3. L_1 was started up on September 25, L_2 on November 5 and L_3 on December 20. For each photoperiod there were three temperature groups, $7 \pm \frac{1}{2}$, $11 \pm \frac{1}{2}$ and $15 \pm \frac{1}{2}\,^{\circ}C$. The temperature groups were started up on September 25 and one week was used to adjust them. For the 10th growth tank was used water with naturally fluctuating temperature (Fig. 2) and the photoperiod was simulated to follow the natural photoperiod for Bergen.

In Fig. 1 the Roman figures I - VI indicate when fishes from each experimental group were tested for saltwater tolerance. The corresponding dates when the test started were September 27, November 5, December 20 1974, March 4, April 21 and May 26 1975.

At the tests 50 fishes from each group were tested. The fishes were starved for 24 hours before beting put into the test tanks. In the three first saltwater tests, I - III, were used static water with airbubbling of 75%, 100% and 110% seawater ($34,5\,^{o}/oo$). In the three last tests, IV - VI, were used only water of 100% seawater. In the test IV the water was static but in test V and VI it was circulating.

The fishes that were going to be tested for saltwater tolerance were taken directly from their freshwater environment and put into a tank with saltwater of the same temperature. Dead fishes were removed from testtanks every second hour during the first 48 hours.

In the tests I - III almost all the fishes were dead after 48 hours. In the tests IV - VI some fishes lived longer and the test continued until no more fishes died and the fishes were taking food again. The three first tests will not be discussed in this paper because among other things the differences in survival between the groups were small.

All fishes in the testgroups were weighed to 0,1 gram and measured to the nearest mm (fork length). The fishes were weighed and measured immediately after death had occured, or for the surviving fishes after 100 hours for test IV and 200 hours for tests V and VI. Conditon factor was calculated from length-weight data as a measure of change in fatness. The condition factor (K) was determined for each fish in a sample using the formula $K = 100\ W/L^3$, where W denotes weight in grams and L denotes fork length in centimeters (HOAR 1939).

During the experimental period from September 25 in 1974 to May 26 in 1975 dead fish were removed dayly, weighed and measured. The growth tanks were cleaned regularly.

The differences in survival between the testgroups were tested for significance by using a x^2 homogenety test and applying Yates' correction (MORONEY 1969). When the value for x^2 corresponded to probabilities of worse fit between the 5 and 1% level the difference was said to be probably significat. When the value was between the 1 and 0,1% level the difference was said to be definitely significant, and below 0,01% highly significant.

In order to evaluate the differences in increase in length and condition factor between the experimental groups, the statistical significance of the difference between the sample means was tested using a formula $Var(\bar{X}_1 - \bar{X}_2) = \frac{\sigma_1^2}{n_1} + \frac{\sigma_2^2}{n_2}$ (MORONEY 1969). A difference of more than two standard errors between sample means is regarded as probably significant and a difference of three or more standard errors is regarded as definitely significant.

RESULTS

Results of the three last saltwater tests are shown in Fig. 3, 4, 5 and 6. Both water temperature and daylength seem to have had effect on growth and on survival during the tests. The two dependent variables, growth rate and survival seem to be closely related. A correlation coefficient of 0.94 was calcualted between per cent of survivals and mean length. This high correlation was calculated independent of date of seawater test and photoperiod, and show that size is very important for euryhalinity. Only about 12% of the variation (residual variance) between groups in proportion of survivors seems to have other reasons than mean size of the fish; for instance, direct influence of photoperiod, age or temperature.

The length distributions for the groups tested on May 26, April 21 and March 4 (tests VI, V and IV) are shown in Fig. 7, 8 and 9 respectively. The figures show clearly an increase in mean length and also an increased variation in length at higher temperatures. The curves are more or less bimodal and the second top seems to become proportionally higher at higher temperatures.

When comparing length distributions for the fishes that survived versus the fishes that died during test VI (Fig. 3) it is evident that also within groups there are strong relations between size and survival. Generally the biggest fishes in each group survived. The smallest fishes that survived were 11 and the largest that died were 14 cm. Worth mentioning is also that no fish smaller than 14 cm survived at 15°C, while at 7°C no fish between 11 and 14 cm died.

In tests V and IV (Fig. 4 and 5) were observed similar differences in length distribution between the temperature groups as for test VI (Fig. 3). There were also observed increased variation in length at increased temperature, bimodality and the second top to be proportionally higher at higher temperatures. A strong relationship between size and survival within groups were also found in the test V and IV.

The last salttolerance test, on May 26, was started about the time when euryhalinity for this population in its normal environment is to be expected. The results of this test, therefore, were submitted to closer analysis. To analyse the influence of the two variable factors water temperature and photoperiod on growth a two way analysis of variance was applied.

Source of variation	d.f.	Mean square
Between temperatures	2	S_t = 36270.29
Between photoperiods	2	S_p = 4287.71
Interaction	4	S_{tp} = 2570.42
Error	802	S_i = 649.58
Total	810	S_s

$F_1 = \frac{StP}{Si} = 3.96$ $\qquad 0.01 < P < 0.05$

$F_2 = \frac{St}{StP} = 14.11$ $\qquad 0.01 < P < 0.05$

$F_3 = \frac{Sp}{StP} = 1.67$ $\qquad p > 0.05$

The first test (F_1) shows that there is a significant interaction between temperature and photoperiod on growth rate of salmon parr, and that both factors have influence on growth. However, second (F_2) and third (F_3) tests show that the effect of temperature will influence growth independent of photoperiod, while the effect of photoperiod depends on water temperature.

By estimating mean squares for the different sources of variations, the following distribution of the total variation was calculated:

Between temperature	29%
Between photoperiod	2%
Interaction	5%
Error (within groups)	62%

When testing the differences in survival in test VI (Fig. 3) by a common X^2 homogenity test, no significant difference between the photoperiods at 7^oC was found. At 11^oC the per cent of survivors at photoperiod L_1 was hightly significant higher that at L_2 and L_3.

A probably significant difference between L_3 at 11 and at 15°C was found where L_3 at 15°C had the higher per cent of survivors. Unfortunately only seven fishes were left in group L_1-15°C when the test started and this low number prevents statistical tests. The per cent of survivors at both 11 and 15°C were highly significant higher than at 7°C and in the NTL-group.

No significant difference in survival between the photoperiods at 7 or at 15°C was found in test V (Fig. 4). At 11°C photoperiod L_2 had a definitely significant higher proportion of survivors than L_3. The proportion of fishes surviving at 11 and 15°C were definitely significant higher than at normal temperature and at 7°C. When tested statistically there was no significant difference between the proportion of surviving fishes at 11 and 15°C.

For test IV (Fig. 5) no statistically significant difference in survival between photoperiods with the same temperature was found nor was there any difference between the temperature groups NTL, 7 and 11°C. The group L_1-15°had proportionally most survivors and the figure was definitely significant higher than for any of the photoperiods at 11°C. Both of the groups L_2-15°C and L_3-15°C had a definitely significant higher per cent of survivors than the group L_3-11°C.

The only significant difference at test VI in mean size between the fishes at different photoperiods with same temperature, was found at 11°C (Fig. 3). Here mean size for fishes at the photoperiods L_1 and L_2 were definitely respectively probably significant higher than for L_3. In tests V and IV, I also found a definitely significant better growth at 11°C for L_1 and L_2 on one hand and L_3 on the other. From Fig. 6 we also see that growth at 15°C during the winter months was much higher at L_1 than in any of the other experimental groups.

Condition factor

There were insignificant differences in condition factor among the photoperiod regimes for the different temperature groups at test VI (Table 1). In test V mean condition factor for the group L_2-11°C was found to be definitely significant higher than for L_3-11°C and probably significant higher than for L_1-11°C. In test IV mean condition factor for L_3-7°C was found to be probably significant higher than for L_2-7°C, and for L_1-15°C to be probably significant higher than for L_2-15°C and L_3-15°C.

There was a clear tendency towards higher condition factor with higher temperature, especially at test IV.

When comparing mean condition factors for the fishes that died with those that survided at 15°C I found significant differences in the three tests IV-VI, (Table 1). The condition factors for the fishes that survived the seawater tolerance tests were definitely significant lower than for the fishes that died. The tendency was the same at 11°C, but here the differences were not statistically significant. At 7°C and at natural temperature (NTL), however, the surviving fishes had higher condition factors than the dead ones.

Mortality

Table 2 shows mortality and mean length of fish that died in the course of the experiment in between the saltwater tests, and mean length of the fishes used in the tests. The NTL-group had lowest mortality rate, the mortality increased with increased temperature and most of the fishes that died at 11 and 15°C died in the period October-December. This high mortality, especially at 15°C, was due to a skin parasite Costia sp.

A high mortality in the group L_3-11°C in December was caused by an accident with the water flow, that caused 33 of the biggest fishes to die of oxygen deficiency. In spring the mortality in all groups was low.

Fish that died between the tests was usually smaller than the fishes at the previous test. At 15°C the dead ones very often had lost one or both eyes. At several occasions the fishes at 15°C were observed to attach each other, especially the eyes.

No fish that were silvery and without the typical parr markings on the sides of the body died in any test, whereas a few fishes that survived had visible parr markings. These fishes did not, however, seem to manage as well as the others, for instance they did not take food during the tests. The fishes that died in the tests had typical parr markings.

DISCUSSION

The results with one year old salmons described above show, that their ability to osmoregulate and as a result from that survive and abrupt transfer from fresh-to saltwater is highly dependent on fish size. This is in good agreement with what PARRY (1960), among others, have found.

As expected, growth was first of all dependent on temperature, but photoperiod was also found to influence growth. Temperature influenced growth independent of photoperiod, while the effect of photoperiod was dependent of temperature.

At the four experimental temperature regimes the best growth was found at 15°C and at the photoperiod, at which the increase in day length started first. The differences in growth between the temperature groups are very clear (Fig. 6) and from these we conclude that salmon in their first year have a better growth rate at higher temperatures up to at least 15°C. This is in agreement with what was found for Atlantic salmon by IVLEV (1960), and JAVAID and ANDERSON (1967). Though using different methods they found similar high preferred temperatures, around 17°C, for underyearling salmon. SAUNDERS and HENDERSON (1969) found that food consumption and efficiency of food conversion and consequently growth rate for Atlantic salmon smolt was higher for any salinity at 14 or 15°C than at 18 or 10°C. BRETT (1971) found for Sockeye salmon (Oncorhynchus nerka), during lake residence, a physiological optium in the region of 15°C. The effect of photoperiod on growth is in accordance with what GROSS et. al. (1965) found for green sunfish (Lepomis cyanellus). He found that an increasing photoperiod enchanced growth considerably more than a constant or a decreasing one. Whether the increased growth in the present experiment is a result of a longer period of increasing daylength influencing some physiological process, or if it is just a result of the fish having got more food because of a longer feeding period, is difficult to say.

As survival of young salmon to a high degree is dependent on growth, which in turn is highly dependent on temperature, it is in no way astonishing to find the highest per cent of survivors of the saltwater tests in the higher temperature regimes (See Fig. 3, 4 and 5).

Significant differences in survival rate between different photoperiods at the same temperature was found only at 11°C. In the test on May 26 the photoperiod with the longest period of increasing daylength had most survivors. From this follows, that, if using the right temperature regime, one will get more salmon smolts in one year if one starts to increase the daylength already in September.

It is interesting to notice that in spite of the significantly better growth at 15 compared to 11°C (Fig. 6), we see from test VI (Fig. 3) that photoperiod L_1 at 11°C had a higher percentage of survivors than L_2 and L_3 at 15°C. We see the same tendency in test V (Fig. 4) for photoperiods L_1 and L_2 at 11 and 15°C. The differences are, however, not statistically significant, but in spite of this it is tempting to compare it with what ZAUGG and WAGNER (1973) found when studying parr-smolt transformation and migration in Steelhead trout. They found that gill Na^+, K^+-stimulated ATPase activity was elevated in smolts exhibiting migratory behaviour, and that ATPase activity was decreased and migration reduced when animals were subjected to temperatures of about 13°C or higher.

These findings that photoperiod influence smoltification and thereby seawater adaptation is not in agreement with what WAGNER (1973) found for Steelhead trout. He concluded that seawater adaptation is independent of photoperiod in that fish.

WAGNER (1973) also suggests that parr-smolt transformation and development of seawater adaptation are two distinct and unrelated physiological processes. This is very difficult to argue against because nobody knows to-day what is really going on in the smoltification process. That parr of Atlantic salmon develope a higher degree of salttolerance with increasing size is well known from the works of PARRY (1960). However, to consider smoltification and seawater adaptation in Atlantic salmon to be two distinct and unrelated physiological processes, based only on a correlation between saltwater tolerance and size, would be an over-simplification. Following observations already mentioned in this study point in the direction that there is a connection between seawater tolerance and smoltification:

i, all fish surviving and taking food during the seawater tolerance tests were silvery and without parr markings,

ii, no fish with above mentioned appearance died during the tests and

iii, all fish not surviving an abrupt transfer from fresh to seawater had typical parr markings.

There was a tendency for the condition factor to be higher for fishes that were reared at higher temperatures (Table 1). This was especially pronounced in test IV. The surviving fishes reared at 11 and 15^{O}C had a lower condition factor than the fishes that died in these temperatures. Under natural conditions, smolts have a low condition factor and this is one of the characteristics that distinguish smolts from parr (HOAR 1939). For the fishes reared at 7^{O}C the tendency seemed to be the opposite of that of 11 and 15^{O}C.

The significant differences in condition factors in tests V and IV when testing the different photoperiods in the same temperature group against each other, indicate that fish will get higher condition factor in a photoperiod where the increase in day length starts earlier than normal.

During the experiment, from September 25 to May 26, there was found an increased mortality in the higher rearing temperatures. To this there may be several explanations, e.g. enchanced risk for outbreak of diseases. The metabolism in fish increases with increased temperature, among other things shown by SAUNDERS (1963), and at high temperatures therefore the individuals will die sooner. It also seems as if fishes were more aggressive at the higher temperatures, something the out-picked eyes should confirm.

SUMMARY

1. Size was found to be the most important factor at seawater adaptation in underyearling Atlantic salmon.

2. In relation to photoperiod, temperature was found to be the most important factor in promoting growth.

3. Best growth in the experimental temperature and photoperiod regimes was found at 15 °C and at the photoperiod with the longest period of increasing daylength.

4. Temperature influenced growth independent of photoperiod, while the effect of photoperiod was dependent of temperature.

5. At the time for seaward migration, the most pronounced effect of photoperiod on seawater adaptation was found at 11 °C. At this temperature a significantly higher per cent of survivors was found at the photoperiod with the longest period of increasing daylength.

6. In the experiment a tendency for the condition factor to be higher at increasing temperatures was shown.

7. The seawater adapted fishes at 11 and 15 °C had a lower condition factor than the fishes that were not adapted at the time for seaward migration. For the fishes reared at 7 °C the tendency seemed to be the opposite of that of 11 and 15 °C.

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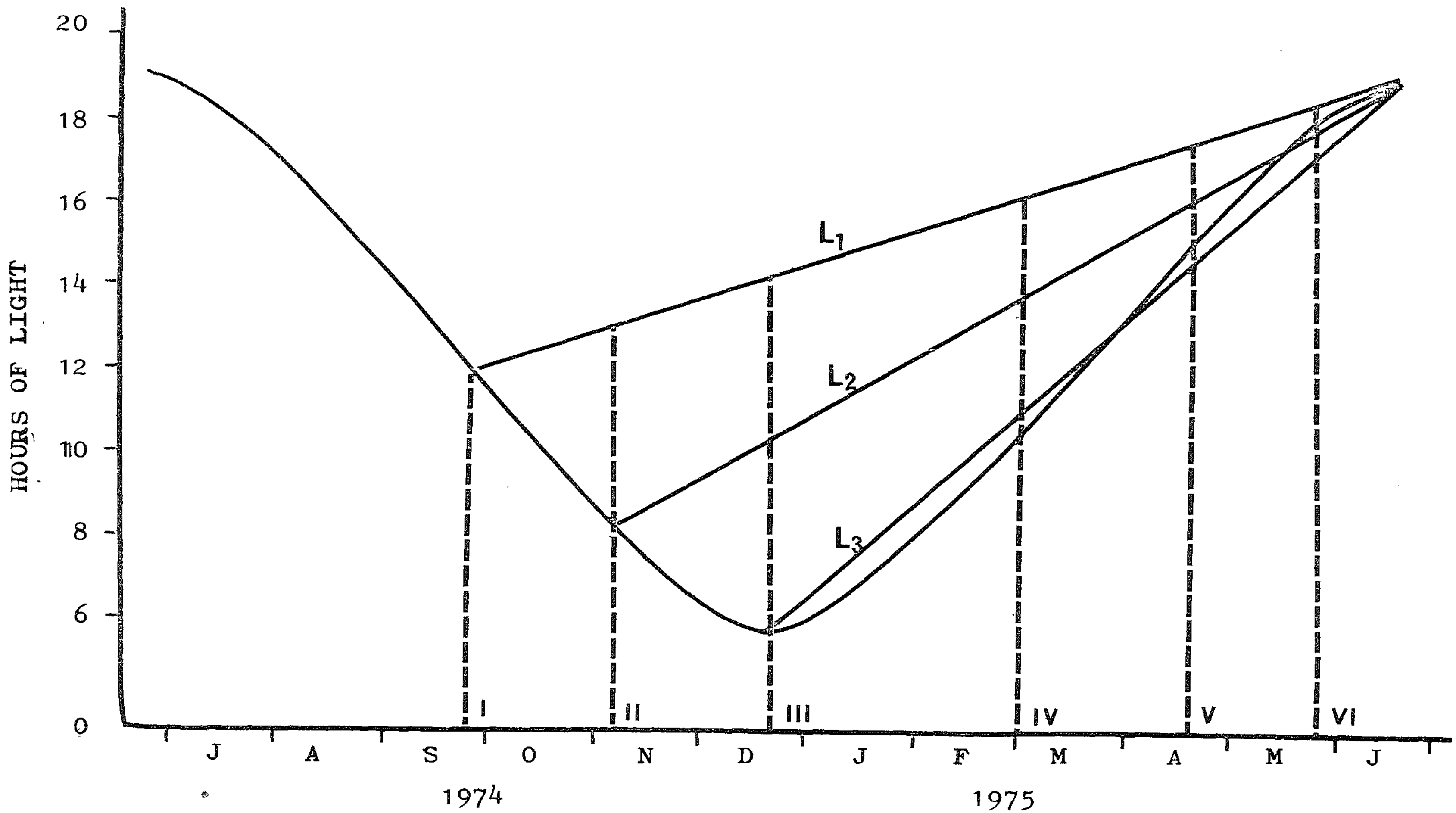

Fig.1. Annual photoperiod cycle at Bergen. L_1,L_2 and L_3 denote the three experimental photoperiods and I-VI time for saltwater tests.

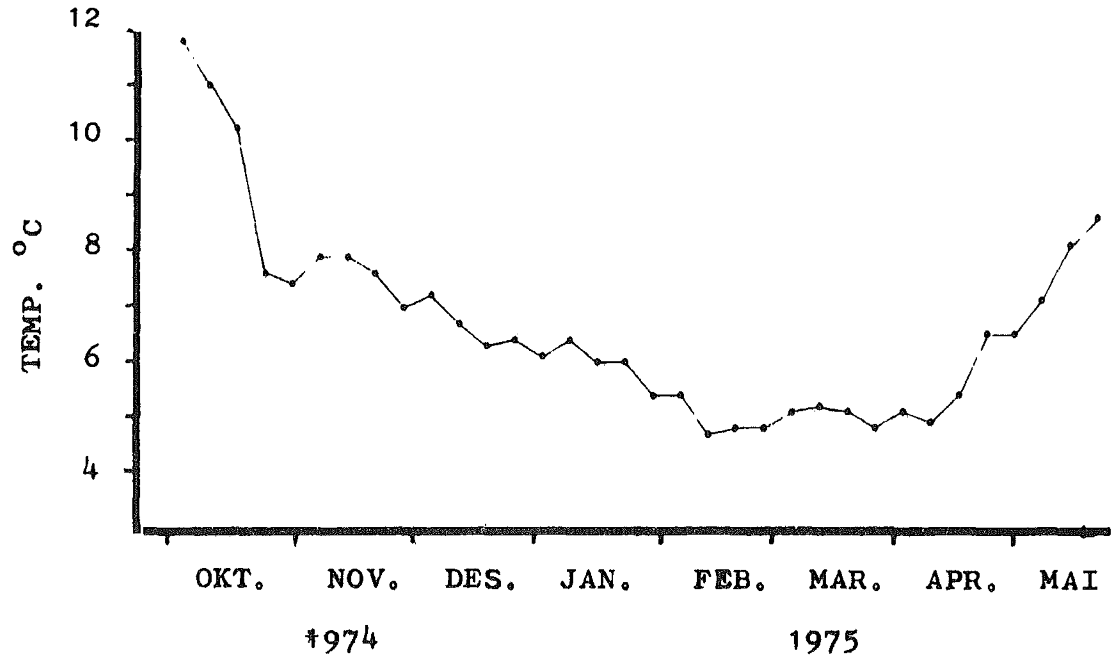

Fig. 2. Annual temperature cycle of freshwater at Bergen.

Test VI 26.5.75.

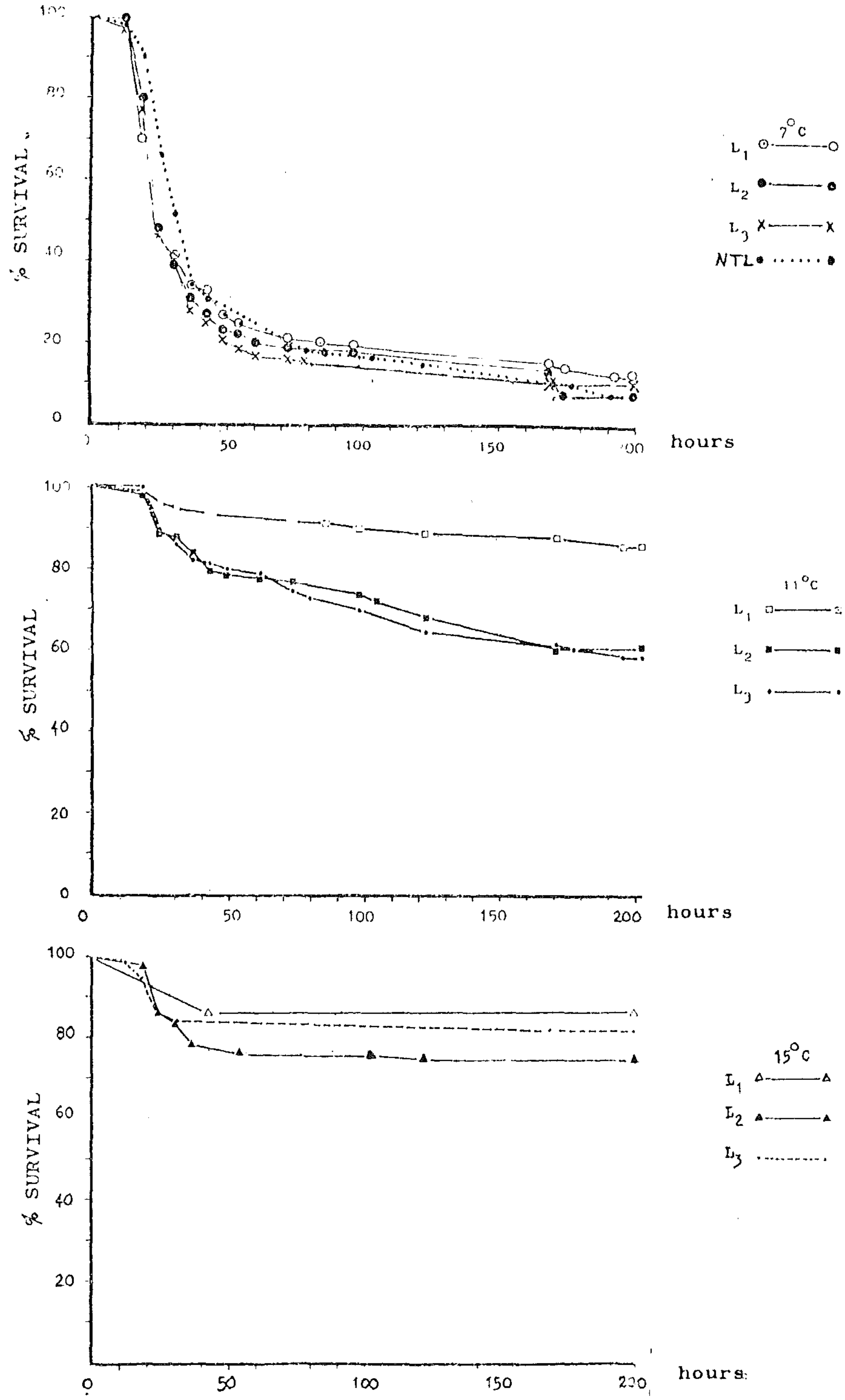

Fig. 3. Mortality rates of young Atlantic salmon exposed to seawater (34.5°/oo) after having been reared at different photoperiod and temperature regimes.

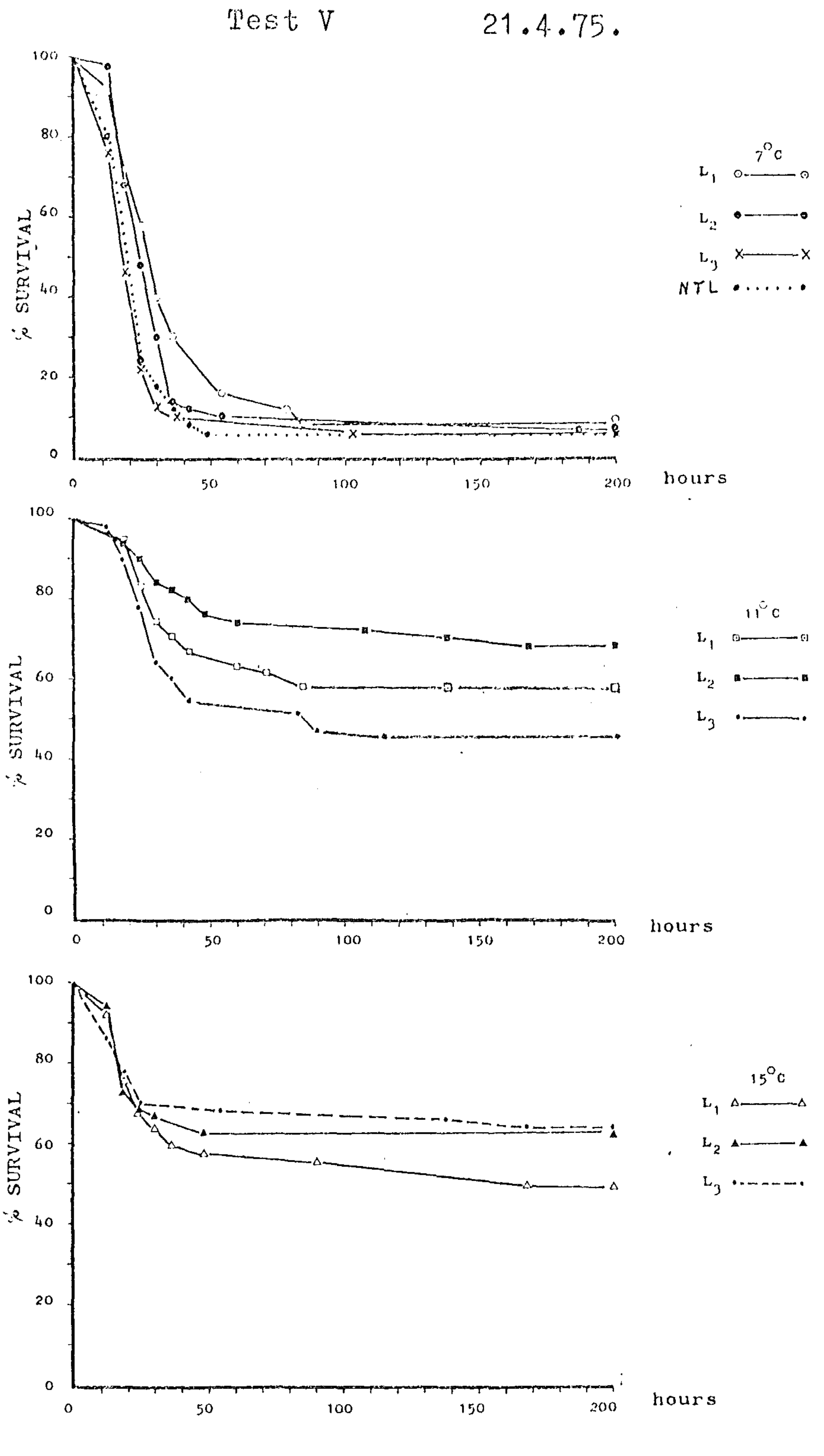

Fig. 4. Mortality rates of young Atlantic salmon exposed to seawater (34.5°/oo) after having been reared at different photoperiod and temperature regimes.

Test IV 4.3.75.

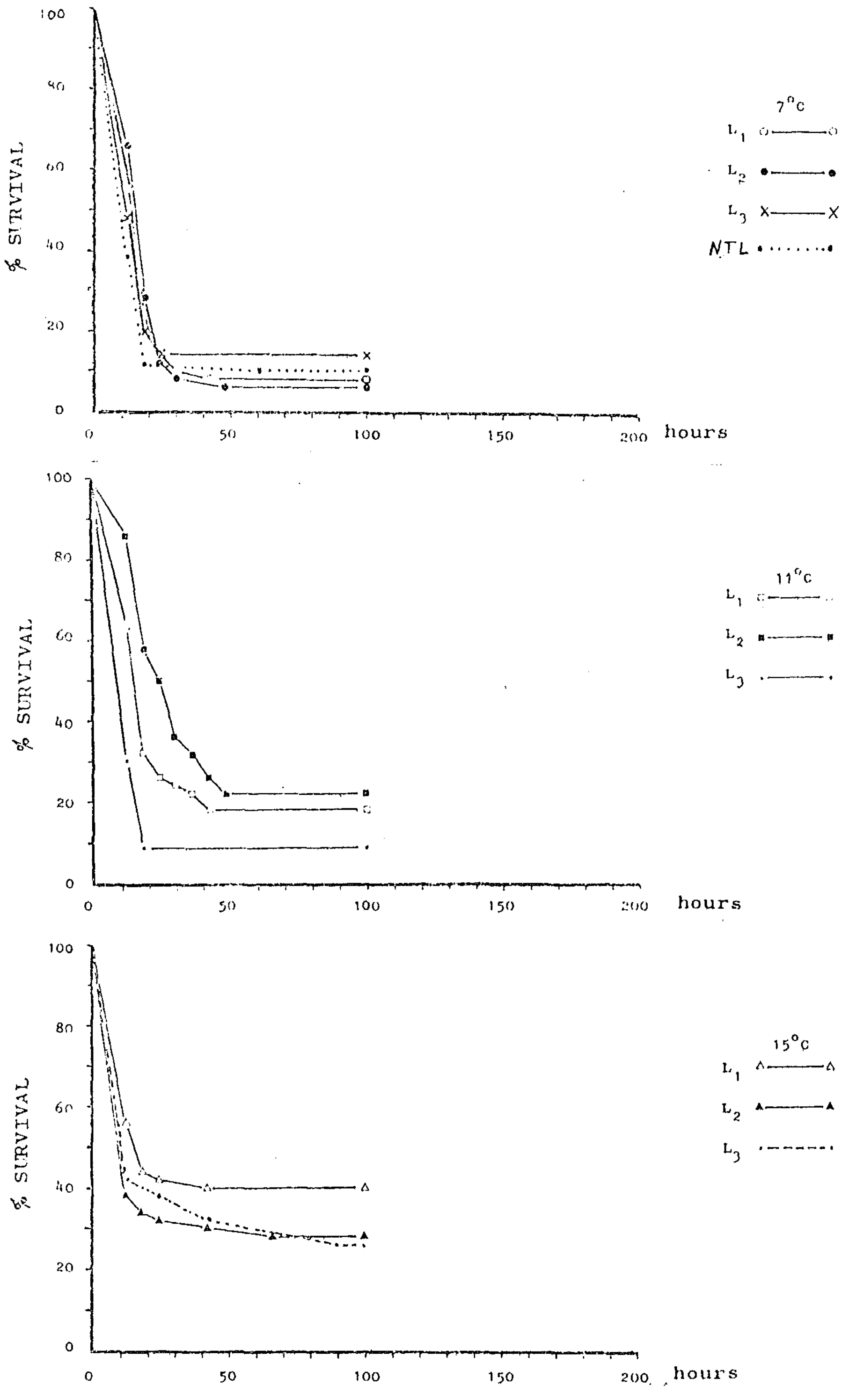

Fig. 5 Mortality rates of young Atlantic salmon exposed to seawater (34.5 °/oo) after having been reared at different photoperiod and temperature regimes.

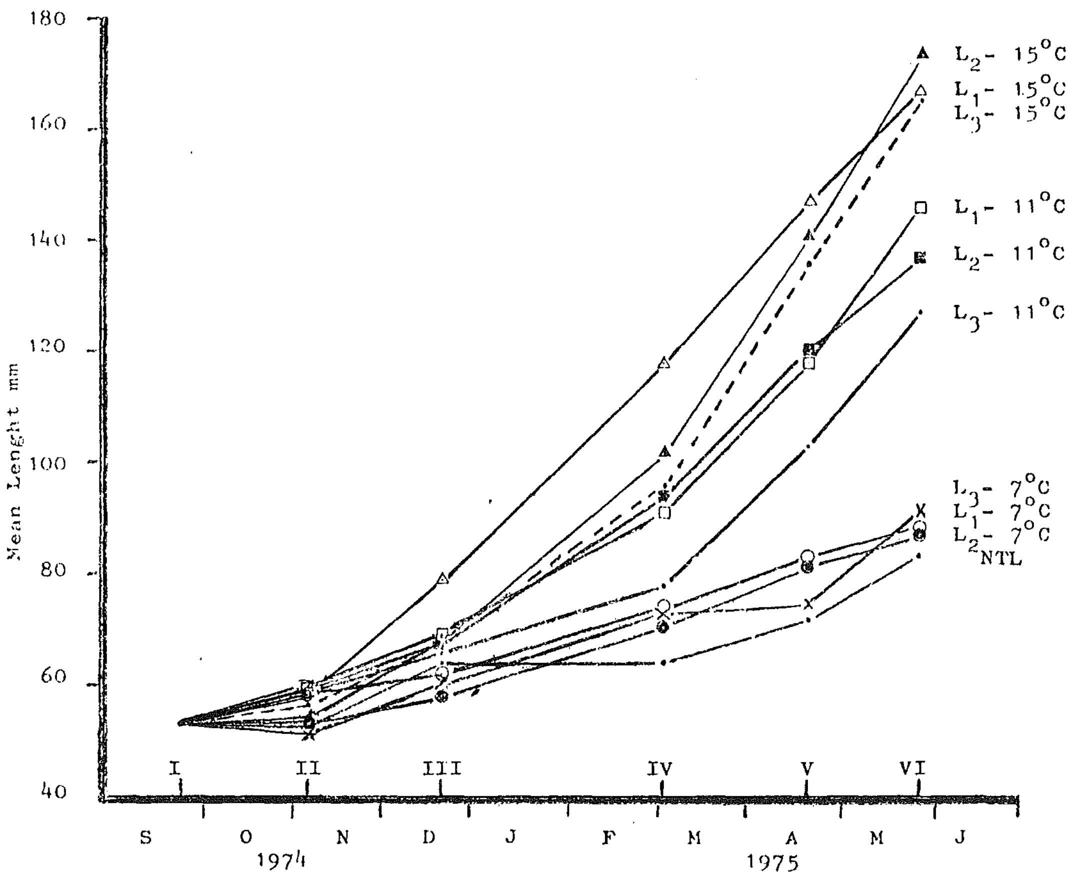

Fig. 6. Mean fish length (fork length) of each experimental group at saltwater tests I - VI.

Test VI 26.5.75.

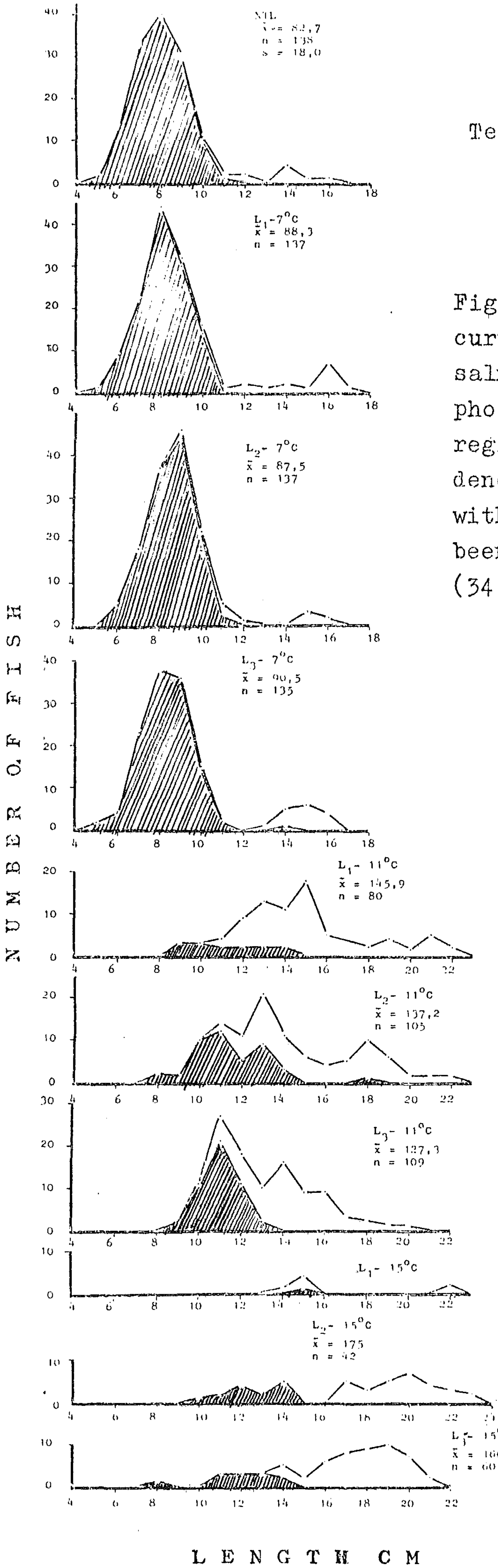

Fig. 7. Length distribution curves for young Atlantic salmon reared at different photoperiod and temperature regimes. The shaded areas denote the fish that died within 200 hours after having been exposed to seawater (34.5°/oo).

Test V 21.4.75.

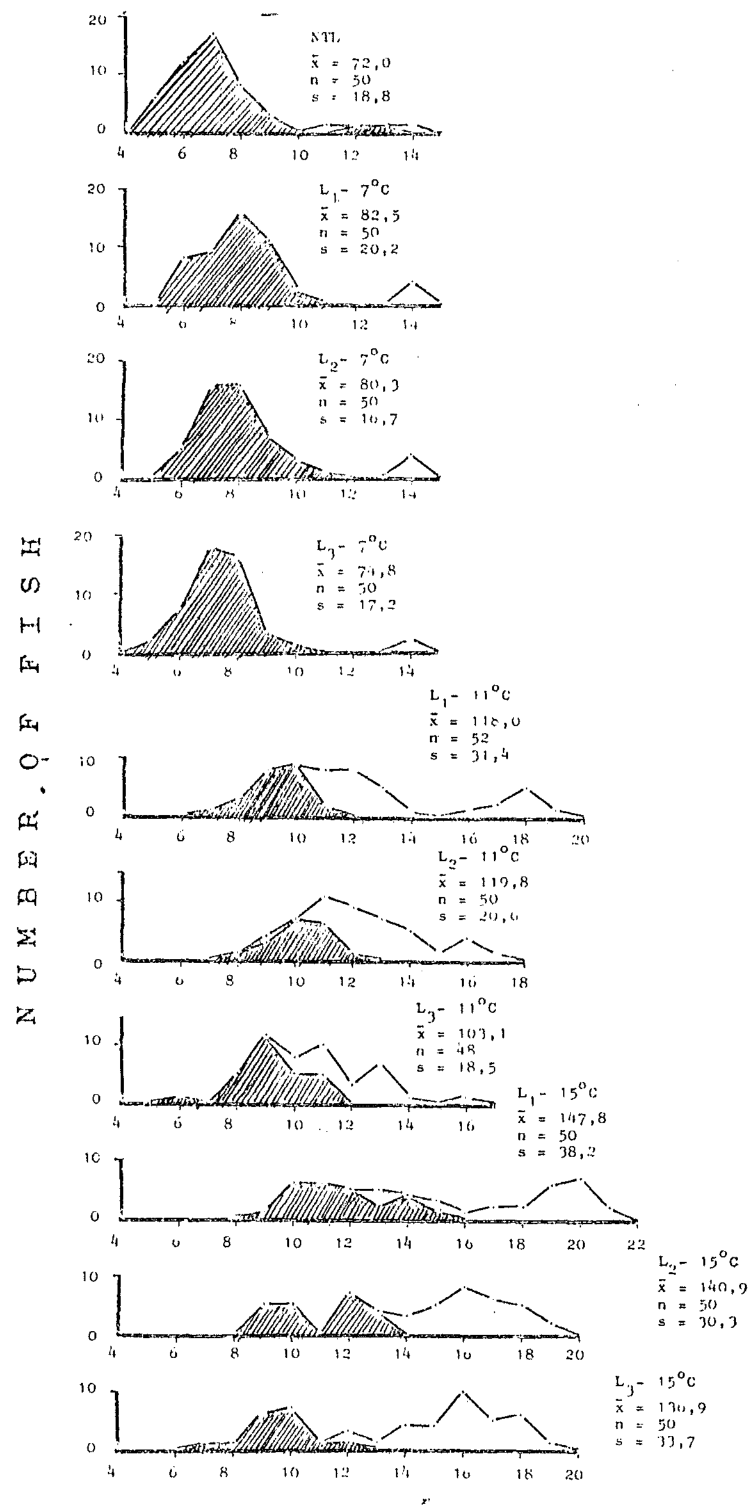

Fig. 8. Length distribution curves for young Atlantic salmon reared at different photoperiod and temperature regimes. The shaded areas denote the fish that died within 200 hours after having been exposed to seawater (34.5‰).

Test IV 4.3.75.

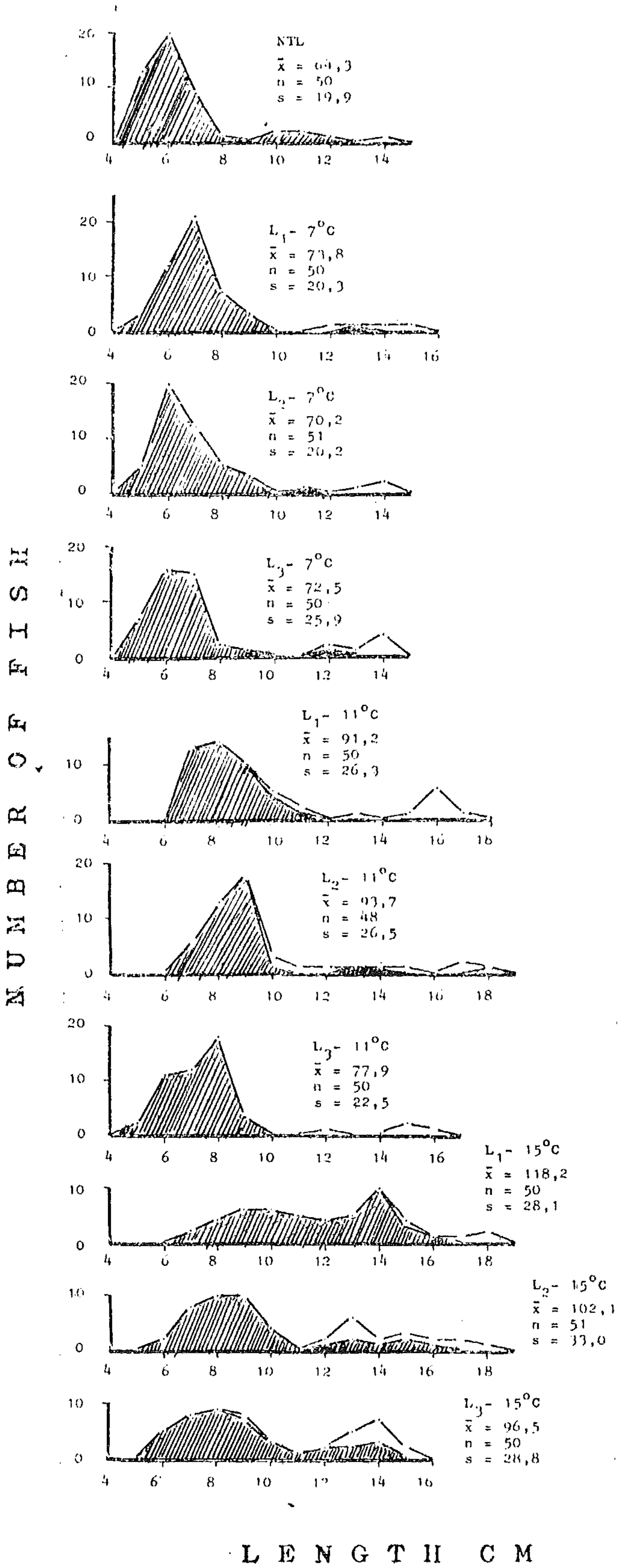

Fig. 9. Length distribution curves for young Atlantic salmon reared at different photoperiod and temperature regimes. The shaded areas denote the fish that died within 100 hours after having been exposed to seawater (34.5°/oo).

Table 1. Mean condition factor of young Atlantic salmon in relation to photoperiod and temperature.

Group	Test IV Total No. fish	Test IV Total K	Test IV Dead No. fish	Test IV Dead K	Test IV Alive No. fish	Test IV Alive K	Test V Total No. fish	Test V Total K	Test V Dead No. fish	Test V Dead K	Test V Alive No. fish	Test V Alive K	Test VI Total No. fish	Test VI Total K	Test VI Dead No. fish	Test VI Dead K	Test VI Alive No. fish	Test VI Alive K
NTL	49	0.96	48	0.86	1	0.93	49	0.91	47	0.91	2	0.87	136	0.93	126	0.93	10	0.98
7°C L_1	48	0.90	45	0.90	3	0.97	50	0.92	46	0.92	4	1.01	136	0.95	117	0.93	19	1.05
L_2	51	0.89	48	0.89	3	0.94	50	0.94	48	0.94	2	1.02	137	0.95	126	0.95	11	1.06
L_3	50	0.95	44	0.94	6	0.96	49	0.90	47	0.89	2	1.06	135	0.98	119	0.98	16	1.01
11°C L_1	50	0.97	42	0.99	8	0.89	52	0.98	23	0.96	29	0.99	80	1.04	14	1.05	66	1.04
L_2	48	0.95	41	0.96	7	0.90	50	1.10	18	1.02	32	1.14	105	1.04	43	1.05	62	1.04
L_3	50	0.97	46	0.97	4	0.93	48	0.96	28	0.96	20	0.95	109	1.01	46	1.03	63	1.00
15°C L_1	50	1.09	46	1.11	4	0.85	50	1.04	25	1.12	25	0.97	7	1.04	1	1.05	6	1.04
L_2	51	1.01	40	1.04	11	0.91	50	1.03	19	1.11	31	0.99	42	1.02	13	1.19	29	0.94
L_3	50	0.98	40	1.02	10	0.85	50	1.02	17	1.09	32	0.98	59	1.01	12	1.17	47	0.97

Table 2. Mean length of young Atlantic salmon reared at different photoperiod and temperature regimes. Number of individuals in brackets.

Mean length (mm)

GROUP		TEST I	MORT. 25.9-5.11	TEST II	MORT. 6.11-20.12	TEST III	MORT. 21.12-4.3.	TEST IV	MORT. 5.3-21.4	TEST V	MORT. 22.4-26.5	TEST VI
NTL		53 (51)	38 (2)	53 (51)	--	64 (51)	45 (1)	64 (50)	63 (1)	72 (50)	66 (2)	83 (137)
7°C	L_1		44 (1)	57 (51)	52 (2)	62 (49)	53 (7)	74 (50)	49 (2)	83 (50)	85 (1)	88 (137)
	L_2		37 (6)	53 (51)	-- (1)	59 (51)	48 (2)	70 (51)	49 (1)	80 (50)	82 (2)	88 (137)
	L_3		39 (8)	51 (52)	42 (1)	60 (51)	47 (3)	73 (50)	--	75 (50)	90 (1)	91 (135)
11°C	L_1		39 (6)	58 (51)	60 (5)	69 (47)	80 (30)	91 (50)	93 (3)	118 (52)	97 (3)	146 (80)
	L_2		35 (4)	58 (47)	55 (8)	67 (50)	82 (9)	94 (48)	82 (9)	120 (50)	101 (2)	137 (105)
	L_3		43 (5)	59 (50)	88 (38)	66 (47)	53 (3)	78 (50)	77 (1)	103 (48)	92 (3)	127 (109)
15°C	L_1		49 (62)	54 (51)	58 (27)	79 (50)	79 (6)	118 (50)	--	148 (50)	--	167 (7)
	L_2		47 (56)	54 (53)	52 (21)	68 (50)	85 (21)	102 (51)	76 (2)	141 (50)	--	175 (42)
	L_3		44 (29)	57 (50)	61 (34)	67 (46)	74 (4)	96 (50)	-- (2)	137 (50)	--	166 (60)