International Council for the Exploration of the Sea

C.M. 1991/M:28
Ref.J
Anadromous and Catadromous Fish Committee.

VARIATION OF GROWTH RATE, TAG-RECOVERY RATE AND TEMPORAL DISTRIBUTION OF TAG-RECOVERIES IN BALTIC SALMON TAGGING EXPERIMENTS

by

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Abstract

The pattern of variation of three basic variables acquired from Baltic salmon tagging experiments - length increment (growth rate), return rate (survival) and temporal distribution of tag recoveries - was analysed. Year of release (year-class) and length at release (smolt size) were used as independent variables, i.e. sources of variation. The data consisted of 352 groups (296613 ind.) of reared smolts released in the northern part of the Gulf of Bothnia (ICES 31) in 1970-1988.

Year-class related factors - probably including changes in marine environment as well as in smolt quality - account for a major part of variation in tagging data. After a correction to smolt size, "year-class" explained 11% of the remaining variation of individual length increment (until A1+ stage), and 54% and 65% of the variation of adult return rate and temporal distribution (A1+percentage) of tag recoveries for each smolt group, respectively.

A significant positive correlation was found between mean length increment and adult return rate for each smolt year-class, indicating that same factors, that regulate growth, affect survival as well - probably via growth rate. Furthermore, the positive correlation between growth rate and A1+ percentage indicates, that the sooner the fish attain legal size and fully recruit to the fishery, the sooner they are caught.

The importance of smolt size is clearly demonstrated by the significant positive regressions of mean size at recapture, return rate and A1+ percentage on smolt length. Length at recapture (A1+) increases by 3.3 cm, A1+ percentage by 13 and return percentage by 3.2 for 5 cm increased smolt length (from 15 to 20 cm). During the study period there was a sligth positive trend in the mean length of A1+ salmon, probably owing to simultaneous rise in smolt size.

The role of gear selectivity, maturity and tag loss as possible sources of biase in the tagging data are discussed.

1. Introduction

Data from tagging experiments (Carlin-tag) are widely used in the assessment and management of Baltic Salmon stocks. Estimates of growth-rate, post-smolt mortality, adult mortality and the distribution of salmon catches by fishing seasons and fishing areas, e.g., are often based on tagging data. Surprisingly little attention has, however, been paid to the pattern of variation of, and - especially - the connection between the parameters used as the bases of these estimates. The stochastic (year-to-year) variation of post-smolt survival (LINDROTH 1965), growth rate (CARLIN 1969, THUROW 1973) and many indices of catch data, is well known, but the correlation between these variables, as well as the consequences of the variation itself, have mainly remained obscure.

I analysed the pattern of variation of three basic variables acquired from tagging experiments - length increment ("growth-rate"), recapture-rate ("survival") and the distribution of tag-recoveries between fishing seasons - and the correlation between these three. Year of release (year-class) and length at release (smolt size) were used as independent variables, i.e. sources of variation. Data from Finnish tagging experiments in the northern part of Gulf of Bothnia in 1970-1988 were used in the analyses.

2. Material and methods

2.1. Tagging data

In all, 352 groups (296613 individuals) of tagged reared salmon smolts were released in the northern part of the Gulf of Bothnia (ICES 31) in 1970-1988 (Table I). All groups belonged to salmon stocks exhibiting a similar pattern of long feeding migration (CARLIN 1969, LUNDIN 1974, IKONEN and AUVINEN 1984) to the Baltic Main Basin (ICES 22-29).

Until May 1991, a total of 24903 tag-recoveries (8,4 %) were reported from these experiments. I devided the recoveries according to the age-group of the fish and fishing season as follows:

Time of recovery	Age-groups	Later referred to as
Year of release - 2nd year April	A+, A1	Post-smolts
2nd year May - 3rd year April	A1+, A2	A1+
3rd year May - 4th year April	A2+, A3	A2+

and so on..

For the growth analysis, all A1+-recoveries (defined above) reported from the Main Basin (ICES 22-29) between November and April were extracted from the data. During this period the growth is assumed to be minimal (LARSSON 1973) and the fish are assumed to be in same state of sexual maturation. The length increment of these fish after release (=length at recapture - individual length at release) was used as a variable describing "growth-rate". Length at recapture was reported for 2675 recoveries. The frequency distribution of length increment is given in Fig 1.

The return-rate of adult salmon (A1+ and older) for each group (352) of tagged smolts was used as a variable describing "survival". The frequency distribution of return-rate is given in Fig 1.

The percentage of A1+ -fish of total adult (A1+ and older) recoveries for each group of tagged smolts was used as a variable describing "temporal distribution" of tag recoveries. Groups with less than 10 adult recoveries (46) were rejected from the data. The frequency distribution of A1+ -percentage is given in Fig 1.

2.2. Statistical methods

Differences in length increment, return-rate and A1+ -percentage were tested by ANOVA for each year-class and between year-classes. Length at release was used as a covariate in the analyses. The frequency distributions of return-rate and A1+ -percentage were normalized by arcsin$\sqrt{\ }$transformation (Fig 1).

Before the application of ANOVA, Bartlett's test of homogenity was used to test for possible differences in the variances for each year-class.

The relationship between average length increment, return-rate (transformated) and A1+ -percentage (transformated) for each year-class was tested by correlation analysis. The dependancy was assumed to be linear (Pearson correlation coefficient).

Regression analysis (linear regression) was used to test the dependency of length-increment (and length at recapture) on individual length at release, and the dependency of return-rate and A1+ -percentage on the mean length at release for each smolt-group. - Same regressions were already included in ANOVA (above), where length at release was used as a covariate.

3. Results

3.1. Between year-class component of variation

Between year-class variation accounts for a substantial part of the total variation (counted from the regression line) of return-rate and A1+ -percentage (54 and 65%, respectively). In the variation of length increment the between-year component is not as important (11 %), though statistically significant (Table II).

3.2. Growth-rate, return-rate and A1+percentage

The correlation between average length increment, return-rate and A1+percentage for each year-class is significant (Table III). Year-classes with good growth (or high mean length at A1+stage) give good returns and high percentages of A1+ fish (Fig 2).

Highest mean values of length increment, 54-56 cm, were obtained in year-classes 1972-1973 and again 1983-1984 and 1988. The A1+percentage for these year-classes varied between 62 and 75, and return-rate between 8 and 24. Growth-rate was, on the other hand, poorest in year-classes 1977-1981 (length increment 47-50 cm), giving only 31-48 % A1+-fish of all adult recoveries (return-rate 3-7%). Year-class 1987 was an exception: low length increment (48 cm) resulted, as expected, in a low return-rate (4.1%), but also relatively high A1+ percentage (66.6%).

3.3. The effect of smolt size

The regression of length increment (and length at recapture), return-rate and A1+ -percentage on smolt size (length at release) is highly significant (Table II, Figures 3 and 4), accounting for 1.6 % (5.4%), 7.3 % and 9.4 % of the total variation, respectively. Length at recapture increases by 3.3 cm, A1+ percentage by 13 and return percentage by 3.2 for 5 cm increased length (from 15 to 20 cm).

The regression of length increment on smolt size is negative, while the regression of length at recapture on smolt size is positive (Fig. 3, Table IV). The pattern is about the same also for separate year-classes (Table IV), but the the values of regression coefficients (slope) and probability seem to vary from year to year.

For year-classes with average or good growth (1984,1985, 1986 and 1988) the regression of length at recapture on smolt size is highly significant (Table III) and the regression coefficient aproaches 1.0, while the regression of length increment on smolt size is not significant. For year-class 1987 with poor growth, on the other hand, the (negative) regression of length increment on smolt size is highly significant, while the regression of length at recapture on smolt size is not as clear.

During the study period there was a slight positive trend in the mean length of A1+ salmon (Fig 2).

4. Discussion

4.1. Evaluation of the growth data

Growth estimates based on tagging data may be biased for several reasons. Fishermen, e.g., don't often have time for accurate length or weigth measurements. This becomes evident from the fact, that the reported lenghts and weights don't always "fit" together. Active size selection is another source of biase: undersized fish are released, or, if taken, not always reported. At A1+ stage 60 cm size limit cuts, at least in year-classes with poor growth, a substantial part of the lower edge of the length distribution (Fig 3, Fig 5). Third, Carlin-tag is known to have an adverse effect on both length (SAUNDERS and ALLEN 1967) and weight increment (ISAKSSON and BERGMAN 1978).

Growth data may be biased by maturity and gear selection, too (THUROW 1973). At A1+ stage (open sea, November-April) all fish were assumed to be in the same stage of sexual maturation. This migth be true, but the grilse, known to be among the smallest individuals by November (SAUNDERS et.al. 1983) have already left for spawning grounds, which may lead to an overestimate of length. The spring emigration of spawners of the year, starting in Mars-April, may, on the other hand, lead to an underestimate (LARSSON 1973).

Male salmon grow faster (CHRISTENSEN and LARSSON 1979) and attain maturity earlier than female. Almost all grilse are known to be males. If the proportion of grilse varies from year to year (see e.g. LARSSON and SVENSSON 1974), so does the sex-ratio of A1+ fish caught offshore. This emphasizes the importance of separating the sexes in growth analysis. Unfortunately, the data doesn't allow of sex separation. Besides precocious males, the salmon can not be sexed as smolts, and there is not much data on sex in the recovery files either.

At present, some 80 % of the total offshore catch of salmon is taken by 160 mm drift nets (Report of...1991), which are highly selective gear, and 20 % by long lines, which are somewhat less selective (CHRISTENSEN and LARSSON 1979) The ratio is, however, by no means constant. Besides "normal" alteration, some major changes have taken place in the salmon fishery during the study period (e.g. 1978), and, probably in the composition and selectivity of off-shore fishery, too. Because of the scarcity of the data, all recoveries regardless to the gear were put together in this study. This probably adds to the variation of length data, but makes it less size selected as well.

At A1+ stage, drift nets select for the largest and fastest growing individuals (CHRISTENSEN and LARSSON 1979, see also Fig 6.). The intensity of selection depends on the size and, hence, on the growth of the fish belonging to a given year-class. Thus, gear selection (passive), as well as the active selection by the fishermen (size limit), tends to "dampen" the real size variation present in the population. - Besides, the largest individuals are probably caugth already in September-October, when the growth still continues.

As a matter of fact, drift nets don't select for fish length, but rather for fish girth. There is some evidence, that the condition factor of salmon varies from year to year. KARLSSON and ERIKSSON (1990), e.g., reported a condition factor 1.24 for the salmon caught offshore in the autumn 1990, which is an exceptionally high figure if compared with a long-term (1977-1990) average (1.10) during September and October. This variation is another source of biase in the growth data, irrespective of whether it is correlated with the length (or growth history) of the fish or not.

Size selection of drift nets may change within a winter season as well. Length increment between November and April is supposed to be minimal (e.g. THUROW 1966, 1973), but CHRISTENSEN (1961) has reported a considerable decrease in the condition factor of salmon during the winter. As a concequence, growth data may be biased by between year chances in the timing of winter fishery.

4.2. Variation of growth rate

Fluctuations in the age-spesific size of salmon have drawn much attention. LINDROTH (1964 and 1965) demonstrated a long lasting size decrease starting from the 1939 year-class. THUROW (1973) found a slight negative trend in the length of A1+ salmon in 1957-1972. According to Swedish tagging experiments in 1953-1972, there was a positive trend in mean weight of older salmon from year-class 1953 to year-class 1959, a negative trend for year-classes 1959-1964, and, again, a positive trend starting from year-class 1964 (LARSSON 1973).

For year-classes 1970-1988 a slight upward trend in the mean length of A1+ salmon was noticed (Fig 1.). However, no such trend can be found in the mean length increment, only ups and downs. This suggests, that the positive trend in mean length of A1+ salmon is mainly caused by the rise in smolt size (Table I).

The negative regression of length increment on smolt size (Fig 3, Table 4) in the whole data suggests better growth rate for small than for large smolts. The same analysis for separate year-classes (1984-1987) reveals, however, that the regression is clearly pronounced only for year-class 1987 with poor growth rate, indicating that the regression is an artifact caused by intensive size selection (Table IV).

Here, again, we have to remember the connection between growth (and size) and maturity and, on the other hand, between maturity and migration as a possible source of biase. The proportion of both precocious males and grilse may vary from year-class to year-class (LARSSON and SVENSSON 1974). Precocious males are known to be among the smallest smolts (CARLIN and OTTOSSON 1967), and there is evidence, that the same holds true for grilse, too (RITTER 1972, LARSSON and SVENSSON 1974 and Fig 6).

CARLIN (1969) explained the 1962-1966 decrease in the mean size of older salmon by intensified offshore fishery, rejecting the possibility of growth variation. More recent study, suggests, however, a major environmental component in determination of growth rate and, accordingly, the age-spesific size of salmon. KUIKKA (1991), e.g., found a positive correlation between the growth rate of salmon and the size of sprat stock. The problem of this kind of approach is, that we don't know, whether the size differences arise already in the post-smolt phase during the first summer, or later. Unfortunately, the scarce post-smolt data doesn't allow of a thorough growth analysis.

If post-smolt phase is critical, one might expect significant differences between the growth rate of southern and northern stocks of salmon. Before taking any regulatory measures, which would affect gear selectivity, e.g. changing the minimum mesh size of drift nets, a comparative growth analysis is of vital importance.

4.3. Growth rate and temporal distribution of tag-recoveries

The positive correlation between growth rate (length increment) and A1+ percentage (Table III), as well as the positive regression of A1+ percentage on mean length of each smolt group (Fig 4), is easy to explain: the sooner the fish attain legal size and recruit to the fishery, the sooner they are caught.

There are, however, some signs that the connection between mean length increment and A1+ percentage is breaking down. Year-classes 1986 and 1987, despite of their average or poor growth, gave exceptionally high percentages of A1+fish (Fig 2.). This might be explained by large smolt size and/or high condition factor of A1+ fish.

So far, there is no information on the connection between temporal and spatial distribution of tag recoveries. One might assume, that the sooner the fish are caught, the smaller is the number of spawning migrants, and vice versa. The connection between growth and maturity makes the picture, however, more complicated. Fish belonging to a year-class with good growth rate probably mature and leave for spawning grouds earlier than fish belonging to a year-class with poor growth rate.

4.4. Growth rate and tag return rate

Positive correlation between growth rate and tag return rate (Table III) indicates, that same factors, that regulate growth, affect survival as well. In addition, the correlation between growth rate and temporal distribution of tag recoveries suggests, that there is one more factor to be taken into account in this context, i.e. the effect of tag loss.

ISAKSSON and BERGMAN (1978), studying the salmon releases in Iceland, reported a 10% tag loss for smolt year-classes 1974 and 1975 between the time of release and time of recovery. The data collected from the Baltic main basin by an ICES programme

(Report of... 1991) indicated a 20 % tag loss for the season 1988/89 (smolt year-classes 1986-1988), 10 % tag loss for the season 1989/90 and 30% tag loss for the season 1990/91.

The problem arising from this kind of approach is, that it doesn't separate between age groups. One might assume that tag loss is not instantaneous, but rather goes on during the whole life span of tagged fish, perhaps with varying speed. As a consequence, the incidence of tag loss migth depend on the length of the sea phase before recapture, which in turn would lead, e.g., to an underestimate of the survival of year-classes with poor growth and to a biased estimate of the distribution of salmon catches between fishing areas.

Indeed, a small data collected from the mouths of rivers Kokemäenjoki and Karvianjoki (trap net -fishery) suggests, that tag loss is a major source of biase in tagging data (Table V). In age group A1+ the number of tagged fish was even higher than expected, in age group A2+ 50 % and in age group A3+ only 25% of the expected number. Besides tag loss, these numbers may, of coarse, indicate, that the tag makes the fish more vulnerable for (trap net) fishery at A1+ phase. It is also possible, that the tagged fish have been larger than the untagged fish - which is not unusual in tagging experiments. In any case, the phenomenon should be taken seriously, and all possible data concerning this issue should be collected and analysed.

4.5. "Year class -effect"

Year class related factors explain a substantial part of the variation in tagging data. But what are these factors ? It is obvious, that the fluctuation of growth rate is mainly caused by changes in marine environment, e.g. in temperature regime and food resources (KUIKKA 1991). The connection between environment and return rate is somewhat more complex. Some factors obviously affect return rate via growth rate - as suggested by the correlation between length increment, return rate and A1+ percentage - some others probably directly. The latter include, e.g., the size of predatory fish stocks (LARSSON 1977) and - in the broader sense of the word "environment" - changes in salmon fishery and tag reporting activity, too.

Changes in smolt quality - and in releasing practice - may add to the year-to-year variation of tagging data as well. One might, however, assume, that if compared with "environmental" chances, these factors are of minor importance - perhaps with the exception of smolt size. On the other hand, differences in smolt quality and releasing methods, etc., probably explain a major part of within year-class variation of tag return rate. In this respect tagged fish are probably more heterogenous than untagged fish belonging to same year-class.

4.6. Smolt age and size

Smolt size is connected with smolt age. In these data the mean length of different smolt groups varied between 132 and 170 mm (mean 155, n=30) for 1+ smolts, between 141-240 (mean 176, n=217) for 2+ smolts and between 143-261 (mean 196, n=105) for 3+ smolts. The regressions of mean size at recapture, A1+ percentage and return rate on smolt size indicate, that the consequences of a large scale shift to younger and smaller smolts, perhaps with a simultaneous change in the minimum mesh size of drift nets from 160 to 180 mm, would be far reaching. During periods of poor growth, practically no A1+ salmon of Gulf of Bothnian origin would be caught from the Main Basin.

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Table I. Releases of tagged smolts in the river mouths of ICES 31 in 1970-1988

Releases				Recovery data				
Year	No of groups	No of smolts	Mean (* size (mm)	Adult return-%	A1+ recoveries Mean length (mm) at Release	Recapture	Mean length increment	A1+ percen-tage
1970	7	8300	154.7	8.0	157.9	673.3	515.3	55.8
1971	4	4000	166.8	14.5	170.6	687.5	516.9	74.4
1972	5	4993	175.2	21.8	179.5	716.4	536.8	64.6
1973	11	8998	159.9	15.2	163.8	706.9	543.1	68.1
1974	7	5500	168.6	9.3	173.5	672.4	498.8	54.2
1975	11	8427	167.1	8.8	172.4	668.9	496.5	48.9
1976	6	5446	169.9	4.4	178.1	697.8	519.8	51.5
1977	18	11973	174.7	3.6	182.7	652.1	469.4	38.5
1978	11	9559	164.6	3.6	177.8	670.8	493.1	37.1
1979	13	8529	177.8	5.2	182.4	646.3	463.9	31.2
1980	31	13840	178.8	6.4	193.9	663.5	469.6	47.9
1981	16	13303	183.5	3.7	198.9	680.6	481.7	44.9
1982	23	20803	177.8	6.2	179.3	713.9	534.7	51.0
1983	17	14895	179.2	8.3	187.1	740.7	553.6	62.0
1984	28	27395	172.2	9.1	179.3	718.6	539.3	67.7
1985	32	30854	183.1	9.2	195.4	706.1	510.7	65.8
1986	41	35622	190.5	6.8	208.8	720.2	511.4	76.5
1987	42	35509	191.1	4.1	212.6	692.9	480.3	66.6
1988	29	28667	190.4	11.8	196.6	759.1	562.4	73.8
TOT.	352	296613	180.1	7.7				63.6

(* Weighed mean of the means for different groups

Table II. Results of ANOVA

ANOVA for length increment					
Source of variation	Sum of Squares	d.f.	Mean square	F--ratio	Sign.level
COVARIATE					
length at release	253657.4	1	253657.4	47.90	* * *
MAIN EFFECT					
year of release	1659697.4	18	92205.4	17.41	* * *
RESIDUAL	14060895.2	2655	5296.0		
TOTAL	15974250.0	2674			

ANOVA for tag-return rate (arcsinV%)					
Source of variation	Sum of Squares	d.f.	Mean square	F--ratio	Sign.level
COVARIATE					
mean length at rel.	884.6	1	884.6	58.24	* * *
MAIN EFFECT					
year of release	6049.5	18	336.1	22.13	* * *
RESIDUAL	5042.9	332	15.2		
TOTAL	11977.0	351			

ANOVA for A1+percentage (arcsinV%)					
Source of variation	Sum of Squares	d.f.	Mean square	F--ratio	Sign.level
COVARIATE					
mean length at rel.	2428.2	1	2428.2	85.27	* * *
MAIN EFFECT					
year of release	15158.5	18	842.1	29.57	* * *
RESIDUAL	8144.4	286	28.5		
TOTAL	25731.1	305			

Table III. Correlation between mean length increment, (growth) tag return-rate (survival) and A1+percentage for each year-class

Correlation analysis

	GROWTH	SURVIVAL	A1+ -PERCENTAGE
GROWTH	1,000	0,622	0,653
	19	19	19
	0,000	0,004	0,002
SURVIVAL	0,622	1,000	0,613
	19	19	19
	0,004	0,000	0,006
A1+PERCENT.	0,653	0,613	1,000
	19	19	19
	0,002	0,006	0,000

Coefficient, sample size, significance level

Table IV Parameters for the regression of individual length at recapture and length increment on individual length at release

Year-class	Length at recapture RC	R^2	F	Length increment RC	R^2	F	Intercept	n
1984	0,660	0,038	11,9***	-0,344	0,011	3,3ns	600,9	301
1985	0,910	0,093	42,4***	-0,088	0,001	0,4ns	528,9	443
1986	0,840	0,097	40,0***	-0,159	0,004	1,4ns	544,7	374
1987	0,430	0,042	7,3**	-0,571	0,072	12,6***	601,1	169
1988	0,990	0,086	21,7***	-0,012	0,000	0,0ns	564,7	234
70-88	0,653	0,054	153***	-0,347	0,016	43,1***	585,6	2675

Table V. The expected (exp) and observed (obs) number of tagged salmon in catch samples from the mouths of rivers Kokemäenjoki and Karvianjoki in 1984-1987 (trap-net fishery)

Releases		Catch samples in 1984-1987														
Year	%	A1+ salmon			A2+ salmon			A3+ salmon			A4+ salmon			A1+ -A4+		
class	tagged	n	exp	obs	n	exp	obs	n	exp	obs	n	exp	obs	n	exp	obs
1982	7.8				63	4.9	2	146	11.4	3	6	0.5	0	215	16.8	5
1983	1.6	22	0.4	2	385	6.2	6	228	3.6	0	11	0.2	0	646	10.4	8
1984	2.7	59	1.6	6	230	6.2	1	128	3.5	1				417	11.3	8
1985	2.6	18	0.5	1	117	3.0	0							135	3.5	1
1986	4.1	50	2.0	3										50	2.0	3
Total		149	4.5	12	795	20.3	9	502	18.5	4	17	0.7	0	1463	44.0	25

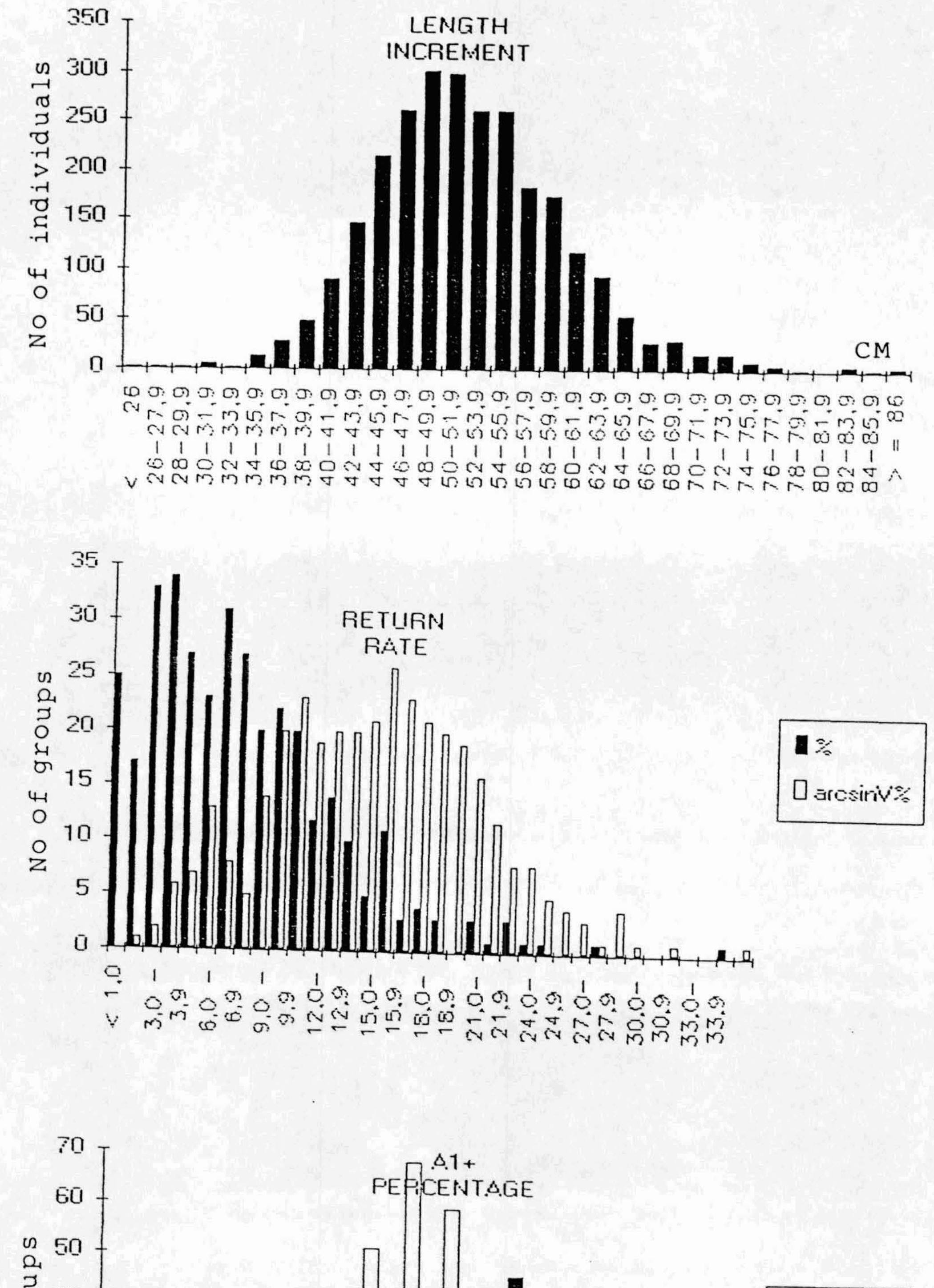


Fig 1. Frequency distributions for "length increment", "return rate" and "A1+ percentage"

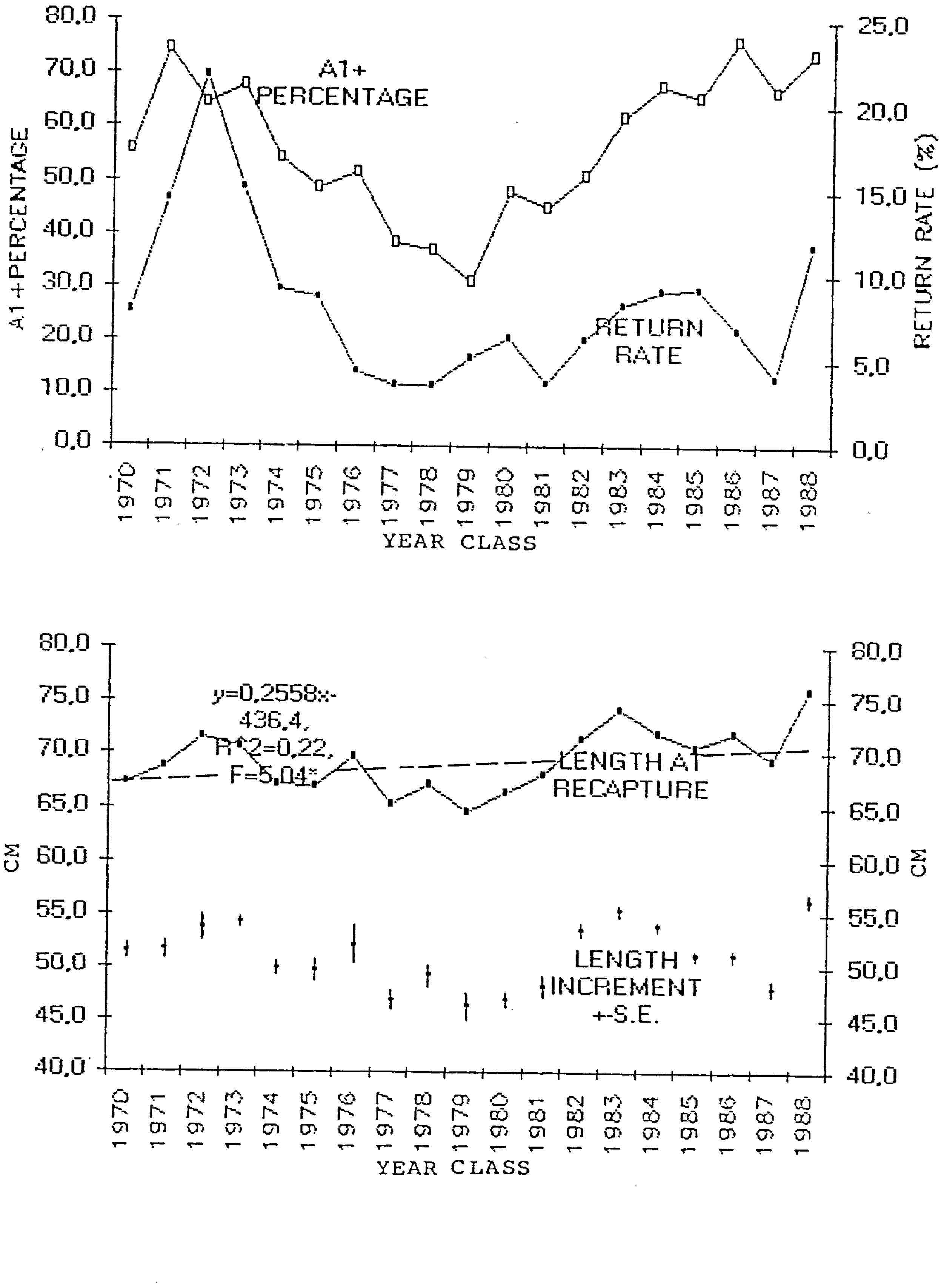
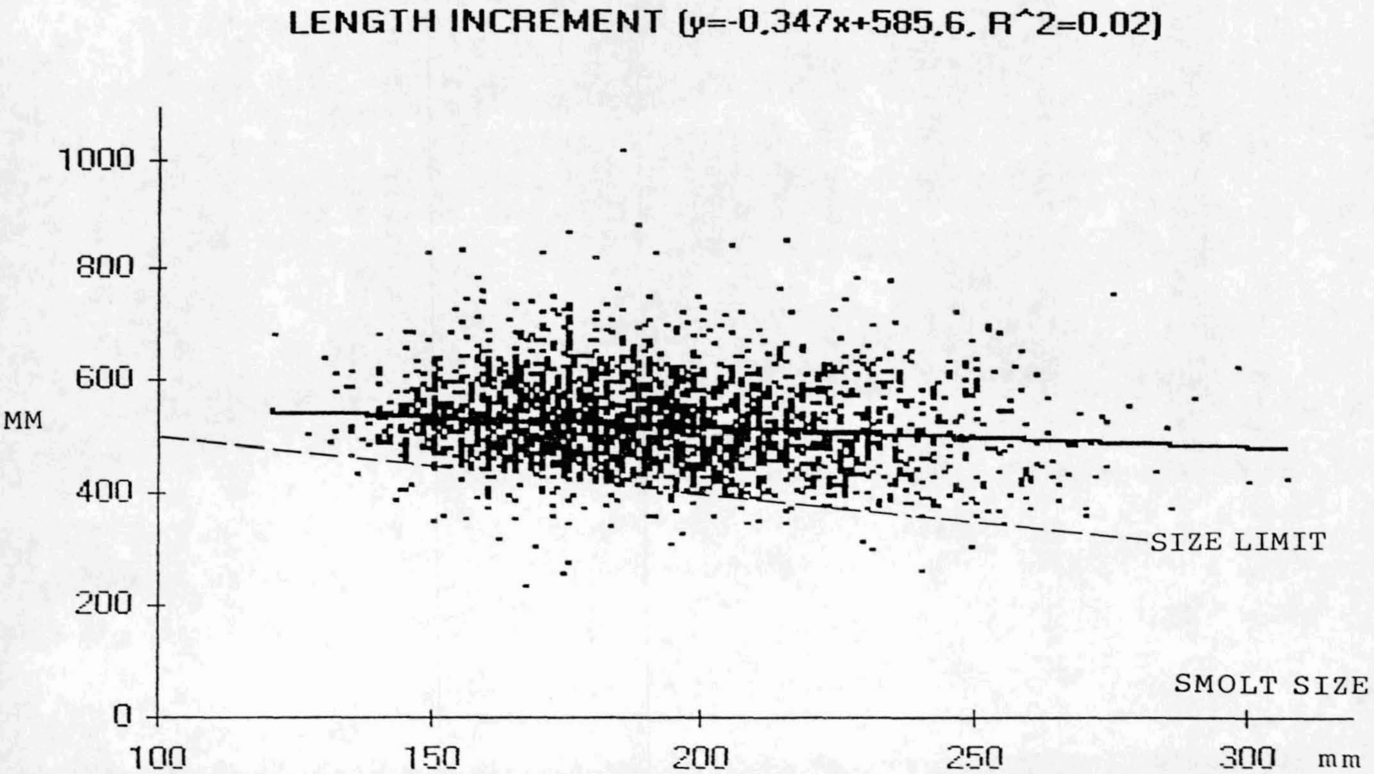


Fig 2. Mean return rates and A1+ percentages (above) and mean lengths at recapture (A1+) and mean length increments (below) for year-classes 1970-1988



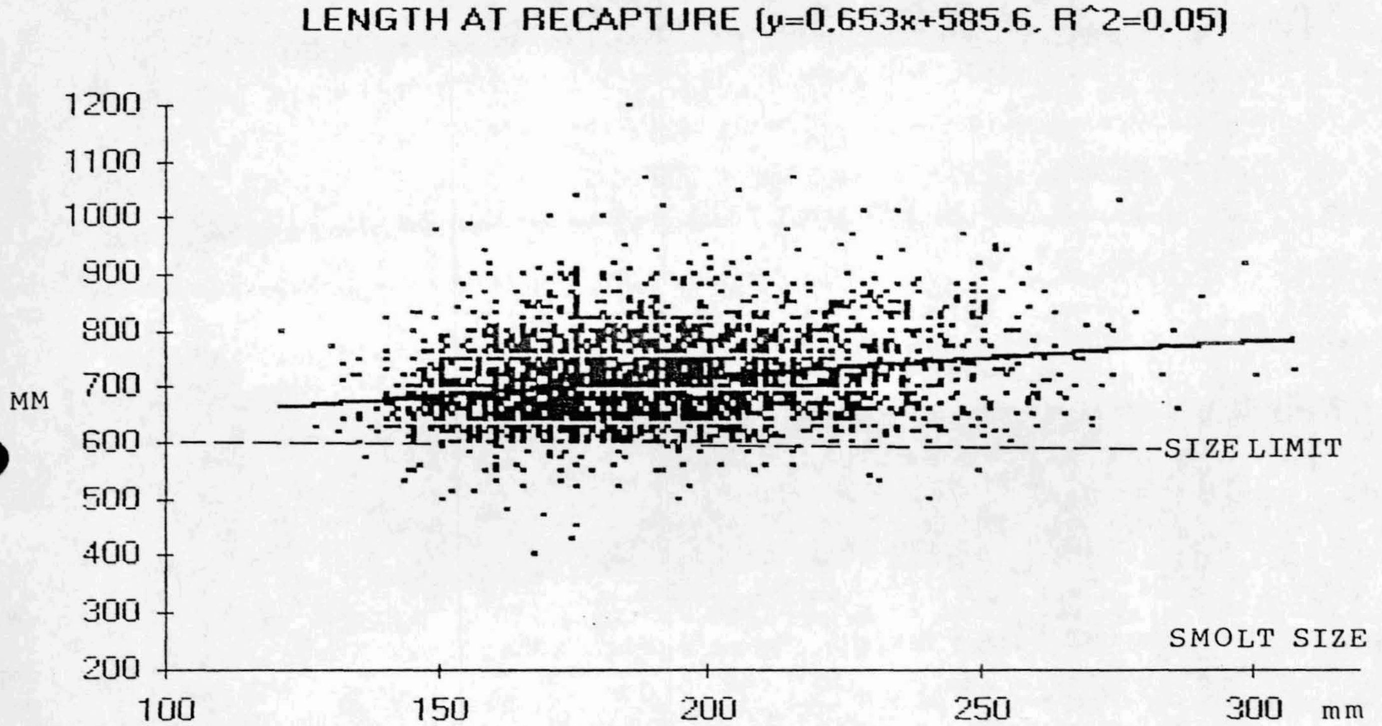
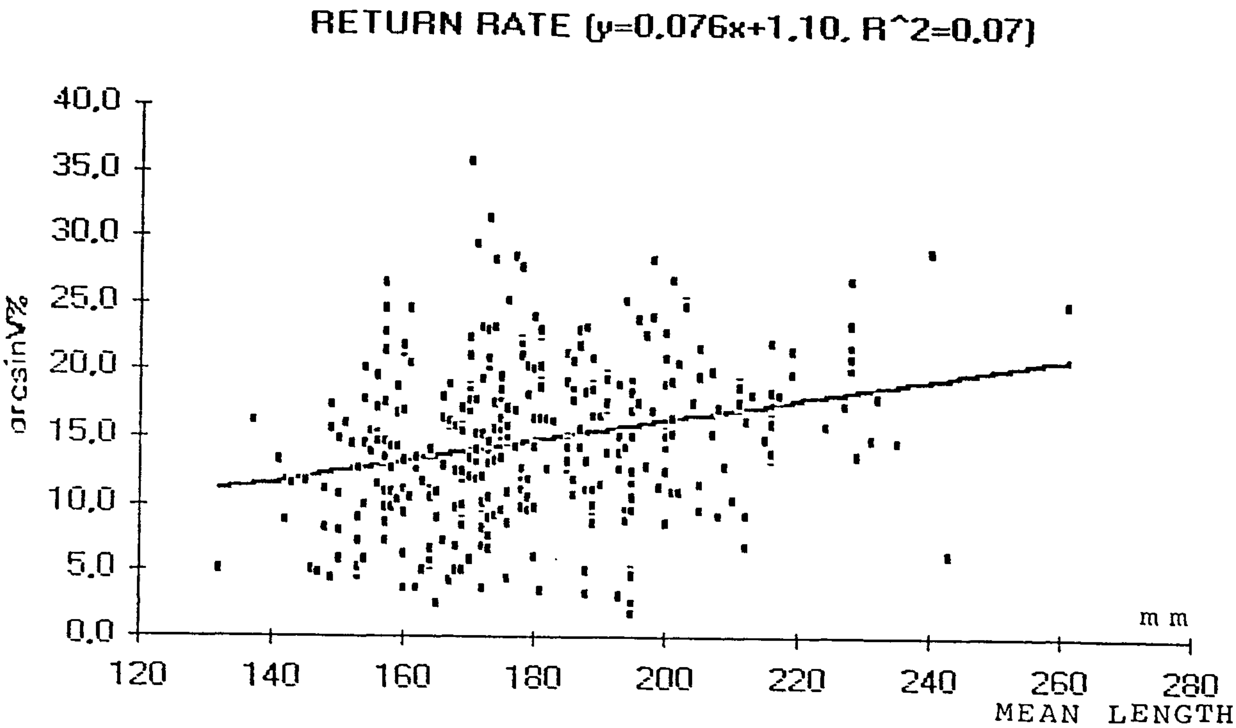


Fig 3. The regressions of length increment (above) and length at recapture (below) on individual length at release



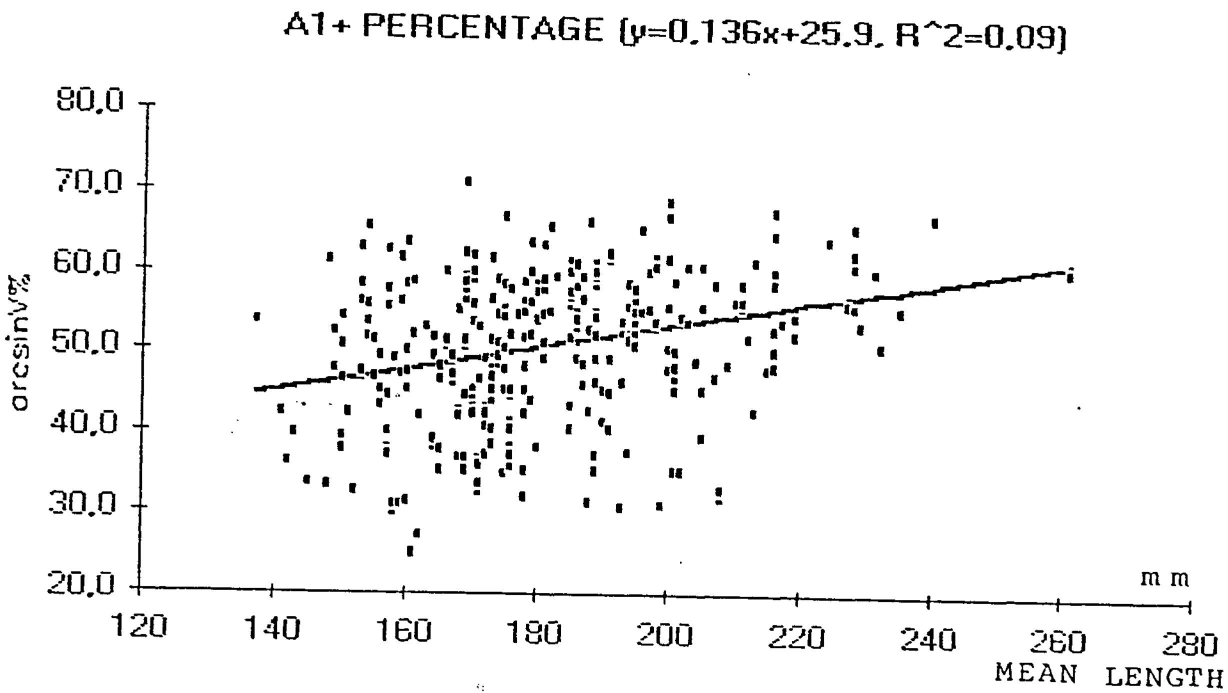


Fig 4. The regressions of return rate (above) and A1+ percentage (below) for each smolt group on mean length of the group at release

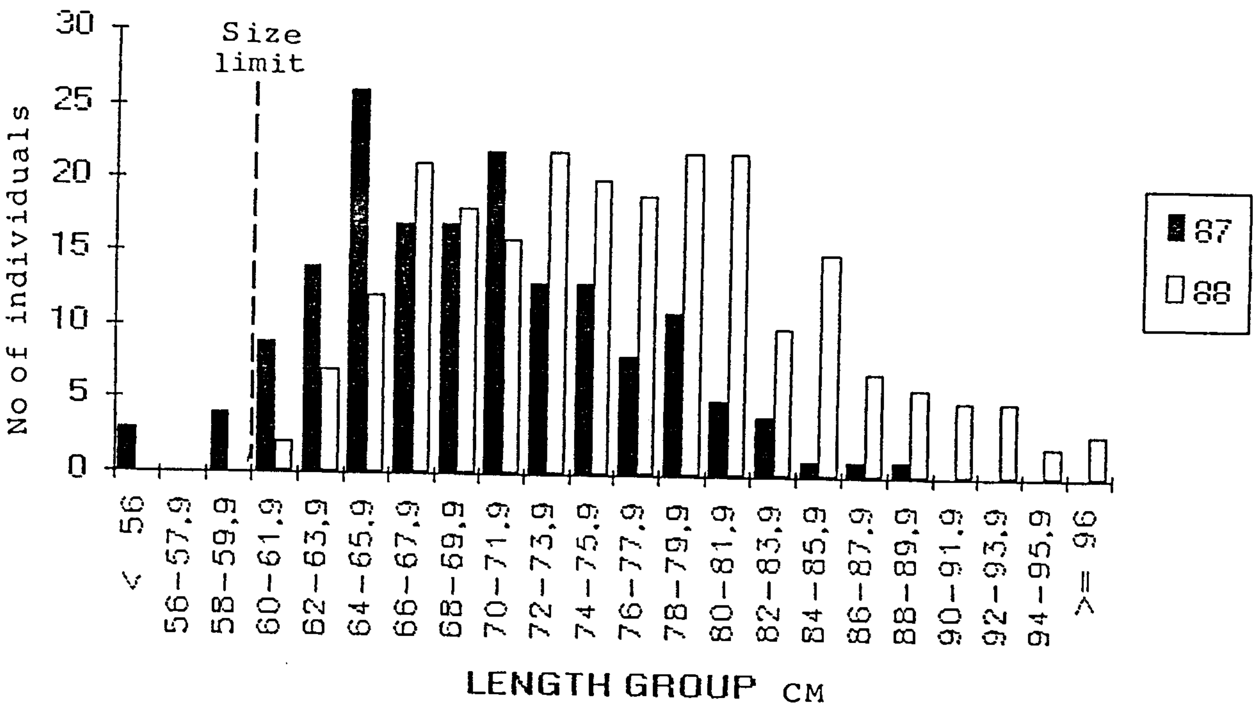


Fig 5. Length distribution of A1+ salmon for year-classes 1987 (poor growth) and 1988 (good growth)

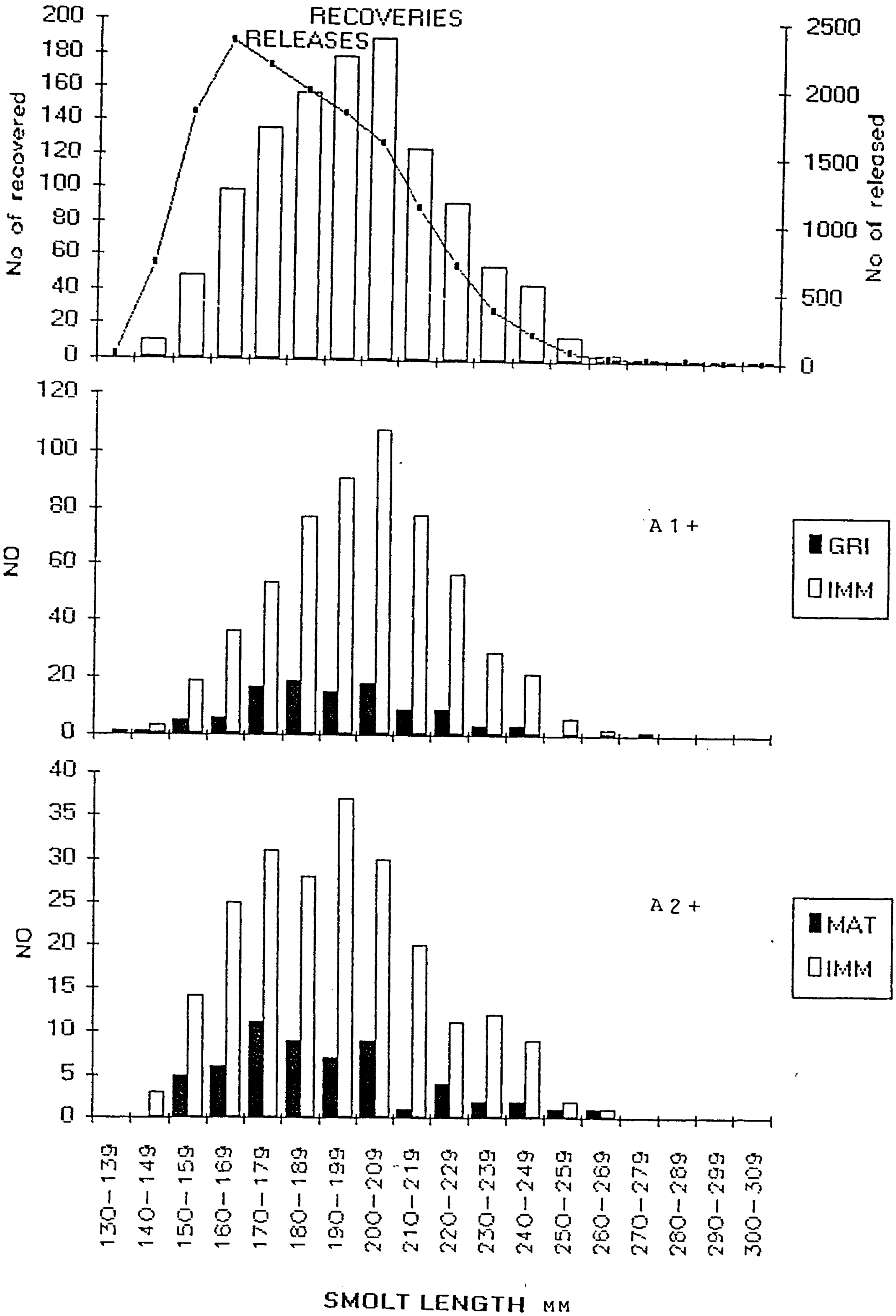


Fig 6. Frequency distributions of smolt length for releases in the mouth of river Iijoki in 1985. Above: All releases and all recoveries. Center: Grilse and immature A1+ salmon. Below: Mature and immature A2+ salmon