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THE DIVERSITY AND SEASONAL SPAWNING MIGRATION OF SALMON (SALMO SALAR L.) IN THE RIVER TORNIONJOKI

by

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ABSTRACT

The age variation within the salmon stock originating from the natural strain in the River Tornionjoki was correlated with the seasonal spawning migration in the river and with the length of the upstream migaration. The more years a salmon spent in the sea, the earlier in the spring it tended to migrate into the river. The female spawners that had spent four years in the river migrated first.

The timing of the seasonal spawning migration of the male was nearly the same for all smolt age groups. Salmon parr usually spend 2 to 4 years in the river. The relative number of salmon that had spent two years in the river among the spawners in the catch was significantly greater in the lower part of the run than in the middle or upper part of the river. The age variation in the salmon stock relative to the length of the upstream spawning migration in the River Tornionjoki indicated that the length of the life history of the spawners increased gradually from south to north.

The drastic reduction in the population density of juvelines, especially in the upstream part of the migration route, is most likely a consequence of preferential removal of the larger and older fish by selective fishery. It is those fish with long life histories that appear to spawn further upstream. The adaptive genetic and ecological diversity of the salmon stock in the River Tornionjoki can be maintained by allowing the upstream migration of a sufficiently large breeding stock to take place throughout the whole spawning season.

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CONTENTS

1. INTRODUCTION

Atlantic salmon (<u>Salmo salar</u> L.) show great variability in phenotypic and genotypic characteristics (Nyman and Pippy, 1972; Schaffer and Elson, 1975; Riddell and Leggett, 1981; Koljonen, 1985). The diversity among salmon stocks from different streams is called stock differentiation, and it results from the adaptation to local environments and the homing behaviour of fish (Leggett, 1977). The stock-specific variation in the life histories of salmon from different rivers in the Baltic region and along the coast of eastern North America is associated with environmental conditions in the native streams (Alm, 1934; Schaffer and Elson, 1975). Both the Baltic and Atlantic salmon stocks exhibit genetic, stock-specific variation (Nyman, 1966; Payne, 1974; Koljonen, 1985).

Salmon stock differentiation in genetic, ecological, or morphological traits occurs also within each water body (Saunders, 1967; Möller, 1970; Ryman et al., 1979; Ståhl, 1981). Saunder's (1967) investigation on salmon stocks in the Miramichi River on the East Coast of North America showed that there were two stocks, one that makes early run and spawns in the upper reaches of the river, and another that undertakes a late run and spawns further downstream. Möller's (1970) data on the transferrin pattern indicates genetic differentiation between these two salmon stocks in the northwestern Miramichi. Ryman et al. (1979) discovered two sympatric populations brown trout (Salmo trutta L.)

with apparently complete reproductive isolation in Lake Bunnersjöarna, Sweden. The genetic difference between these brown trout stocks was very small, but they showed great variability in their ecological and morphological characteristics. A pattern of stock subdivision in natural Baltic salmon populations of the main drainage system between the Lainio and Tornio Rivers in northern Sweden has also been found (Ståhl, 1981).

In this drainage system, stock differentiation of salmon and trout is often associated with the spawning migrations (Saunders, 1967; Saunders and Allen, 1967; Schaffer and Elson, 1975). On the northeastern coast of North America, the larger salmon tend to migrate upstream in the spring when the run-off is greatest, and smaller fish do so in the summer when water velocities are slowest (Schaffer and Elson, 1975). In the Miramichi river system, the early-run spawners have spent more years in the river than those making the late runs (Saunders, 1967).

Salmon stock differentiation has recently attracted interest for investigations on life history evolution. It can be assumed that variation in the demographic parameters among and within semi-isolated salmon stocks is adaptive and the result of natural selection (Schaffer, 1979).

In this paper, the age and size variation within salmon stock originating from the natural strain in the River Tornionjoki have been related to the timing of the seasonal spawning migration and the length of the upstream migration. This kind of knowledge about the ecological and genetic variation within a salmon strain is necessary for monitoring the performance of the strain and for monitoring the effects of stocking activities. The data on stock-specific variation in salmon is useful in conjunction with the planning of temporal and local control of fishing and in rehabilitation and breeding programmes.

The upstream migration of salmon in the River Tornionjoki starts at the beginning of June and continues as late as September and October (Petersson, 1975). The spawning migration of salmon can cover over 400 km from the mouth of the river to the farthest upstream spawning areas in Finland and Sweden (Nordqvist, 1904; Toivonen, 1962; Karlström, 1963). Spawning continues for about six weeks from September to the end of October (Karlström 1963).

2. MATERIALS AND METHODS

The salmon studied were caught in 1983 and 1984 in the Rivers Tornionjoki , Muonionjoki, and Könkämöeno by fishermen (Pruuki et al., 1985 ; pers. comm.) (Fig. 1). They included 74 wild spawning salmon in 1983 and 164 wild and 7 hatchery-reared ones in 1984. Only wild fish were examined in this investigation. The other 393 wild spawning salmon came from the coast between the mouths of the Rivers Tornionjoki and Kemijoki in 1982 and 1984 (Kallio, 1986). These wild fish from the coast probably belonged to the natural salmon strain of the River Tornionjoki since there is no any other large natural salmon stock in the northern part of the Botnian Bay region (Ikonen and Auvinen, 1984). These salmon were caught for stripping and selected from the catch because of their large size.

The size, sex, and time and place of capture of the salmon were recorded. I. Antere of the Finnish Game and Fisheries Research Institute examined the scales to determine how many years had been spent in the river and how many in the sea, as well as to detect possible hatchery origins (Antere and Ikonen 1983).

The dates of capture of the salmon were assumed to mark the progress of the seasonal migration in the river. The length of the upstream migration is the distance between the mouth of the river and the site of capture.

The effect of the time spent in the stream on the age and size at maturation of the salmon was determined by comparing the smolt age groups with each other. The significance of the differences between these groups was calculated using the t-test (Dixon, 1981).

The relationship of the age variation within a salmon stock to the timing of the upstream migration was determined by comparing the regression lines between the years of life in the sea with the dates of upstream migration by the different smolt age groups, and computing the mean times of the upstream spawning migrations by each group establish accorging to the number of years the fish spent in the sea. The distributions of the years of stream life by spawners in the different parts of the river were tested using the chi-squared test. The statistics were compiled using BMDP programs (Dixon, 1981).

3. RESULTS

3.1. Association of river life with age and size at maturation

The age and size at maturation were not found to vary with the length of time spent in the river by the spawners either in 1983 or in 1984 in the river material (Table 1). In contrast, a comparison of the smolt age groups with spawners at the mouths of the Rivers Kemijoki and Tornionjoki revealed that the number of years in the stream increases with the number of years in the sea. The female spawners that had spent four years in the river were larger and older at maturity than the female spawners after three years in the river ($p < 0.05$ and $p < 0.1$; Table 2). The male spawners after three years in the river had spent more years in the sea and had reached a larger size than migrants after only two years in the river ($p < 0.05$; Table 2).

3.2. Age variation and upstream migration

The number of years of spawning salmon spent in the sea was correlated with the timing of the seasonal spawning migration (Fig. 2; Table 3). The more years a salmon had spent in the sea, the earlier in the spring it tended to migrate upstream. After three years in the sea, most spawners migrated upstream in June, while after only two years in the sea, they can be found migrating from the middle of June to the end of August. After only one year in the sea, the salmon began to migrate upstream at the beginning of July (Table 4).

The length of time female spawners have spent in the river is also correlated with the timing of the seasonal upstream migration. Most female spawners after four years in the river migrated at the end of June, while after only three years, the females swam upstream mainly in the middle of July. All salmon caught before June 10 were females that had spent four years in the river (Table 3; Fig. 2).

The entry of female spawners into the rivers occurred earlier in the season than in the males (Fig. 2; Table 3). The females in all smolt age groups had also averaged more winters in the sea than the males. The smolt age composition of the male spawners was the same during the whole season (Fig. 2).

Salmon parr usually spent 2 to 4 years in the River Tornionjoki. The percentage of spawning salmon that had spent only two years in the river was significantly higher in the catch from the lower part of the run than in those from the middle or upper parts of the river (Table 5).

4. DISCUSSION

4.1. Effect of smolt age on sea life

Many fishery scientists have recognized stock-specific variation in the age and length of the time spent in the river or sea by species in Salmonidea. Alm (1934), Hutton (1937), Stewart (1949), Ritter (1974) and Thorpe (1980) reported inverse ratios between the numbers of years in the rivers and in the sea. However, Dahl (1937) did not observe any relationship between smolt age and the number of spent years in the sea by salmon stocks. The data on fishes from the coast revealed that when the number years in the river increased, so did the number years in the sea, but the data on fishes from the river did not indicate this kind of relationship.

Variation within a stock is not nessesarily the same as variation between the stocks. It is obvious that relationship between the number years in the river and those in the sea is not constant, either between or within stocks of Atlantic salmon. Rather, the variation in these traits is stock-specific and sexually dependent and has to be explained on the basis of several variables.

Slow-growing parr were found to spend more years in the river than the fast growning parr, on the average (Menzies, 1927; Elson 1957; Jones 1959; Shearer 1973). The growth rate in streams seems to affect age at smoltification, if this occurs at a definite size. It is probable that salmon grow more slowly in the northern part of the river, where the growth period is shorter, than in the southern part. That a greater procentage of spawners with only two previous years in the river are found in the lower reaches than in the middle or upper part of the river provides evidence for this. The observations of Dahl (1916) and of Alm (1959) that the number of years salmon spend in the rivers increase from south to north in the Northern Hemisphere lend additional weight to this theory. The relationship between the growth rate in the river and the size and age of the smolts was not investigated by scale examination.

4.2. Age variation and upstream migration

The age variation of spawners during the whole seasonal upstream migration was investigated. It was clear that both male and female salmon that had spent more years in the sea undertook the upstream migration earlier. Moreover, the female spawners after four years in the river, migrate upstream at the beginning of summer, but female salmon after only two years in the river migrate during the whole season.

The age distribution of smolt in various parts of the river indicated that most salmon with only two years in the river were caught in the lowest part and near the mouth of the river. The majority of the data came from the lowest part of the river, where some spawners just beginning the longer upstream migration were probably also caught. These observations support the hypothesis that big, old salmon, especially female spawners, migrate further up the river than young, small ones. It has also been observed during investigations on the differences among salmon stocks that the spawners in a long river are older on average, than the salmon in a short river (Schaffer and Elson, 1975; Thorpe and Mitchell, 1981) and that the percentage of salmon that have spent only one year in the sea is lower in longer rivers (Scarnecchia 1983).

Homing, reproductive isolation and natural selection form amd maintain adaptive sub-stocks. The salmon strain of the River Tornionjoki can be divided into the genetically separate populations (Ståhl, 1981). The correlations of the age and size variation with the timing and length of the upstream migration by salmon of the strain in the River Tornionjoki is insufficient to indicate that there the salmon stocks differ considerably in life history traits. However, it is evident that the life history traits change gradually from south to north.

4.3. Age of female and male salmon at maturation

The variation in the life history within the stock was correlated with sex. The male spawners had spent fewer years in the sea than the females, and they migrated upstream later. The differences between males and females may be explained by the allocation of energy to reproduction and by the reproductive capacity of the sexes.

The resources available to an organism in any particular age class for reproduction, growth and maintenance are always limited. Increasing the resource allocation to reproduction can be expected to increase the immediate reproduction, but this can reduse the survival or fecundity in the future. The organism maximizes fitness during its whole life cycle (Gadgil and Bossert, 1970; Schaffer, 1979). The salmon may reproduce several times during its life, but the likelihood of its breeding at least twice is very low. According to the observations of Järvi (1932), 3.8 % of the salmon in the catch from the River Tornionjoki in 1930 and 1931 had reproduced earlier. The percentage of such fish among present spawners is below 1 % (Pruuki et al., 1985). Thus, the first breeding essentially represents the reproductive effort of the whole life.

Egg production by females is associated with the size of the fish (Pope et al., 1961; Larsson and Pickova, 1978; Kallio, 1986). The female salmon obviously benefit from spending several years in the sea, which increases their reproductive capacity and allows them to store up energy for the spawning migration. The farther upstream the female salmon migrate the more they have to produce eggs in relation to the cost of upstream migration. The cost of migrating upstream to the Atlantic salmon is demonstrated in various ways, for instance by the fact that large salmon migrate during periods of high water flow, and the small salmon travel during periods of low water flow (Schaffer and Elson, 1975).

The reproductive capacity and weight of male salmon do not increase as much as those of females in the sea. Large males have better chances of breeding with a large female salmon (Belding, 1934; Jones and King, 1949; Jones 1959). However, small, precocious males and grilses are able to take part in breeding along with the large male spawners as so-called satellite males, and as such, when they attempt to fertilize some of the eggs. If precocious males or those that have spent only one year in the sea do indeed manage to fertilize eggs, natural selection maintains maturation as a parr or after one year in the sea. The maturation of precocious males and their age at maturation in the sea are two independently heritable traits (Glebe et al,. 1980; Gjerde 1984).

4.4 Changes in size and age distribution in spawning population

A comparison of the present age distribution of the salmon stock of the River Tornionjoki with the age distribution at the beginning of the century reveals that the proportion of young fish in the spawning population has increased. For example, the procentage of three sea year salmon has fallen from 29 % to 13 % in the period between 1930 and 1970, and the percentage of spawners that have spent four years in the river, had fallen from 28 % to 21 % in the same period (Järvi, 1938; Pruuki et al,. 1985). The relatively great decrease in the oldest class of fish is assumed to be due to a decline in the spawning population reaching the uppermost part of the river. The decreases in the juveline densities have been most marked in this part (Karlström, 1983).

The age of salmon at maturation has been shown to be a heritable trait that can be affected by selection (Schaffer and Elson, 1975; Saunders, 1981; Thorpe et al,. 1983). The age composition of the spawning stock has tended to become younger, and the age-specific mean weight has decreased (Toivonen, 1983; Pruuki et al,. 1985). This age-specific mean weight decrease is greatest in those fish that have spent many years in the sea. Apparently, selective fishing causes the heritable changes in those genes affecting the age at maturation. Moreover, selective fishing takes fast growing salmon more often from the later-maturing groups than from the earlier maturing ones. Both these points have obviously affected the observed changes in the spawning salmon stock in the River Tornionjoki. The changes in the growth rate in the sea among different groups of spawners that have spent different periods of the time in the sea are not known, but it is possible to investigate this by scale examinations.

4.5. Conclusions

Since the salmon stock in the River Tornionjoki consists of differentiated substrains with different life cycles and homing behaviour it is necessary to maintain as much diversity as possible within the stocks and among sub-stocks by rehabilitation management and fishing limitations. The fishery should be regulated so that the spawning stock remains of adequate size during the whole seasonal upstream migration, and so that the natural stock is able to use all the nursery grounds of the species. In particular, it should guarantee the spawning success of the large salmon that have spent many years in the sea, because the substrains in the upper part of the river have decreased the most. It is reasonable to identify mating groups from captured salmon spawners, established on the basis of the time of the seasonal upstream migration, the age of the fishes, and their size at maturation.

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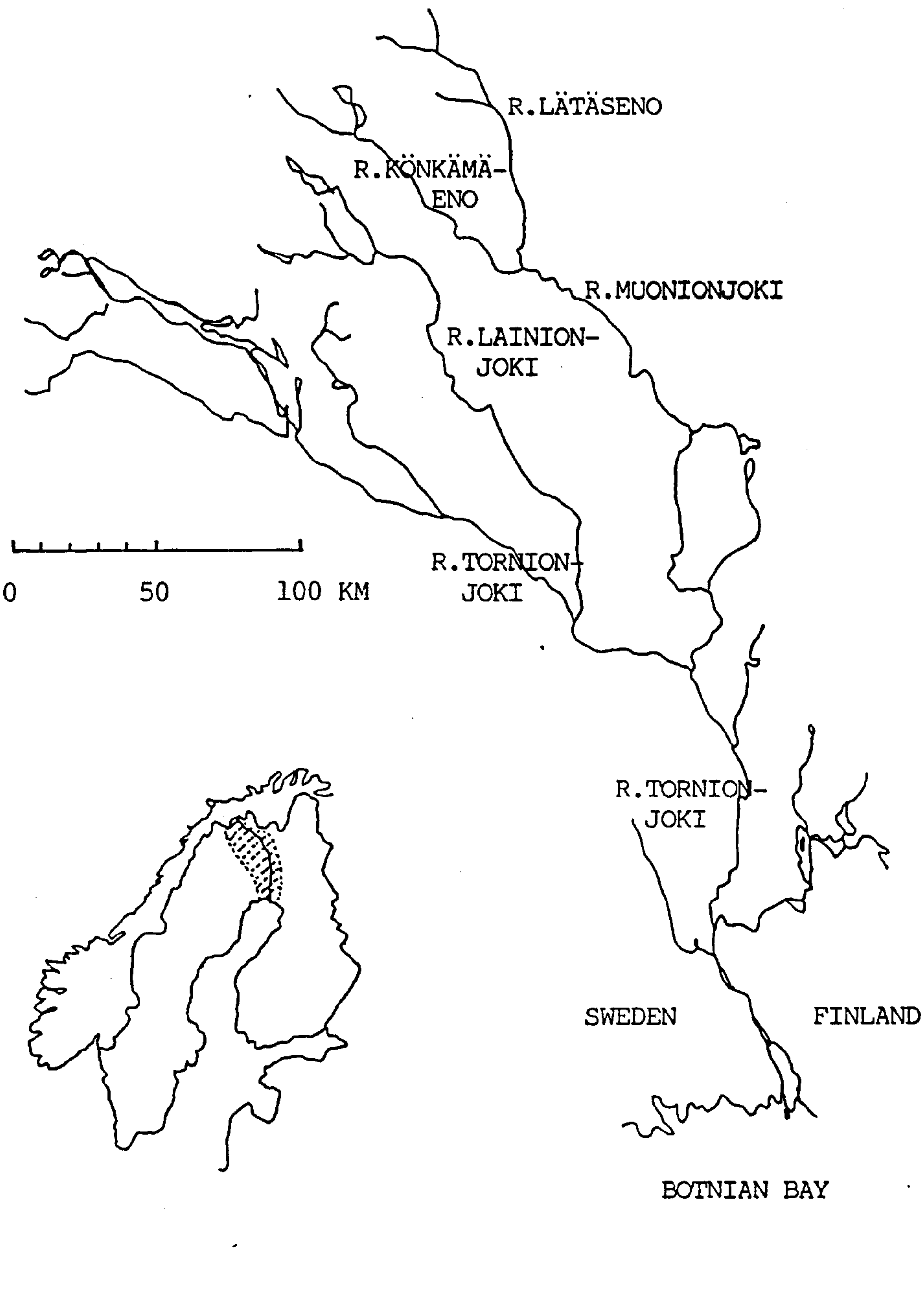

Figure 1. The main drainage system of the River Tornionjoki.

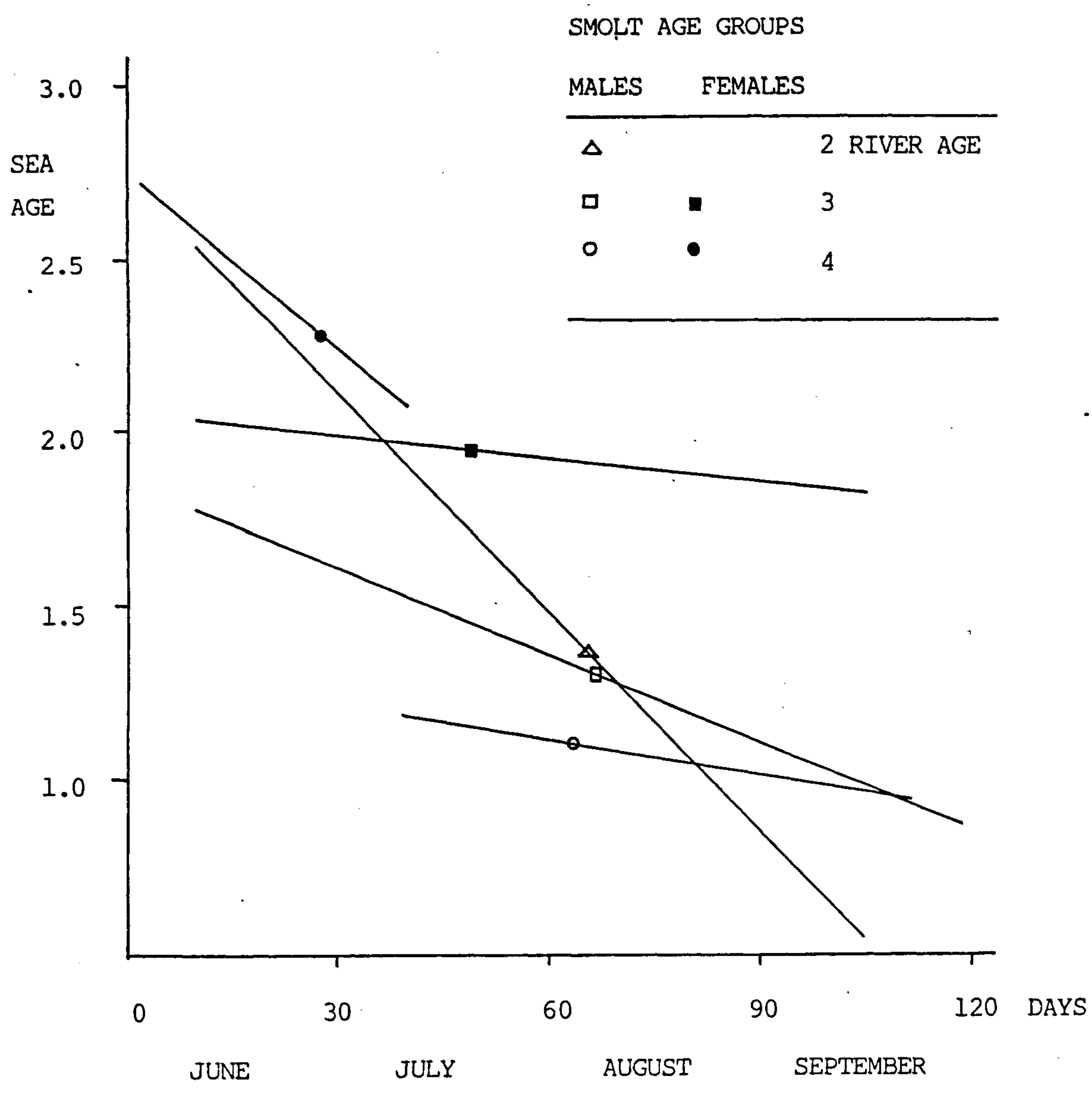

Figure 2. The regression lines between years in the sea and date of upstream migration by male and female salmon spawners in the different smolt age groups in the River Tornionjoki in 1984. The parameters can be found in Table 3.

Table 1. Weight, length and years in the sea of salmon spawners in the different smolt age groups in the River Tornionjoki in 1984. The differences between the smolt age groups have been determined using the t-test. Mean = $\bar{x}$, standard deviation = s, number of fish = n. Significance levels; $p < 0.05$ *, $p < 0.10^{o}$, $p > 0.1^{ns}$.

MATERIALS AND TRAITS	SMOLT AGE GROUPS 2.a				3.a				4.a		
	$\bar{x}$	s	n	p	$\bar{x}$	s	n	p	$\bar{x}$	s	n
FEMALES AND MALES											
WEIGHT (KG)	4.13	3.82	16	o	2.76	2.81	119	ns	3.46	3.16	29
LENGTH (CM)	73.6	28.1	16	ns	62.7	14.5	119	ns	66.0	16.2	29
SEA YEARS (Y)	1.60	0.73	15	ns	1.42	0.59	117	ns	1.55	0.82	29
FEMALES											
WEIGHT (KG)	9.16	6.33	3	*	4.43	3.17	25	ns	6.36	4.08	9
LENGTH (CM)	110.0	50.4	3	ns	75.3	15.5	25	ns	80.6	18.6	9
SEA YEARS (Y)	2.50	0.70	2	ns	1.91	0.58	24	ns	2.33	0.86	9
MALES											
WEIGHT (KG)	2.96	1.92	13	ns	2.30	2.50	93	ns	2.15	1.40	20
LENGTH (CM)	65.2	12.5	13	o	59.1	12.3	93	ns	59.4	9.8	20
SEA YEARS (Y)	1.46	0.66	13	ns	1.29	0.52	92	ns	1.20	0.52	20

Table 2. The weight, length and years in the sea of salmon spawners in the different smolt age groups near the coast and the mouths of the Rivers Kemijoki and Tornionjoki in 1982 and 1984. The differences between smolt age groups have been determined using the t-test. Mean = $\bar{x}$, standard deviation = s, number of fish = n. Significance levels; $p < 0.001^{***}$, $p < 0.01^{**}$, $p < 0.05^{*}$; $p < 0.10^{o}$, $p > 0.1^{ns}$.

MATERIALS AND TRAITS	SMOLT AGE GROUPS 2.a $\bar{x}$	s	n		3.a $\bar{x}$	s	n		4.a $\bar{x}$	s	n
FEMALES AND MALES											
WEIGHT (KG)	4.19	2.21	94		4.41	2.10	228		5.34	2.44	35
p				ns				*			
LENGTH (CM)	76.6	11.9	95		80.4	10.1	260		83.5	12.3	38
				**				o			
SEA YEARS (Y)	2.04	0.51	90		2.19	0.49	252		2.43	0.60	37
				*				*			
FEMALES											
WEIGHT (KG)	4.96	2.15	62		4.54	1.85	176		5.54	2.32	29
				ns				*			
LENGTH (CM)	80.7	10.2	62		81.1	9.1	194		84.5	11.9	31
				ns				ns			
SEA YEARS (Y)	2.21	0.41	61		2.25	0.45	194		2.48	0.62	31
				ns				o			
MALES											
WEIGHT (KG)	2.69	1.40	32		3.99	2.91	52		4.37	3.01	6
				*				ns			
LENGTH (CM)	69.0	11.2	33		78.2	12.3	66		78.9	13.8	7
				***				ns			
SEA YEARS (Y)	1.68	0.54	29		1.98	0.57	58		2.16	0.40	6
				*				ns			

Table 3. The regression lines between years spent in the sea and the date of upstream migration for the different salmon smolt age groups in the River Tornionjoki in 1984. Parameters: a = intercept, b = regression coefficient, s_b = standard error of the coefficient, r = correlation coefficient, 100 x r^2 = total proportion variation explained, F_1 = the F ratio that tests significance of the regression, F_2 = the equality of the regression lines.

MATERIALS NUMBER OF FISH		MEAN AND RANGE OF SEA YEARS	OF TIME OF UPSTREAM MIGRATION	REGRESSION STATISTICS a	b	s_b	r 100x r^2%	F_1	F_2
FEMALES AND MALES									
131	3.a, 4.a	1.41 1-3	61.3 2-119	2.06	-.010	.001	-.504 25.47	44.0^{***}	
105	3.a	1.41 1-3	63.2 10-119	2.02	-.009	.001	-.496 24.61	33.6^{***}	1.7^{ns}
26	4.a	1.42 1-3	53.8 2-111	2.35	-.017	.004	-.591 34.99	12.9^{**}	
FEMALES									
26	3.a, 4.a	2.03 1-3	43.6 2-105	2.34	-.007	.004	-.284 8.06	2.1^{ns}	
19	3.a	1.94 1-3	49.3 10-105	2.12	-.003	.004	-.180 3.25	0.6^{ns}	1.4^{ns}
7	4.a	2.28 1-3	28.0 2-40	3.23	-.033	-023	-.547 30.02	2.1^{ns}	
MALES									
113	2.a,3.a,4.a	1.27 1-3	65.8 10-119	1.88	-.009	.001	-.511 26.14	39.2^{***}	
8	2.a	1.37 1-3	65.6 10-105	2.72	-.020	.006	-.778 60.63	9.2^{*}	2.4^{*}
86	3.a	1.30 1-3	66.3 10-119	1.91	-.009	.001	-.529 28.01	32.6^{***}	
19	4.a	1.10 1-2	63.3 39-111	1.30	-.003	.003	-.220 4.85	0.86^{ns}	

Table 4. The timing of the seasonal spawning migration in the River Tornionjoki by salmon in different groups according to the time spent in the sea.

		MALES			FEMALES		
		NUMBER OF YEARS IN THE SEA			NUMBER OF YEARS IN THE SEA		
		1	2	3	1	2	3
MEAN TIME OF UPSTREAM MIGRATION	(DAY)	73	47	10	41	57	19
RANGE OF UPSTREAM MIGRATION	(KM)	39-119	15-111	10-11	32-53	14-105	2-36
NUMBER OF FISH	(N)	86	26	4	6	13	8

Table 5. The distribution of spawning salmon according to the number of years spent in the Rivers Tornionjoki and Muonionjoki in 1984. The differences have been tested with the chi-squared test. N = number of fish. X^2 = Chi-squared test. Significance levels; $p < 0.05^{*}$, $p < 0.01^{**}$.

DISTANCE FROM THE MOUTH OF THE RIVER, KM	YEARS SPENT BY SPAWNING SALMON IN THE RIVER								X^2
	2		3		4		ALL AGE GROUPS		
	N	%	N	%	N	%	N	%	
0 - 50	13	23	36	64	7	13	56	35	12.9**
51 - 100	1	2	34	68	15	30	50	31	9.0*
OVER 100	2	4	47	85	6	11	55	34	6.0*