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The Biology of Salmon from Southern Norway

Fluctuations in Age and Growth

by

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With Financial Support from „Nansenfondet"

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PREFACE.

This report presents the results of some investigations on the biology of salmon from Southern Norway. Special attention has been paid to the annual fluctuations in the age and growth of the fish. — The material has been collected partly from the rivers Nidelven and Tovdalselven, partly from the sea outside Arendal and Flekkefjord.

The material forming the basis of these investigations has been placed at my disposal by Dr. philos. *Alf Dannevig,* Director of the Floedevig Sea Fish Hatchery at Arendal. The work has been carried out at this station where I have had the opportunity of utilizing the entire technical equipment, and where I have got valuable help and advice.

Observations on the temperature of the surface water have been kindly placed at my disposal by the Floedevig Sea Fish Hatchery, and the Norwegian Meteorological Institute.

The collection of the material and the present investigations have been carried out with financial support from »Nansenfondet«, Oslo.

I wish to express my sincere thanks to those who have made it possible for me to carry out these investigations or have assisted me in some way or other.

Floedevigen, January 1946.

Gunnar Dannevig.

INTRODUCTION.

The salmon stock of Nidelven has previously been examined by *A. Dannevig* (1914). During the years 1911—1913 the small salmon were dominating; the grilse were also numerous, whereas large salmon were scarce. Previous spawners appeared to be more abundant than in most other Norwegian rivers. — Most of the fish had spent 2 or 3 winters parr life. In a later report *A. Dannevig* (1930) has drawn attention to the fact that younger emigrants seem to stay a longer time in the sea than older ones.

In Tovdalselven *Dahl* (1912) found the grilse to be dominating in the year 1910. This result has been confirmed by *Huitfeldt-Kaas* (1946). According to *Dahl* (1937) and *Huitfeldt-Kaas* (loc. cit.) the salmon caught at this locality have spent about 2.80 years in the river.

Salmon caught in the waters near Krisiansand in the years 1908 and 1909 were examined by *Dahl* (1910). The vast majority of the material from this locality consisted of grilse and small salmon, the latter group dominating. — Salmon with 2 and 3 years river life were most abundant, older emigrants being rather scarce.

Dahl (1913 a) and *A. Dannevig* (1914, 1930) have drawn attention to the great annual fluctuations in the average size of the fish from these waters. This phenomenon is often very marked, and the fishermen are quite familiar with it. A biological analysis of the present material may give further contribution to our knowledge of these fluctuations, which may be assumed to be of importance to the yield of our rivers.

Material and Methods.

The material here dealt with has been collected at 4 different localities at the Skager Rack coast of Norway (fig. 1). The samples have been taken partly from salmon ascending the rivers Nidelven and Tovdalselven, partly from salmon caught in the sea outside Arendal and Flekkefjord.

Only the lower part of the river Nidelven is passable for salmon, the dam at Eivindstad forming the upper limit. There is also a dam at Rygene, and the fish can only ascend through a salmon pass which has been built there. Between Rygene and Helle there are several small water falls, but they do not form any hindrance to the salmon. From Helle to Arendal the river runs quite slowly.

According to the official statistics (compiled by *K. Dahl* and *E. Dahl* (1942) the output of the fishery in Nidelven shows strong fluctuations, as will be seen from fig. 2. In the later years the output has been rather small. The statistics, however, may not be considered to give more than an approximate expression of the actual fluctuations.

The most important fishery takes place in special traps at Rygene. The efficiency of this fishing gear is highly dependant on the water level. Most of the material from Nidelven has been collected at this locality, but in some years also a few specimens caught below Rygene by rod and line, or in nets, have been included. — The salmon caught at Rygene may be assumed to be representative of the stock, with the exception perhaps of salmon exceeding 10—12 kg; fish of that size occur sparsely in the lower part of the river, but they are less frequent as far upstream as Rygene.

Tovdalselven has previously been a very rich salmon river. According to *Dahl* (1939) this river holds the world record for number of salmon caught by one tenant in a season. Here, as in most rivers in the Southern part of the country, the output has been decreasing during the last century (fig. 2). Only the lower part of the river is passable for salmon. — The material has been secured from fish caught in bagnets (»kilenøter«) and stakenets in the estuary of the river.

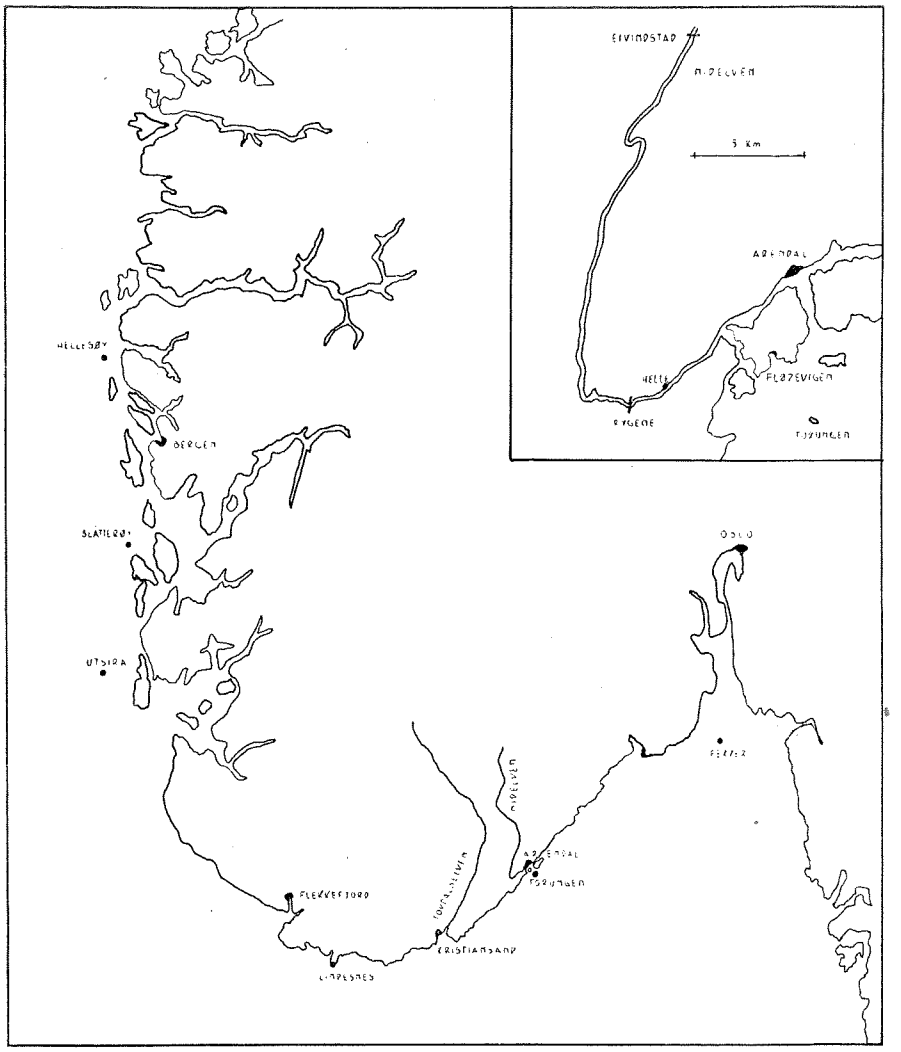

Fig. 1. The Area Investigated.

The material from Arendal and Flekkefjord has been obtained from bagnets which every year have been placed in the same localities among the outer skerries.

The salmon of our material has generally been caught by ordinary fishing gear in the usual fishing season. For fixed engines there is an annual close season from August 26th to April 14th, and a weekly close time from Friday at 6 p.m. to Monday at 6 p.m. — The meshes of the nets may not be smaller than 5.8 cm between the knots, and the

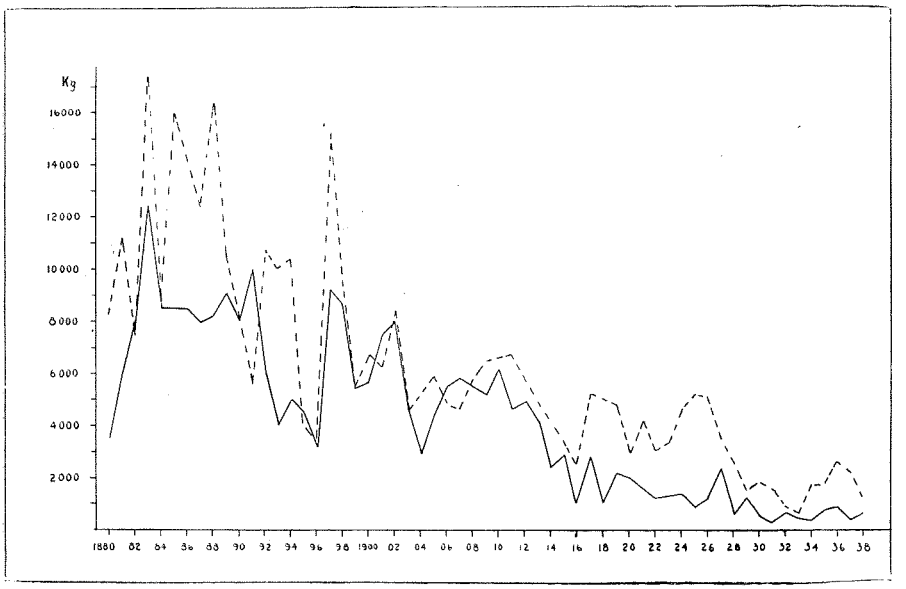

Fig. 2. The Output of the Salmon Fisheries in Nidelven (————) and Tovdalselven (— — — —).

spaces between the bars in the wooden traps not smaller than 5.6 cm. Some of the smallest grilse therefore escape capture.

The most important fishing season in the sea is from the middle of May to the end of June. There may, however, be some variations from one year to another owing to weather and current conditions. — The material from Tovdalselven has mainly been collected in the month of June. — The fishery at Rygene begins in the summer as soon as the salmon occur, which seldom happens before the middle of June. And it is carried on throughout the season if the conditions are suitable. — It may be of importance to note that some salmon enter the river in the close season (later than 26th of August).

The present material comprises 2849 specimens. Of each fish the length has been measured and age and growth have been estimated from the scales. For salmon from Nidelven and Arendal the weight is also given. The number of fish examined is recorded in tab. 1. — The most extensive investigations have been carried out in Nidelven where samples have been secured through 18 consecutive years. — The scanty material in 1927 and 1929 is due to bad fishing seasons. — It will appear that simultaneous investigations have been carried out at 3 localities during 7 consecutive years (1925—1931), and at 4 localities during 4 years (1927—1930).

Tab. 1. Number of Salmon examined from each Locality.

Year	Nidelven	Arendal	Tovdals-elven	Flekkefjord
1922	113			
1923	80			
1924	95			
1925	136	43	22	
1926	299	71	121	
1927	17	37	30	16
1928	80	117	41	35
1929	21	48	88	36
1930	58	47	66	38
1931	65	48	52	
1932	111		53	
1933	131			
1934	65			
1935	109			
1936	147			
1937	88			
1938	107			
1939	118			
Total	1840	411	473	125

Johnston (1905) was the first one to show that the life history of salmon can be read from the scales. *Dahl* (1910) found the method to be valid also in Norwegian waters. — *A. Dannevig* (1928) has shown that in salmon with exceptionally poor growth the first winter band may be little characteristic and difficult to detect, the winter band being indicated by 2 or 3 narrow ridges only. *Dannevig* and *Høst* (1931) found that the first winter band may be lacking in scales from the foremost part of the body. They, therefore, suggest that the scales should always be taken from the region in which they are first formed, viz. about the lateral line between the dorsal and adipose fins.

The individual growth has been calculated according to the methods worked out for the herring by *Lea* (1910, 1919). This method is based upon the assumption that the growth of the scales is proportional to the growth in length of the fish. It must be pointed out, however, that as to the salmon it has not yet been established to what extent this assumption really holds good. The attempts which have been made by *Dahl* (1910), as well as by *Lindsay* and *Thompson* (1932) to ascertain the applicability of the method are not satisfactory. In this connection I will draw attention to *Lea's* (1933, 1938) criticism of the methods usually employed.

Thus we do not know to what extent the calculated growth figures correspond to the actual size of the fish. There seems, however, to exist a definite connection between the growth of the fish and that of the scales. The estimated growth figures may, therefore, be comparable when calculated for fish of approximately the same size, provided that the scales are secured from the same part of the fish. As shown by *Dannevig* and *Høst* (1931) the figures for calculated growth vary according to the part of the fish from which the scales are taken.

The present scale material is not quite uniform. From 1922—30 the scales were taken from the side of the fish between the dorsal and pectoral fins, later between the dorsal and adipose fins. The fact that several persons have been engaged in the collection of the material has also given rise to errors. Thus the scale samples from Flekkefjord proved to be unsuitable for estimating the river-life period since they had been taken too near the pectoral fins. For the same reason some of the samples from Tovdalselven were difficult to interpret. Thus the readings for this river are somewhat uncertain, and the material is, therefore, not dealt with explicitly. Salmon, the river-period of which could not be satisfactorily estimated, have been marked in the tables with a query.

The zones formed during sea life as well as the spawning marks were generally very characteristic and easy to discern. For previous spawners the reservation must be made that errors in the readings may occur owing to absorption of essential parts of the scales. — On the whole it must be borne in mind that the method of estimating the age and growth from the scales to a certain extent is dependent on personal judgment. — The details as to age, growth, and size are given in tab. I—VI.

MAIDEN SALMON.

Parr Life.

Salmon with 3 years of river life dominate in all localities, the percentages varying between 56 % in Nidelven and 66 % in Tovdalselven (tab. 2). Salmon with 2 years of river life are also numerous, between 32 % in Tovdalselven and 41 % in Nidelven. In all localities there is also a small number of salmon with 4 years of river life. — Thus the salmon from these localities seem to have spent approximately the same length of time in the river. It is of special importance to note that this is also the case as regards fish caught in the sea outside Arendal. Salmon belonging to tribes with a shorter or longer parr life is, therefore, not represented to any appreciable degree in the catches made at

this locality. The results from Nidelven and Tovdalselven are in close agreement with those previously obtained, see tab. 3.

The material from Nidelven and Arendal is sufficiently abundant for investigations into the annual fluctuations of the smolt age, with the exception, however, of the material from the bad years 1927 and 1929. For each year the relative frequency (%) of fish respectively with 2, 3, 4, and 5 years parr life has been calculated; the annual deviations from the mean for the whole period are given in figs. 3 and 4, open colums.

In Nidelven (fig. 3) the greatest deviation (18 %) occur in 1931 when fish with 2 years parr life were rather scarce. In 13 years, however, the deviations are less than 10 %, and in 8 years less than 5 %. In the material from Arendal (fig. 4) the annual deviations from the mean are not more than 8 % with the exception of 1930.

In most years, therefore, the present material exhibits no great fluctuations as to the duration of river life. The small differences which may occur may be due to fluctuations in the strength of the year-classes.

Also *Alm* (1934) found only small variations in the duration of river life. He therefore considers the age at emigration to be typical for the different rivers. *Huitfeldt-Kaas* (1946) has arrived at the same results, but points out that minor differences may occur.

Tab. 2. Duration of River Life.

Locality	N	River life				
		1 year	2 years	3 years	4 years	5 years
Nidelven 1922—1939 ..	1497		41%	56%	3%	0.2%
Tovdalselven 1925—1932	375	0.3%	32%	66%	2%	
Arendal 1925—1931 ...	366		34%	61%	5%	

Tab. 3. Duration of River Life of Salmon entering Nidelven and Tovdalselven in different Periods.

	1 year	2 years	3 years	4 years	5 years	R
Nidelven 1911—13[1]	1%	49%	46%	4%		
» 1922—39		41%	56%	3%	0.2%	
Tovdalselven 1909[2] ..		37%	63%			2.63
» 1910[2] ..		26%	65%	9%		2.82
» 1910[3] ..						2.77
» 1925—32	0.2%	32%	66%	2%		2.69

[1] A. Dannevig (1914). [2] Huitfeldt-Kaas (1946). [3] Dahl (1937).

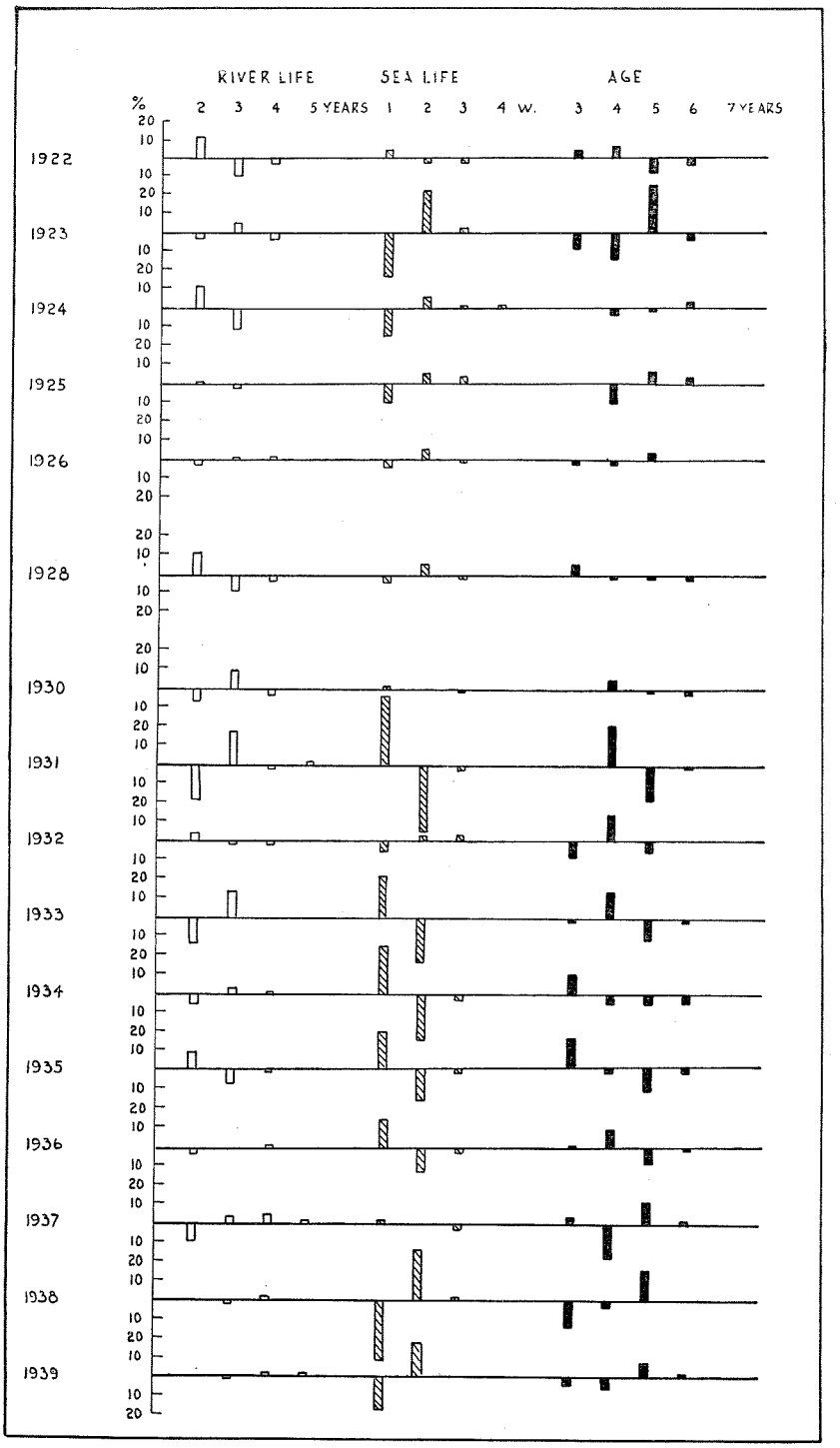

Fig. 3. Nidelven. Fluctuations in River Life (open columns), Sea Life (hatched columns), and Age (black columns).

Sea Life.

Salmon with 2 full years of sea life dominate in all localities, the percentage varying between 54 % at Arendal and 72 % at Flekkefjord (tab. 4). The remaining maiden salmon are mostly grilse (between 39 % in Nidelven and 25 % in Tovdalselven). Large salmon, as mentioned above, are probably not duly represented in the material from Nidelven. Also a few very large salmon have been caught at Arendal and in Nidelven. — Evidently the salmon caught in the various localities have generally spent about the same time in the sea before the first spawning migration.

Different authors have previously discussed whether the age of the emigrating smolt may influence the duration of sea life. In order to elucidate this problem the material from Nidelven and Arendal has been arranged in contingency tables according to Fisher (1932), see tables 5 A and 5 B. It appears that the grilse are more abundant among 3 years old emigrants than should be expected if the two variants were independent, whereas the large salmon (3 winters in the sea) generally have stayed a shorter time in river. The probability (P) that these deviations from the theoretical frequencies may have arisen by chance is less than 0.01. The material indicates, therefore, that a short river period is generally correlated with a long sea period.

The same observation has previously been made in most localities where extensive investigations have been carried out, thus in Swedish rivers (*Alm* (1934)), in the River Wye (*Hutton* (1925, 1937)), and in Newfoundland waters (*Lindsay* and *Thompson* (1932)). — *Huitfeldt-Kaas* (1946) has found that the smolt age is approximately the same in grilse and small salmon, but somewhat lower in large salmon. — *Rosén* (1918 b) and *Dahl* (1937) did not find any differences between the various classes. — Fluctuations as to the relative abundance of the different year-classes may, however, influence the results to some extent when dealing with the material of a single year.

It is well known that there are fluctuations from one year to another in the relative abundance of grilse and small salmon. It may, therefore, be of interest to compare the present results with those of previous investigations in the same localities (tab. 6). — In Nidelven the relative abundance of grilse and small salmon is approximately the same in the two periods 1911—13 and 1922—39. In Tovdalselven the grilse were dominating in the years 1909 and 1910 whereas the small salmon constituted the main part of the catch in the period 1925—32.

A. Dannevig (1930) has dealt with the catches of salmon in Tovdalselven on the basis of the statistics from the salmon fisheries at Hamre and Boen. The salmon has been classified according to weight: »svele«

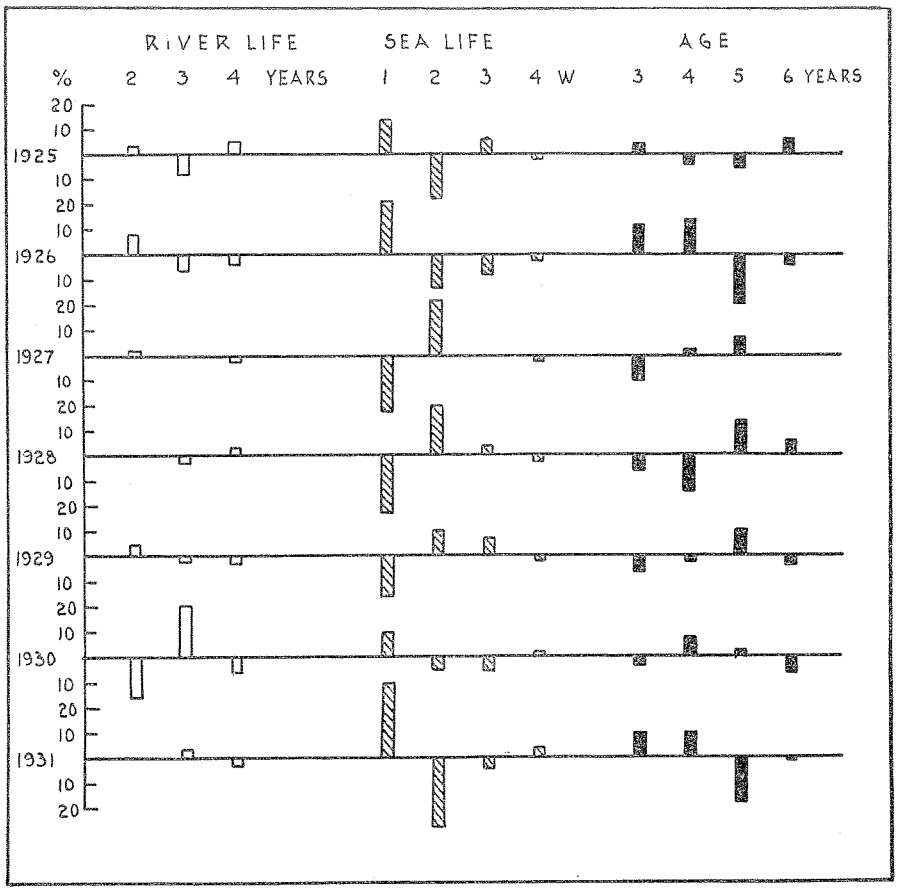

Fig. 4. Arendal. Fluctions in River Life (open columns), Sea Life (hatched columns), and Age (black columns).

< 3 kg, i. e. grilse and some small salmon, and »laks« > 3 kg. During the years 1899—1927 the catches at Boen consisted on an average of 37 % »svele« and 63 % »laks«, the grilse thus constituting less than 37 %. — During the years 1925—32 we found that the grilse on an average amounted to 25 % of the catch.

Further it was shown by *A. Dannevig* (loc. cit) that there are great annual fluctuations from one year to another in the abundance of »svele« and »laks«. In the year 1910 the catch of »svele« at Boen was 98 % above average, the catch of »laks« being only 20 % up. Also at Hamre there was in that year caught a rather high number of »svele«. Thus it appears that in the year 1910 the grilse must have been exceptionally abundant in Tovdalselven. This conforms

Tab. 4. Duration of Sea Life.

Locality	N	Sea Life (winters)			
		1 w	2 w	3 w	4 w
Nidelven 1922—1939	1596	39%	59%	2%	0.06%
Tovdalselven 1925—1932.....	409	25%	69%	5%	
Arendal 1925—1931	383	36%	54%	9%	1%
Flekkefjord 1927—1930	123	25%	72%	3%	

Tab. 5a. Duration of River and Sea Life of Salmon from Nidelven. (Figures in Brackets Indicate the Theoretical Frequencies if the two Variates were Independent).

River Life	Sea Life			Totals
	1 w	2 w	≧ 3 w	
2 w	204 (238.4)	388 (358.5)	15 (10.1)	607
3 w	366 (331.1)	468 (497.8)	9 (14.1)	843
≧ 4 w	18 (18.5)	28 (27.8)	1 (0.8)	47
Totals	588	884	25	1497

$X^2 = 17.12 \quad P < 0.01$

Tab. 5b. Duration of River and Sea Life of Salmon from Arendal.

River Life	Sea Life			Totals
	1 w	2 w	≧ 3 w	
2 w	37 (45.8)	67 (69.2)	22 (11.0)	126
3 w	90 (81.0)	123 (122.5)	10 (19.5)	223
≧ 4 w	6 (6.2)	11 (9.3)	0 (1.5)	17
Totals	133	201	32	366

$X^2 = 20.22 \quad P < 0{,}01$

Tab. 6. Duration of Sea Life of Salmon Entering Nidelven and Tovdalselven in different Periods.

Duration of sea life (winters)	1 w	2 w	3 w	4 w
Nidelven 1911—1913 (Dannevig (1914))	41%	53%	6%	
» 1922—1939	39%	59%	2%	0.06%
Tovdalselven 1909 (Huitfeldt-Kaas (1946))	71%	29%		
» 1910 »	65%	35%		
» 1910 (Dahl (1912))	65%	35%	0.02%	
» 1925—1932.....	25%	69%	5%	

well with the results of *Dahl* and *Huitfeldt-Kaas* who found that the grilse were dominating in that year.

For the material from Nidelven and Arendal the relative abundance of respectively grilse, small and large salmon has been calculated for each year and for the whole period. In figs. 3 and 4 the hatched columns represent the annual deviations from the mean for the whole period; as is clearly seen the fluctuations are great in grilse and small salmon, but extremely small in large salmon. — The annual fluctuations in the relative abundance of grilse in Nidelven and at Arendal are shown in fig. 5. The changes in the composition of the stock seem to be very much the same in the two localities.

These great fluctuations have previously been discussed by various authors. (*Dahl* (1913 a), *A. Dannevig* (1914, 1930), *Jacobsen* and *Johansen* (1921), *Alm* (1934), *Järvi* (1938).) — *Dahl* and also *Alm* suggest that this phenomenon may be due to fluctuations in the relative abundance of the year-classes, or to a shorter or longer period of sea life. *Jacobsen* and *Johansen* maintain that a high temperature in the coastal waters during summer may cause some of the salmon, which normally would stay another winter in the sea, to make for the rivers. This view is also supported by *Alm*. I have not been able, however, to find any connection between the duration of sea life and the temperature of the surface water along the South-Eastern coast of Norway.

If the fluctuations in the relative abundance of small salmon and grilse are caused by variations in the strength of the year-classes to which they belong, it may be expected that a year rich in grilse will be followed by a year rich in small salmon. From figs. 3 and 4 it appears that this is generally not the case. The grilse for instance, may be exceptionally abundant through 2 or more consecutive years, and so also the small salmon. — It seems as if the sea life of salmon is not always of equal duration. In some years the fish enter the river as grilse, in other years they may stay another year in the sea for some reason or other. It is seldom, however, that salmon from these localities stay as long as 3 winters in the sea before spawning.

Age distribution.

The maiden salmon caught in Nidelven, Tovdalselven and at Arendal are between 3 and 6 years old, see tab. 7. The vast majority of the fish is spawning for the first time at an age of 4 or 5 years. Thus a particular year-class will occur in the catches through 4 subsequent seasons, but only in two years is it of special importance.

In the case of herring, cod and several other species one has obtained information as to the relative strength of the year-classes by

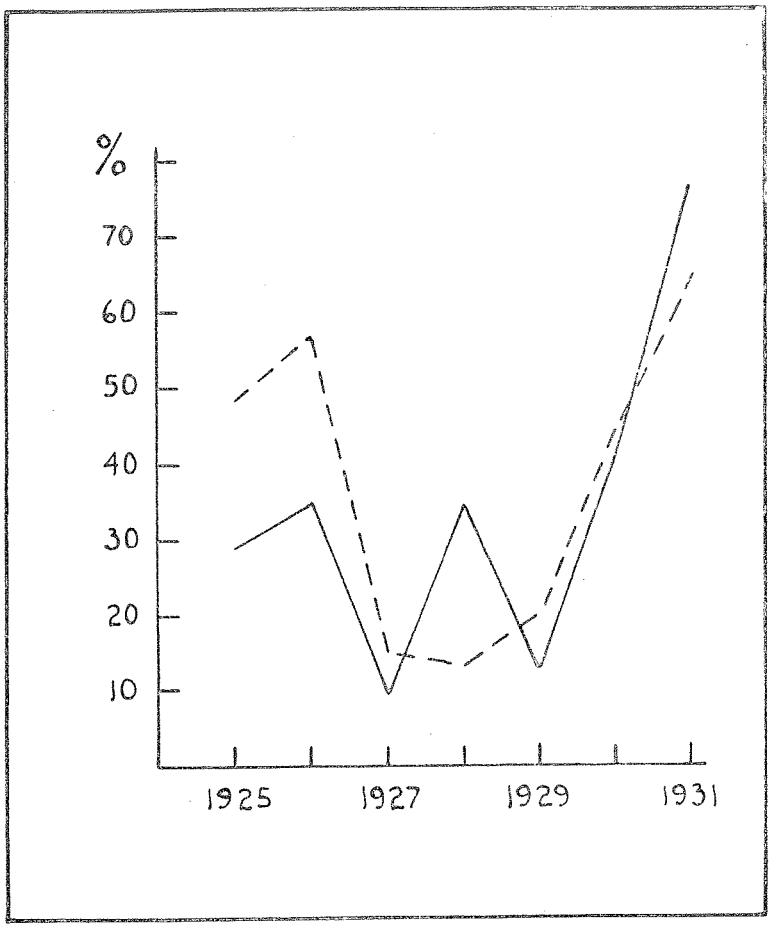

Fig. 5. Percentage of Grilse in Nidelven (————) and at Arendal (– – – –).

comparing the age distribution in the shoals in several subsequent seasons. In the case of the salmon, such investigations are, however, more complicated. The reservation must be taken that the relative abundance of the different age-groups is influenced, not only by the year-classes, but also by fluctuations in the duration of sea life. This fact is particularly significant as a single year-class is of importance only during two years. Slow and gradual fluctuations are difficult to discern. On the other hand it may be supposed that accentuated fluctuations in the strength of the year-classes may have a strong effect on the age distribution in periods during which the duration of sea life is approximately the same.

Tab. 7. Age of Maiden Salmon.

	3 years	4 years	5 years	6 years	7 years
Nidelven 1922—1939	14%	50%	33%	3%	0.1%
Tovdalselven 1925—1932 ...	9%	38%	51%	2%	
Arendal 1925—1931	10%	43%	41%	6%	

The frequency of the different age groups has been calculated for each year for the material from Nidelven and Arendal. In figs. 3 and 4 the black colums represent the deviations from the mean for the whole period. — At both localities there are variations from one year to another as to the age of the fish, and in each year there is rather a close agreement between the age composition of the stock and the relative abundance of grilse and small salmon.

In most cases it is difficult to find any connection between the age distribution in one year and the next as might be expected if the fluctuations in age were caused mainly by variations in the strength of the year-classes. In the material from Nidelven only 2 year-classes have been more than usually abundant through 3 years. The 1918-group shows a surplus of 4-year old fish in 1922, of 5-year olds in 1923, and of 6-year olds in 1924. In the same way the year-class of 1932 is more abundant than the preceding and following year-classes. — In the material from Arendal there are indications that the year-class of 1922 is richer than usual.

Size and Growth.

It has previously been established that in each river quick-growing specimens will generally emigrate at an earlier age than slow-growing ones. (*Rosén* (1918 a, b), *Alm* (1919, 1924), *Menzies* (1925, 1927), *Pentelow, Southgate* and *Bassindale* (1933), *Nordqvist* and *Alm* (1927), *Went* (1938), and *Huitfeldt-Kaas* (1946).) — It may be of interest to ascertain whether younger emigrants also during sea life have a more rapid growth. In tab. 8 and 9 the mean values of 1, L_1 etc. are given for grilse and for small salmon with 3 years of parr life; the letter δ indicates how much these figures are larger or smaller than those for fish with 2 years of parr life. In the smolt stage the older fish is somewhat bigger than the younger ones (2.3 cm in the case of the grilse from Nidelven). It is seen, however, that during sea life the younger emigrants grow a little quicker. The original difference in size succesively diminishes and finally quite disappears. This holds good for the grilse as well as for the small salmon. During the fol-

Tab. 8. Nidelven. The Growth of Grilse with 3 Years of River Life. δ indicates how much these Figures are Larger or Smaller than the Figures for Grilse with a River Period of 2 Years.

Year	N_2	N_3	l	δ_l	L_1	δ_{L_1}	L	δ_L	W	δ_W
1922 ...	18	22	13.6	—0.3	44.0	—1.6	55.8	—1.2	1.48	—0.01
1923 ...	4	6	13.2	+1.4	42.5	+0.7	54.0	—1.5	1.45	—0.03
1924 ...	12	9	15.5	+4.2	46.0	+0.3	56.3	+0.9	1.59	+0.10
1925 ...	13	13	14.6	+2.5	44.5	+1.3	55.9	+1.5	1.51	+0.08
1926 ...	32	59	13.7	+2.2	47.7	+0.8	57.5	0.0	1.63	—0.07
1928 ...	13	10	12.9	+1.0	42.1	0.0	51.0	—1.6		
1930 ...	6	16	14.5	+2.0	45.8	+1.5	57.1	—0.6	1.61	—0.07
1931 ...	8	36	15.2	+3.3	49.3	+0.7	59.6	+1.0	1.71	+0.04
1932 ...	5	26	15.7	+3.7	45.6	+1.0	57.2	—0.4	1.62	—0.38
1933 ...	13	49	15.2	+2.0	48.4	+1.1	59.8	+1.4	1.88	+0.09
1934 ...	14	19	14.7	+3.3	49.2	+1.6	58.5	+0.1	1.71	+0.06
1935 ...	29	27	14.2	+2.7	48.4	0.0	58.6	+0.6	1.69	+0.09
1936 ...	16	40	14.8	+2.3	49.8	+1.4	59.4	+1.8	1.75	+0.29
1937 ...	12	13	14.6	+2.8	46.4	+0.9	58.1	+0.5	1.55	0.0
1939 ...	9	13	13.5	+1.0	46.7	—0.9	57.2	—1.0	1.55	—0.14
Mean difference				+2.3		+0.6		+0.1		+0.003

Tab. 9. Nidelven. The Growth of Small Salmon with 3 Years of Parr Life. δ indicates how much these Figures are Larger or Smaller than the Figures for Fish with a River Period of 2 Years.

Year	N_2	N_3	l	δ_l	L_1	δ_{L_1}	L_2	δ_{L_2}	L	δ_L	W	δ_W
1922	34	25	13.2	+1.7	42.7	—1.4	66.6	—0.7	72.5	—0.5	3.30	—0.02
1923	18	35	12.5	+1.1	46.8	+0.2	70.8	—0.5	76.0	+0.2	4.02	+0.17
1924	27	24	13.6	+3.5	43.6	+2.6	69.3	+2.5	74.4	+2.2	3.95	+0.70
1925	25	36	13.4	+2.6	46.9	+0.8	72.9	+0.7	77.4	—0.7	4.26	—0.25
1926	69	95	12.8	+1.2	44.5	—0.4	69.1	0.0	74.0	+0.2	3.65	+0.01
1928	23	22	13.6	+2.1	47.3	+0.6	68.9	+0.4	72.8	+0.5	3.28	—0.11
1930	10	15	14.5	+2.2	43.3	+0.5	67.6	—0.3	74.8	+0.5	3.90	+0.34
1931	5	7	12.9	+2.1	44.4	+0.4	69.0	—1.0	75.2	+1.0	3.87	+0.53
1932	35	23	13.6	+1.8	49.2	+0.6	73.0	+0.6	78.0	+1.4	4.35	+0.24
1933	13	19	15.1	+2.0	47.6	0.0	72.0	+1.4	76.3	—2.4	3.82	—0.68
1934	6	14	15.8	+2.8	51.1	+1.8	75.8	—1.2	81.0	—1.0	4.67	—0.15
1935	19	19	14.2	+2.6	50.8	+1.4	75.5	+1.0	79.1	+1.0	4.61	+0.45
1936	26	22	14.2	+3.4	50.6	+1.5	73.0	—0.1	76.3	0.0	3.98	—0.14
1937	8	26	14.1	+1.5	49.7	—0.6	73.3	—2.3	77.4	—3.2	3.98	—0.57
1938	32	37	15.4	+2.5	48.7	+2.3	73.5	+0.7	79.0	+1.4	4.27	+0.32
1939	29	39	15.5	+2.6	47.3	+2.7	73.1	+2.4	77.4	+0.4	3.96	+0.04
Mean difference				+2.2		+0.8		+0.2		+0.1		+0.06

lowing, therefore, no attention is paid to the duration of river life when the growth during sea life is discussed.

The present results are in close agreement with those of *Järvi* (1938), *Huitfeldt-Kaas* (1946), and *Went* (1938). — *Lindsay* and *Thompson* (1932) have found that in the case of grilse the growth of younger and older emigrants is approximately the same. As regards the small salmon they found older emigrants to grow slower than the younger ones. — *Dahl* (1910) maintains, however, that during sea life older emigrants exhibit a quicker growth than younger ones.

The size of the grilse and that of the small salmon caught during the period 1925—31 will appear from fig. 6 and tab. 10. As shown by the length frequencies in fig. 6 the two classes of fish may in most cases be separated by their length, the grilse being generally smaller than 66 cm, the small salmon being larger. — The mean size of corresponding groups is very much the same at the four localities, that of the grilse between 56.8 and 59.1 cm, and that of the small salmon between 74.9 and 76.4 cm. As regards the latter group, the differences between the means may not be considered significant. It will appear from tab. 11 that the values of D/ε_D in most cases are rather small, and not larger than 2.2. There are, however, distinct indications that the grilse from Nidelven is significantly smaller than the grilse from the other localities (tab. 12). This difference is probably due to the selective action of the traps at Rygene which catch smaller fish than the bagnets do. From fig. 6 it appears that the material from Nidelven even comprises some specimens smaller than 50 cm. Fish of that size are never caught in the bagnets.

The mean length of the large salmon, which is not very numerous, is given in tab. 13. The average size is about 100 cm, and there is no great difference between the various localities.

There are, however, strong fluctuations from one year to another in the size of grilse and in that of small salmon. Thus the mean length of the small salmon from Nidelven varies between 72.6 and 82.3 cm (the curves at the top in fig. 7). It has previously been shown by *Alm* (1934) that such fluctuations occur in Swedish rivers also. *Alm* assumes that the varying size may be due to an early or late run, or to a varying growth during sea life. It will appear from fig. 7 that the increase in length during the year of capture (T) varies within narrow limits, in Nidelven between 3.3 and 6.9 cm. It is the growth during the first year of sea life (T_1) which displays the greates fluctuations, in Nidelven between 29.4 and 38.2 cm. During the second year of sea life the fluctuations are generally smaller.

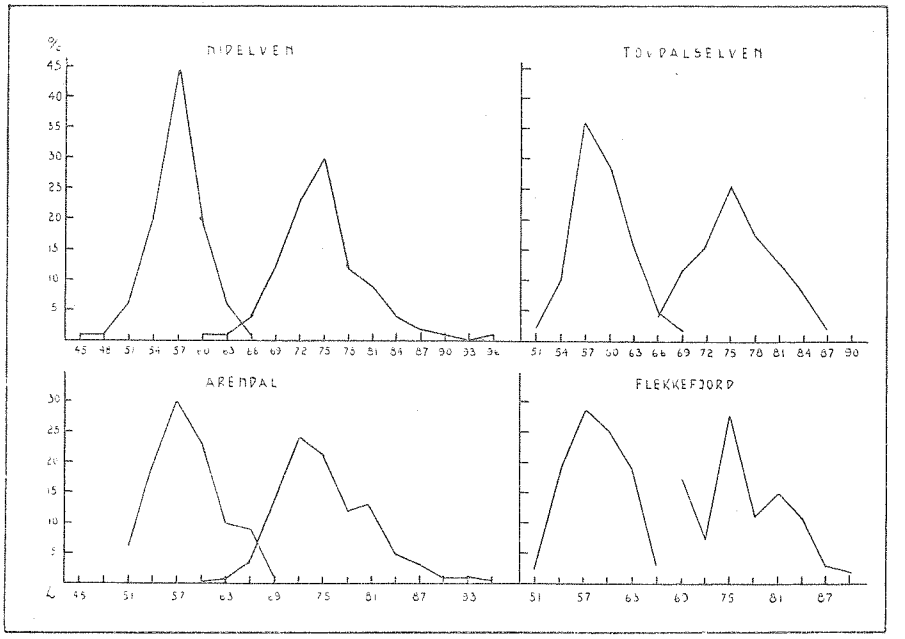

Fig. 6. Size Distribution of Grilse and of Small Salmon.

In order to obtain a closer knowledge of the annual fluctuations in the growth during the first year of sea life, we will also take the grilse from Nidelven into consideration, and calculate the growth for the year in which it took place, fig. 8. (The years 1926 and 1928 have been excluded, as there are no figures for T_1 of the grilse.)

For the year 1930, for instance, we get one value for T_1 on the basis of the grilse caught in 1931, and one value on the basis of the small salmon caught in 1932. The general trend of the two curves is very much the same. The close agreement between the two independent series of observations may be taken as a proof that the variations met with are significant.

The calculated increment during the first year of sea life is always somewhat greater for small salmon than for grilse. It cannot be decided whether this is due to methodical errors, or to biological selection.

The material from Nidelven has given clear evidence that the growth during the first year of sea life is subject to strong annual fluctuations. In order to find out whether these are of more general character, we will take into consideration the material of small salmon from all localities. (The material of grilse from Arendal, Flekkefjord and Tovdalselven is too scarce to be dealt with in this connection).

Tab. 10. Mean Length of Grilse and Small Salmon Caught During the Period 1925—1931.

	Grilse				Small salmon			
Locality	N	$\bar{L}$	σ	ε	N	$\bar{L}$	σ	ε
Nidelven	222	56.8	3.50	0.23	361	74.9	5.62	0.30
Arendal.....	137	58.3	4.10	0.35	208	75.3	6.00	0.41
Tovdalselven.....	100	59.1	5.79	0.58	256	75.6	5.11	0.32
Flekkefjord	31	58.5	3.59	0.65	88	76.4	5.76	0.61

Tab. 11. Small Salmon. Difference (D) in Length between the various Localities. D/ε_D in brackets.

	Nidelven	Arendal	Flekkefjord
Tovdalselven	0.7 (1.5)	0.3 (0.6)	0.8 (1.2)
Arendal	0.4 (0.7)		
Flekkefjord	1.5 (2.2)	1.1 (1.5)	

Tab 12. Grilse. Difference (D) in Length between the various Localities. D/ε_D in brackets.

	Nidelven	Arendal	Flekkefjord
Tovdalselven	2.3 (3.7)	0.8 (1.2)	0.6 (0.7)
Arendal	1.5 (3.6)		
Flekkefjord	1.7 (2.5)	0.2 (0.3)	

Tab. 13. Mean Length of Large Salmon.

Locality	N	L
Nidelven 1922 - 1939	29	98.9
— 1925—1931	10	101.1
Arendal 1925 - 1931	35	100.3
Tovdalselven 1925 - 1931	20	103.2
Flekkefjord 1927—1930	4	99.0

The increase in length during the various periods of sea life is presented in fig. 9 for the years in which the growth took place. — In each year the salmon from the various localities exhibit approximately the same increase in length during the first year of sea life, the greatest difference observed in any year being 2.8 cm (1927). The general trend of the

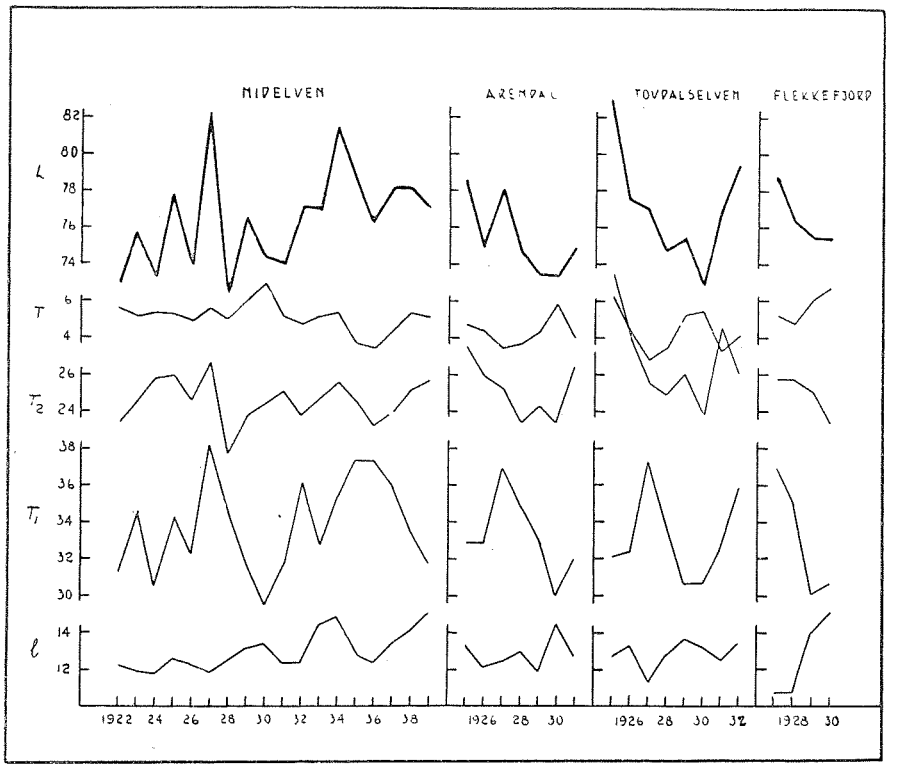

Fig. 7. Size and Growth of Small Salmon caught in different Years.

curves representing T_1, is the same. The salmon caught in the various localities therefore exhibit rather corresponding fluctuations in the growth during the first year of sea life.

As to the growth during the second year of sea life there is a rather close conformity between the salmon from Arendal, Tovdalselven and Flekkefjord. The curve representing Nidelven, however, differs to some extent from the other ones. The correspondence between the various localities is on the whole less marked during the second than during the first year of sea life. — Also the increment in length during the year of ascent is subject to corresponding fluctuations. Only in the year 1927 smaller discrepancies occur.

In the case of the material from Nidelven we find that the general trend of the curves representing T_1 and T_2 is rather different. In the other localities we find decreasing values for T_1 and T_2 from 1925 to 1927, and increasing values from 1929 to 1930; in 1931 they are again smaller. In the years 1924 and 1928 the values for T_1 are relatively

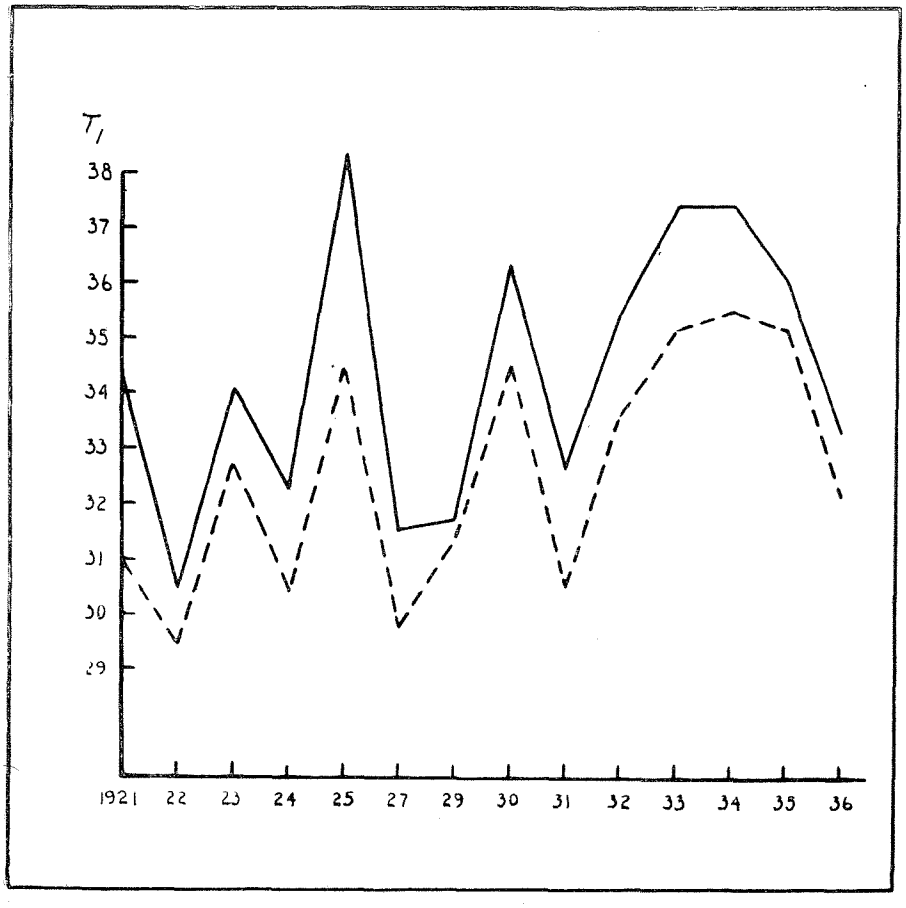

Fig. 8. Nidelven. Increment in Length during the first Year of Sea Life for Small Salmon (————) and Grilse (– – – –) for the Years in which the Growth took Place.

small, whereas the values for T_2 are large. — The variations in T seem on the whole to correspond well with the fluctuations in T_1. Only in the year 1927 there are some irregularities.

From these results it may be safe to conclude that during the first year of sea life the salmon from these waters live under rather similar conditions. To some extent this is also the case during the second year of sea life, and in the year of ascent. — It is of interest to note, however, that in some cases fish spending their second year in the sea probably live under other conditions than do the salmon which spend their first year in the sea.

Among the factors which may influence the growth, the temperature and the amount of food are of great importance. Our knowledge as to

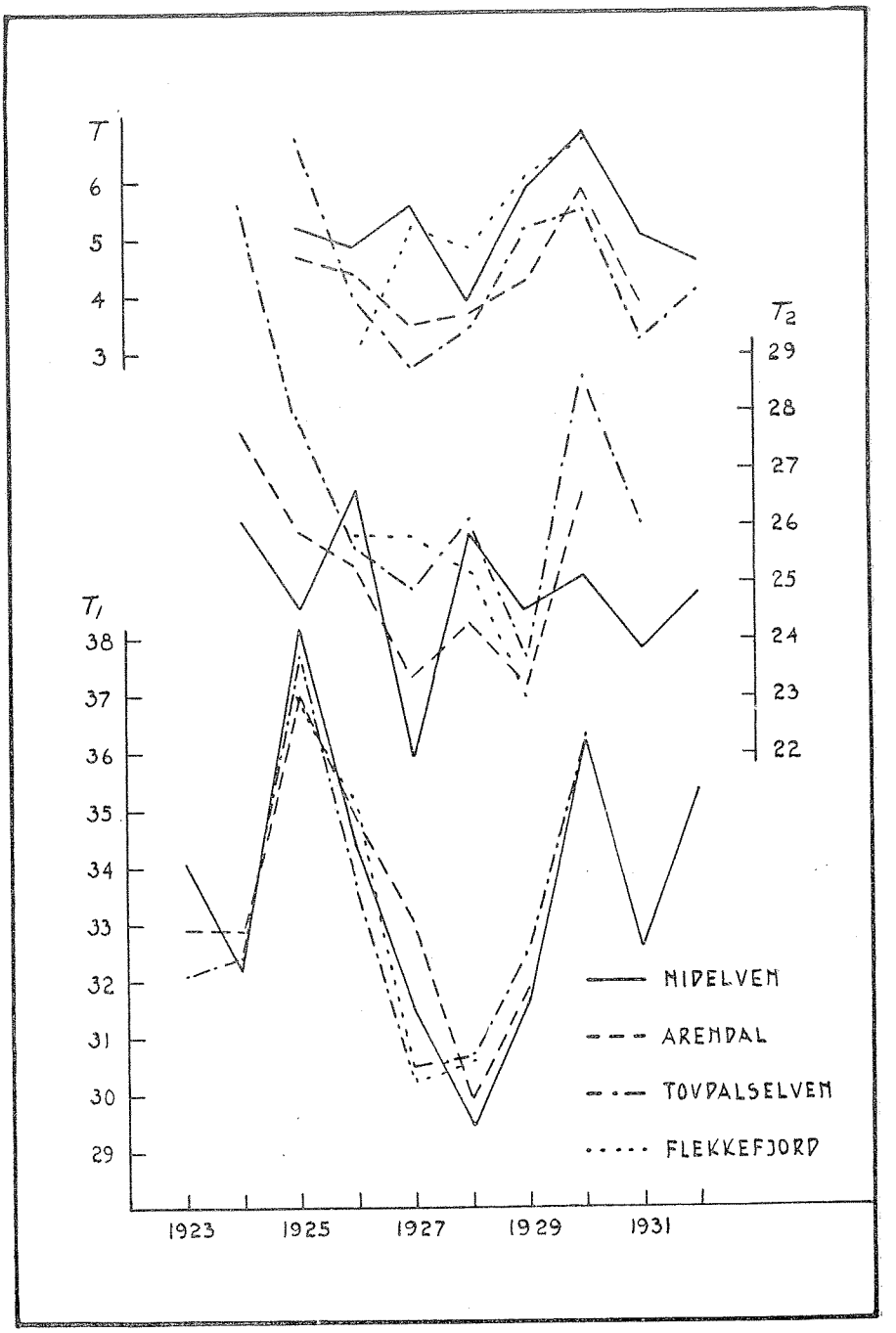

Fig. 9. Small Salmon. Increment in Length in the various Periods of Life for the Years in which the Growth took Place.

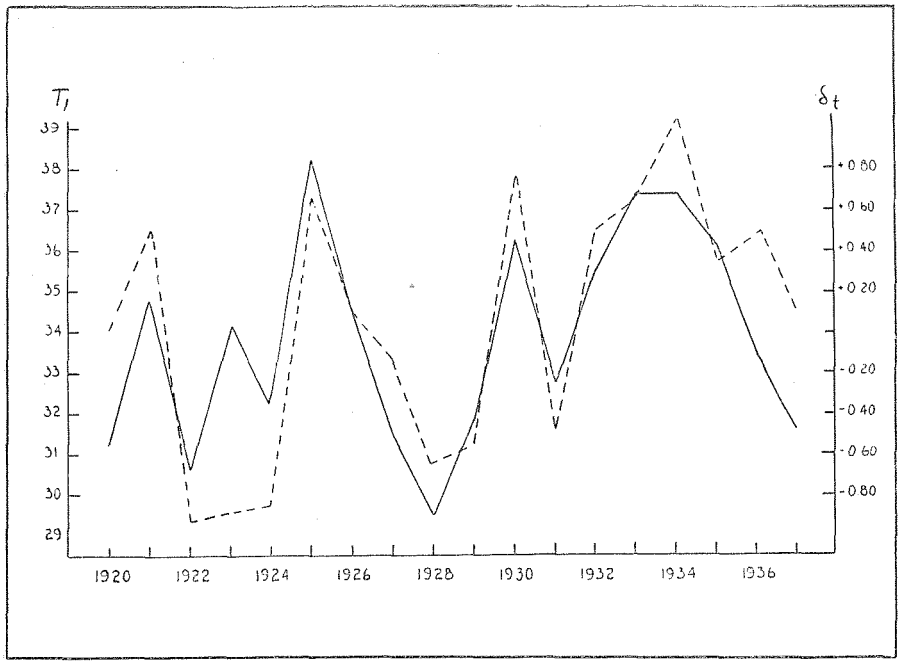

Fig. 10. The Growth during the first Year in the Sea (T_1) for Small Salmon from Nidelven (————), and the Annual deviations (δ_t) from the Mean Temperature at Floedevigen (– – – –).

the feeding grounds of the salmon is very limited and we have no information as to the quantity of food available. —

Certainly we are not able to give a picture of the temperature conditions under which the salmon live. The conditions in the coastal waters may, however, be of some importance to the descending smolts. — The temperature at 1 m depth is observed every working day at the Floedevig Sea Fish Hatchery which is situated close to the open sea at Arendal. The Norwegian Meteorological Institute has informed me that the variations in temperature of the surface water recorded at Floedevigen have proved to be of a rather general character. The temperature here fluctuates in accordance with the temperature of the surface water at several other localities among the outer skerries at the south-eastern as well as the western coast of Norway. (Ferder, Torungen, Lindesnes, Utsira, Slåtterøy, and Hellisøy, see fig. 1).

The annual deviations from the normal at Floedevigen are presented in fig. 10 together with the fluctuations in T_1 for small salmon from Nidelven. There can be no doubt that the trend of the two curves is very much the same. The growth of salmon spending their first

year in the sea, is on the whole better in years with a high temperature than in years with a low temperature in the surface water.

We do not know if the conditions under which the salmon really live have been subject to corresponding fluctuations. If this has been the case, the temperature may have had a direct effect upon the growth, and the correlation may be explained. — The temperature is, however, only one of the factors of importance to the growth of the fish, factors which may vary independently, or be more or less related to each other. Thus displacement of the Baltic water along the Skager Rack coast of Norway may involve changes in temperature, salinity, and in the abundance of several food components such as herring, mackerel, and pelagic crustaceans. Variations in temperature may, therefore, indicate more general changes in the surroundings.

Weight and Condition.

The average size of respectively grilse, small salmon, and large salmon in Nidelven and at Arendal, is given in tab. 14. The factor γ which indicates the relative weight of the fish, has been calculated on the basis of the average weight and length.

The mean weight of the grilse caught at Arendal is 1.84 kg, and that of the small salmon 4.48 kg. Thus the increase in weight during the second year in the sea amounts to 2.64 kg; in the third year of sea life the increase is much larger, viz. 7.2 kg, the average weight of the large salmon being 11.7 kg.

The average weight of corresponding groups from Nidelven is somewhat smaller. For grilse, small salmon, and large salmon the difference from the fish caught at Arendal amounts to 0.25 kg, 0.53 kg, and 2.0 kg respectively. — Considering the factor γ it appears that the relative weight of the fish is somewhat smaller in Nidelven. This difference in weight and condition may be ascribed to the fact that the salmon from Nidelven have stayed a shorter or longer time in the river before capture.

There are great fluctuations from one year to another in the mean weight of corresponding groups (tab. V). Thus the weight of grilse caught at Arendal varies between 1.58 kg (1927) and 2.16 kg (1926), the deviations from the mean for the whole period being — 14 % and + 17 % respectively. For the small salmon from the same locality the annual deviations may amount to ± 16 %. — In Nidelven the weight of the grilse fluctuates between 1.33 kg and 1.87 kg, and that of the small salmon between 3.30 and 4.71 kg. — These variations are related not only to the growth, but also to the condition of the fish.

Tab. 14. Size and Conditon of Salmon from Arendal and Nidelven.

	Grilse			Small almon			Large Salmon		
	L	W	γ	L	W	γ	L	W	γ
Arendal . . . .1925—31	57.5	1.84	0.97	75.6	4.48	1.04	100.3	11.7	1.15
Nidelven . . .1922—39	57.0	1.59	0.86	76.5	3.95	0.88	98.9	9.7	1.01

SALMON WHICH HAVE PREVIOUSLY SPAWNED.

Relative Abundance.

Considering the material from each locality as a whole, we find the following percentages of previous spawners:

Nidelven	1922—1939	13 %
Tovdalselven	1925—1932	14 »
Arendal	1925—1931	7 »
Flekkefjord	1927—1930	2 »

The figures for Nidelven are in close agreement with those found by *A. Dannevig* (1914) during the years 1911—1913 when previous spawners constituted 14 % of the catch. — In Tovdalselven *Dahl* (1912) and *Huitfeldt-Kaas* (1946) found only 6 % of salmon with spawning mark in the year 1910. The results of a single year may not, however, be considered characteristic to a river as great annual fluctuations may occur. In Nidelven the relative frequency of previous spawners varies between 4 % in 1922 and 22 % in 1936 and 1938 (tab. VI). In Tovdalselven there are still greater variations, between 2 % (1931) and 38 % (1932).

Fish which have previously spawned are almost equally frequent in Nidelven and Tovdalselven, whereas they are more scarce in the catches made in the sea. This is the case for the whole period as well as for the single years. Such differences may occur if fish on their second spawning migration enter the rivers late in the season when the fishery in the sea has come to an end. The salmon caught in the sea may also to some extent be composed of fish from other rivers with a lower percentage of survivors.

According to *Alm* (1934) there is also in Swedish waters the same difference between river and sea as to the abundance of fish which have previously spawned (on an average 7.5 % in rivers and 3.2 % in sea). *Alm* is apparently of the opinion that the habits of the latter ones differ from that of maiden fish. — In the Southern Baltic, however, *Dixon* (1931) has in some years found between 12 and 20 % with spawning marks, and this is more than what generally is found

in most rivers. *Dixon* expresses the opinion that a considerable part of the previous spawners caught in this locality is fish which have lost their faculty of propagation. His material is not, however, adequate for such a conclusion.

Fish which have survived previous spawning migrations are more abundant in Nidelven and Tovdalselven than is the case in most European rivers where this group generally constitute about 7 % of the catch. (*Dahl* (1910, 1913 b), *Hutton* (1925), *Storrow* (1932), *Alm* (1934), *Järvi* (1938), *Otterstrøm* (1938), *Went* (1938), *Huitfeldt-Kaas* (1946).) — From the works of *Alm, Huitfeldt-Kaas,* and *Järvi* it appears, however, that in some years they may constitute about 16 % of the stock.

Previous spawners seem to be more abundant on the other side of the Atlantic. According to *Hutton* (1927) 19 % of the salmon in a Canadian river had previously spawned. He also refers to *Calderwood* (1926) and *Menzies* (1926) who in two rivers in Eastern Canada found 34 % and 17 % respectively. From the investigations of *Lindsay* and *Thompson* (1932) it appears that in Newfoundland waters fish which have previously spawned generally constitute 16.5 % of the stock; in some rivers still higher numbers were found.

The previous and present investigations have thus shown that there are great fluctuations from one year to another in the relative abundance of fish which have spawned on a previous occasion. There are also great differences between the various localities. The fluctuations occurring in a single river may to some extent be due to variations in the relative strength of the year-classes. The mortality during the spawning migration may, however, vary from year to year and from one locality to another.

As will be shown later the present material indicates that the mortality during the first spawning migration is more severe among small salmon than among grilse. The relative abundance of fish which have previously spawned may, therefore, be related to the composition of the stock in previous years.

The relative high percentage of survivors in Nidelven and Tovdalselven may be ascribed to the fact that the spawning here takes place a short distance from the sea. The mortality may be assumed to be more severe in rivers in which the spawning grounds are situated far from the sea.

The marking experiments of *Dahl* and *Sømme* (1936, 1937, 1938, 1942) have shown that at least 50 % of the salmon marked on their spawning migration, are recaptured. The fishing intensity will therefore influence the mortality during this period of life.

Life Cycle Classes.

The material from Nidelven consists of 1596 maiden fish, 224 specimens with 1 spawning mark, 19 specimens with 2 spawning marks, and 1 specimen with 3 spawning marks. Thus we find that 14 % of the stock survive the first spawning migration and enter the river for a second time. Of these individuals 8 % survive and enter the river for a third time. Only in rare cases the salmon survive a third spawning and enter the river for a fourth time. Thus the percentage of survivors decreases for each spawning. — In Tovdalselven there were 64 specimens with spawning marks. Of these only one had spawned twice. At Arendal and Flekkefjord no specimens proved to have spawned more than once.

To find out from which groups the previous spawners are mostly derived, the time spent in the sea before spawning is given in tab. 15 for fish with one spawning mark and for maiden fish. It is evident that the majority of the previous spawners has entered the river as grilse, whereas the small salmon dominated among the maiden fish. The present material indicates, therefore, that in these waters the mortality during the spawning migration is more severe among small salmon than among grilse. This is in conformity with the results previously obtained in these waters by *Dahl* (1910) and *A. Dannevig* (1914). — *Lindsay* and *Thompson* (1932) as well as *Järvi (1938),* dealing respectively with salmon from Newfoundland and Finnish waters, have found the percentage of survivors to be approximately the same in grilse and small salmon.

Tab. 15. Duration of Sea Life (Winters) before Spawning for Maiden Fish and for Fish with 1 Spawning Mark.

Winters in sea before spawning		1 w	2 w	3 w	4 w
Nidelven	maiden fish	39%	59%	2%	0.06%
	previous spawners	77%	22%	1%	
Tovdalselven	maiden fish	25%	69%	5%	
	previous spawners	83%	17%		
Arendal	maiden fish	36%	54%	9%	1%
	previous spawners	54%	46%		

The time spent in the sea between two spawning migrations, the intermediate migration period, is given in tab. 16. Some of the salmon which have survied the spawning enter the river in the subsequent season. The vast majority (between 89 % and 93 %) spend one winter in the sea before starting on their second migration. In some rare cases the salmon may stay even two winters in the sea. These

results are in conformity with those previously obtained in Nidelven by *A. Dannevig* (1914), and the conditions seem to be very much the same in most localities (*Dahl* (1910), *Lindsay* and *Thompson* (1932), *Järvi* (1938)). — According to *Menzies* (1912) annual spawning may, however, be rather frequent in certain localities.

Tab. 16. Salmon with one Spawning Mark. Intermediate Migration Period.

	+	1 w	2 w
Nidelven	7%	93%	
Tovdalselven	11%	89%	
Arendal	7%	89%	4%

Size and Growth.

The average size of the fish belonging to the same groups of salmon which have previously spawned, is very much the same in the different localities (tab. 17). — The mean length of fish which have spawned as grilse and enter the river the subsequent season, exceeds that of the grilse by about 6 cm. The growth during the last summer in the sea has, therefore, been very slight. If they stay another winter in the sea before the second spawning migration (.1G1), they have approximately attained the size of small salmon. — The strain of the spawning migration seems to be more severe to the small salmon. Fish belonging to the group .2G1 have not by far attained the size of maiden fish which have also spent 3 winters in the sea. The results obtained in the various localities are very much the same in this respect.

Tab. 17. Size of Maiden Salmon and Previous Spawners. (1925—1931)

		Nidelven		Tovdalselven		Arendal	
		L	W	L	W	L	W
Grilse	.1 +	56.8	1.6	59.1		58.3	1.8
Previous spawners.....	.1 G +	63.8	2.1	63.5		(65)	(2.9)
Small salmon	.2 +	74.9	3.8	75.6		75.3	4.5
Previous spawners.....	.1 G 1	75.4	3.9	75.4		71.3	3.7
Large salmon	.3 +	100.1	10.5	103.2		100.3	11.7
Previous spawners	.2 G 1	90.6	6.7	90.9		89.4	7.5

ANNUAL FLUCTUATIONS IN THE SIZE OF THE SALMON.

There are great fluctuations from one year to another as to the average size of the salmon entering Nidelven. The mean weight of the fish varies between 2.2 kg (1931) and 4.3 kg (1938), the mean for all years being 3.3 kg. From the previous discussion it is evident that these fluctuations to a certain extent depend on the growth of the fish. Thus it has been found that the average weight of the small salmon varies between 3.3 and 4.7 kg, and that of the grilse between 1.3 and 1.9 kg.

The composition of the stock is of still greater importance. The grilse may in some years constitute the vast majority of the maiden fish (77 % in 1931), in other years the small salmon may dominate (88 % in 1938). — The maiden fish entering Nidelven have on an average spent 1.63 winters in the sea. The annual deviations — δ — from this mean are presented in fig. 11 together with the average weight (W) of the fish in the different years. Apparently the varying weight of the ascending salmon may to a great extent be ascribed to fluctuations in the relative abundance of grilse and small salmon. *Dahl* (1913 a) has arrived at the same results.

It is evident that the fluctuations as to the size of grilse and small salmon are of importance to the yield of the river. In some years a number of 100 small salmon may yield only 330 kg, in other years 470 kg, or 42 % more. The effect upon the total output of the river will be in proportion to the relative abundance of the group in question.

The importance of the varying duration of sea life is more difficult to ascertain as we have no information as to the rate of mortality during this period of life. — Calculating with a mortality of 20 %, we find that 100 specimens entering Nidelven in the grilse stage, on an average will yield 159 kg, whereas they will yield 316 kg if staying another year in the sea. Assuming a mortality of 40 %, the two groups will yield 159 and 237 kg respectively. It is evident that even with a mortality of 40 %, the output of the fishery in a river will be greater in periods in which the salmon spend 2 winters in the sea than in periods in which the salmon enter the river as grisle.

The factors here dealt with will of course only cause smaller fluctuations in the yield of a river, the main factor being the strength of the year-classes. As far as we may judge from the present material and from the official statistics, greater changes in this respect have not occurred within the period of investigation.

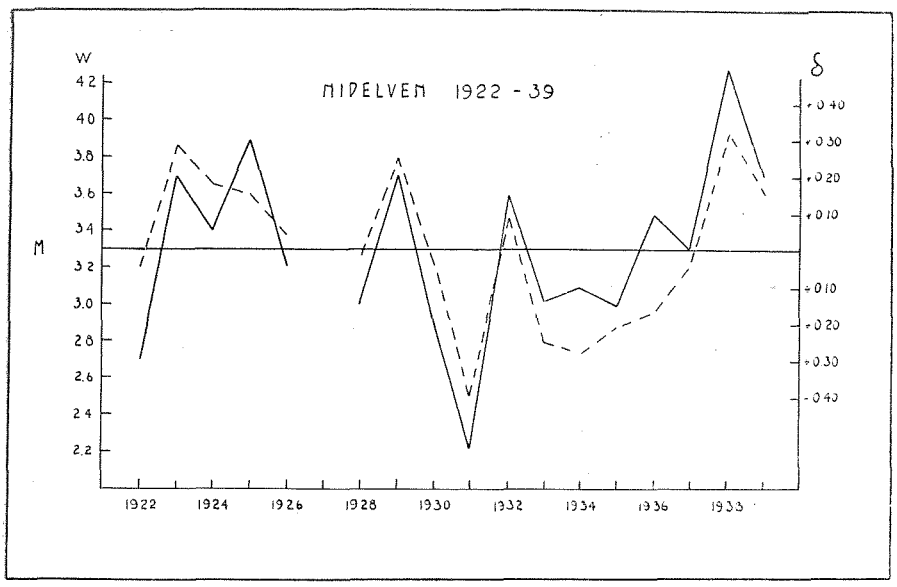

Fig. 11. Nidelven. Annual Fluctuations in the Weight (W) of the Ascending Salmon (————), and the deviations (δ) from the average Duration of Sea Life of Maiden Fish (— — — —).

Summary.

The material here dealt with comprises salmon ascending the rivers Nidelven and Tovdalselven, and salmon caught in the sea off Arendal and Flekkefjord.

River life. There is no considerable difference as to smolt age between the various localities. Salmon with 3 years of river life dominate; emigrants 2 years old are also numerous, whereas fish with 4 years of river life only constitute a small percentage of the stock. Older emigrants are extremely scarce. Generally there are no great fluctuations from one year to another as to the duration of river life, even if such fluctuations may occur in some years. — On the whole the duration of river life of large salmon is shorter than that of small salmon and grilse.

Sea life. Salmon with 2 years of sea life generally dominate in all localities; the grilse are also numerous, whereas large salmon are scarce. There are, however, great annual fluctuations as to the relative abundance of grilse and small salmon. There are periods in which the grilse dominate, and periods in which the small salmon dominate. These fluctuations are very much the same in Nidelven and at Arendal. It seems as if the salmon do not always stay for the same period in the sea; in some years they enter the river in the grilse stage, in other

years they spend another winter in the sea. It is seldom, however, that salmon from these waters stay 3 winters in the sea.

Age. A single year-class appears in the catches through 4 consecutive years. In two years only it is of some importance. The age of the fish fluctuates according to the time spent in the sea. In some years also fluctuations in the relative abundance of the year-classes may influence the age distribution.

Size and Growth. The length and weight of the salmon are not influenced by the duration of river life. — Grilse, as well as small and large salmon caught within the same period, are of approximately the same size in the various localities. — There are great annual fluctuations in the size of grilse and small salmon. — The fluctuations in growth are especially marked during the first year of sea life. When the growth during the first year in the sea is calculated for the year in which the growth occured, the grilse and the small salmon from Nidelven exhibit corresponding variations. There is also correspondence between the various localities in this respect.

The growth during the first year of sea life seems on the whole to be more rapid in years with a high temperature in the surface water along the coast than in years with a low temperature. The growth may be directly influenced by fluctuations in the temperature. Such fluctuations may, however, also indicate more general variations in the growth conditions in the sea.

The frequency of *previous spawners* varies considerably from one year to another. Generally this group is more abundant in the material from the rivers than in the material from the sea. The mortality at the first spawning seems to be more severe among small salmon than among grilse. — Generally the salmon spend 1 winter in the sea between the two spawning migrations. Specimens occur, however, which enter the river in the succeeding season, or stay 2 winters in the sea.

The size of the salmon entering Nidelven varies considerably from year to year owing to fluctuations in the relative abundance of the various classes of salmon. Fluctuations in the size of individuals belonging to the same group are also of importance. — The varying duration of sea life and the varying growth are of importance to the yield of a river.

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Tab. I. Material from Nidelven 1922—1939. Number of Salmon in each Life Cycle Class. (Percentage in Brackets).

Year	River life	Sea life (winters) 1 w	2 w	3 w	4 w	Total	Previous spawners	N
1922 ...	2 years	18	34			52 (52)		
	3 -	22	25			47 (47)		
	4 -			1		1 (1)		
	?	6	2			8		
Total ..		46 (43)	61 (56)	1 (1)		108	5 (4)	113
1923 ...	2 years	4	18	4		26 (39)		
	3 -	6	35			41 (61)		
	?		8			8		
Total ...		10 (13)	61 (81)	4 (5)		75	5 (6)	80
1924 ...	2 years	12	27	1	1	41 (53)		
	3 -	9	24	2		35 (45)		
	4 -		2			2 (3)		
	?		8			8		
Total ...		21 (24)	61 (71)	3 (3)	1 (1)	86	9 (9)	95
1925 ...	2 years	13	25	2		40 (42)		
	3 -	13	36	4		53 (55)		
	4 -		3			3 (3)		
	?	7	11	1		19		
Total ...		33 (29)	75 (65)	7 (6)		115	21 (15)	136
1926 ...	2 years	32	69	3		104 (39)		
	3 -	59	95			154 (57)		
	4 -	2	8			10 (4)		
Total ..		93 (35)	172 (64)	3 (1)		268	31 (10)	299
1927 ...	2 years	1	6			7		
	3 -		3			3		
	4 -							
Total ...		1	9			10	7	17
1928 ...	2 years	13	23			36 (53)		
	3 years	10	22			32 (47)		
	?	1				1		
Total ...		24 (35)	45 (65)			69	11 (14)	80
1929 ...	2 years		3			3		
	3 -	2	7			9		
	?		5			5		
Total ...		2	15			17	4 (19)	21

(*Tab. 1 continued*).

Year	River life	Sea life (winters) 1 w	2 w	3 w	4 w	Total	Previous spawners	N
1930 ...	2 years	6	10			16 (34)		
	3 -	16	15			31 (66)		
	?		6			6		
Total ...		22 (41)	31 (59)			53	5 (9)	58
1931 ...	2 years	8	5			13 (22)		
	3 -	36	7			43 (74)		
	4 -	1				1 (2)		
	5 -	1				1 (2)		
	?	1	2			3		
Total ...		47 (77)	14 (23)			61	4 (6)	65
1932 ...	2 years	5	35	3		43 (45)		
	3 -	26	23	2		51 (54)		
	4 -		1			1 (1)		
Total ...		31 (33)	59 (62)	5 (5)		95	16 (14)	111
1933 ...	2 years	13	13	1		27 (27)		
	3 -	49	19			68 (70)		
	4 -	1	2			3 (3)		
	?	7	4	1		12		
Total ...		70 (64)	38 (35)	2 (2)		110	21 (16)	131
1934 ...	2 years	14	6			20 (36)		
	3 -	19	14			33 (60)		
	4 -	2				2 (4)		
	?	2				2		
Total ...		37 (65)	20 (35)			57	8 (12)	65
1935 ...	2 years	29	19			48 (50)		
	3 -	27	19			46 (48)		
	4 -	1	1			2 (2)		
	?	1	3			4		
Total ...		58 (58)	42 (42)			100	9 (8)	109
1936 ...	2 years	16	26			42 (38)		
	3 -	40	22			62 (56)		
	4 -	4	2			6 (5)		
	?	2	2			4		
Total ...		62 (54)	52 (46)			114	33 (22)	147

(*Tab. I continued*).

Year	River life	Sea life (winters)				Total	Previous spawners	N
		1 w	2 w	3 w	4 w			
1937 ...	2 years	12	8			20 (31)		
	3 -	13	26			39 (60)		
	4 -	3	2			5 (8)		
	5 -	1	0			1 (2)		
	?	2	8			10		
Total ...		31 (41)	44 (59)			75	13 (15)	88
1938 ...	2 years		32			32 (41)		
	3 -	5	37			42 (54)		
	4 -	2	2			4 (5)		
	?		3	3		6		
Total ...		7 (8)	74 (88)	3 (4)		84	23 (22)	107
1939 ...	2 years	9	29			38 (40)		
	3 -	13	39	1		53 (55)		
	4 -		4			4 (4)		
	5 -		1			1 (1)		
	?		3			3		
Total ...		22 (22)	76 (77)	1 (1)		99	19 (16)	118
1922/39	2 years	204	388	14	1	607 (41)		
	3 -	366	468	9		843 (56)		
	4 -	16	27	1		44 (3)		
	5 -	2	1			3 (0,2)		
	?	29	65	5		99		
Total ...		617 (39)	949 (59)	29 (2)	1 (+)	1596	244 (13)	1840

Tab II. Material from Arendal 1925—1931. Number of Salmon in each Life Cycle Class. (Percentage in Brackets).

Year	River life	Sea life				Total	Previous spawners	N
		1 w	2 w	3 w	4 w			
1925 ...	2 years	5	4	4		13 (36)		
	3 -	10	7	2		19 (53)		
	4 -	2	2			4 (11)		
	?	2	1			3		
Total ...		19 (49)	14 (36)	6 (15)		39	4 (9)	43
1926 ...	2 years	14	15			29 (44)		
	3 -	22	13	1		36 (55)		
	4 -	1				1 (2)		
	?	2				2		
Total ...		39 (57)	28 (41)	1 (1)		68	3 (4)	71
1927 ...	2 -		10	2		12 (36)		
	3 -	5	14	1		20 (61)		
	4 -		1			1 (3)		
Total ..		5 (15)	25 (76)	3 (9)		33	4 (11)	37
1928 ...	2 years	4	22	9		35 (33)		
	3 -	9	48	5		62 (59)		
	4 -	1	8			9 (8)		
Total ...		14 (13)	78 (74)	14 (13)		106	11 (9)	117
1929 ..	2 years	2	9	3		14 (38)		
	3 -	6	15	1		22 (59)		
	4 -	1				1 (2)		
	?		4	3		7		
Total ...		9 (20)	28 (64)	7 (16)		44	4 (8)	48
1930 ...	2 years	3	4	1		8 (18)		
	3 -	18	18			36 (82)		
	?		1	1	1	3		
Total ...		21 (45)	23 (49)	2 (4)	1 (2)	47	0	47
1931 ...	2 years	9	3	1	2	15 (34)		
	3 -	20	8			28 (64)		
	4 -	1				1 (2)		
	?		1	1		2		
Total ...		30 (65)	12 (26)	2 (4)	2 (4)	46	2 (4)	48
1925/31	2 years	37	67	20	2	126 (34)		
	3 -	90	123	10		223 (61)		
	4 -	6	11			17 (5)		
	?	4	7	5	1	17		
Total ...		137 (36)	208 (54)	35 (9)	3 (1)	383	28 (7)	411

Tab. III. Material from Tovdalselven 1925—1932. Number of Salmon in each Life Cycle Class. (Percentage in Brackets).

Year	River life	Sea Life (winters)			Total	Previous spawners	N
		1 w	2 w	3 w			
1925	2 years	4	4		8		
	3 -	7	3		10		
	4 -	1			1		
Total		12	7		19	3 (14)	22
1926	1 year		1		1		
	2 -	22	18	3	43		
	3 -	34	26	1	61		
	4 -		1		1		
Total		56	46	4	106	15 (12)	121
1927	2 years	4	11	2	17		
	3 -	1	6		7		
	?			1	1		
Total		5	17	3	25	5 (17)	30
1928	2 years		3		3		
	3 -		30		30		
	?		3		3		
Total			36		36	5 (12)	41
1929	2 years		21	4	25		
	3 -		28	1	29		
	4 -		3		3		
	?		16	7	23		
Total			68	12	80	8 (9)	88
1930	2 years		11	1	12		
	3 -	10	35		45		
	?	1	1		2		
Total		11	47	1	59	7 (11)	66
1931	2 years	2	4		6		
	3 -	14	26		40		
	?		5		5		
Total		16	35		51	1 (2)	52
1932	2 years	2	4	1	7		
	3 -	2	23		25		
	4 -		1		1		
Total		4	28	1	33	20 (38)	53

(*Tab. III continued*).

Year	River life	Sea Life (winters)			Total	Previous spawners	N
		1 w	2 w	3 w			
1925—32 ..	1 year		1		1 (0.3)		
	2 years	34	76	11	121 (32)		
	3 -	68	177	2	247 (66)		
	4 -	1	5		6 (2)		
	?	1	25	8	34		
Total		104 (25)	284 (69)	21 (5)	409	64 (14)	473

Tab. IV. Material from Flekkefjord. Number of Salmon in the different groups.

	N	Grilse	Small salmon	Large salmon	Spawned fish
1927	16		15	1	
1928	35		33	2	
1929	36	11	23		2
1930	38	20	17	1	

Tab. V. Size, Growth, and Condition.

Year	Grilse						Small salmon						
	N	l	L_1	L	W	γ	N	l	L_1	L_2	L	W	γ
Nidelven.													
1922	46	13.5	44.5	56.3	1.49	0.84	61	12.3	43.5	67.0	72.7	3.30	0.86
1923	10	12.6	42.2	54.6	1.46	0.90	61	12.0	46.3	70.7	75.8	3.92	0.90
1924	21	13.1	45.8	56.0	1.53	0.87	61	11.9	42.4	68.2	73.5	3.59	0.90
1925	33	13.2	43.6	54.6	1.45	0.89	75	12.5	46.6	72.6	77.8	4.35	0.92
1926	93	13.0	47.5	57.5	1.66	0.87	172	12.3	44.5	69.0	73.9	3.63	0.90
1927	1	11	45	56	—	—	9	11.8	50.0	76.7	82.3	—	—
1928	24	12.2	42.0	51.9	1.33	0.95	45	12.5	46.9	68.7	72.6	3.41	0.89
1929	2	18	47	56	1.5	—	15	13.2	44.7	70.5	76.5	3.95	0.88
1930	22	13.9	45.4	57.2	1.63	0.87	31	13.5	42.9	67.4	74.3	3.73	0.91
1931	47	14.7	49.2	59.3	1.71	0.82	14	12.4	44.1	69.2	74.2	3.60	0.88
1932	31	15.1	45.5	57.3	1.68	0.89	59	12.5	48.8	72.6	77.2	4.21	0.92
1933	70	14.6	48.2	59.5	1.87	0.89	38	14.5	47.2	72.0	77.1	4.08	0.89
1934	37	13.5	48.7	58.5	1.68	0.84	20	15.0	50.5	76.1	81.4	4.71	0.87
1935	58	12.8	48.3	58.2	1.65	0.84	42	13.0	50.4	75.1	78.7	4.38	0.90
1936	62	14.3	49.5	58.9	1.67	0.82	52	12.4	49.8	73.0	76.3	4.06	0.91
1937	31	13.8	45.9	57.8	1.53	0.79	44	13.7	49.8	73.8	78.2	4.20	0.88
1938	7	15.8	44.0	56.6	1.47	0.81	74	14.2	47.5	72.7	78.1	4.10	0.86
1939	22	13.1	47.0	57.6	1.61	0.84	76	14.6	46.2	72.0	77.2	3.96	0.86

(Tab. V continued).

Year	Grilse						Small salmon						
	N	l	L_1	L	W	γ	N	l	L_1	L_2	L	W	γ
Arendal													
1925	19	13.3	44.7	56.2	1.70	0.96	14	13.4	46.3	73.9	78.6	5.00	1.03
1926	39	13.1	48.8	60.3	2.16	0.99	28	12.2	45.1	71.0	75.4	4.33	1.01
1927	5	11.6	41.0	54.0	1.58	1.01	25	12.5	49.4	74.7	78.2	5.20	1.09
1928	14	13.9	45.1	55.7	1.69	0.98	78	13.0	47.8	71.2	74.9	4.25	1.01
1929	9	13.0	45.7	57.7	1.87	0.97	28	12.0	45.0	69.3	73.6	3.77	0.95
1930	21	15.3	47.3	59.8	2.00	0.94	23	14.5	44.4	67.6	73.5	3.90	0.98
1931	30	14.6	49.1	58.3	1.90	0.96	12	12.7	44.7	71.3	75.2	4.88	1.15
Tovdalselven													
1925	12	13.0	45.0	58.3			7	12.7	44.6	76.2	83.0		
1926	56	12.7	47.8	60.3			46	13.3	45.7	73.6	77.7		
1927	5	11.6	46.8	58.0			17	11.3	48.8	74.4	77.2		
1928	0						36	12.8	46.5	71.4	74.9		
1929	0						68	13.7	44.2	70.3	75.5		
1930	11	14.8	46.3	57.7			47	13.3	44.0	67.7	73.2		
1931	16	13.4	49.0	58.0			35	12.5	45.1	73.7	77.0		
1932	4	13.8	46.8	58.2			28	13.5	49.5	75.5	79.6		
Flekkefjord													
1927	0						15	10.8	47.7	73.5	78.7		
1928	0						33	10.7	45.8	71.6	76.5		
1929	11	13.2	43.6	56.3			23	14.1	44.3	69.5	75.6		
1930	20	15.4	46.3	59.4			17	15.1	45.7	68.7	75.5		

	Large salmon						
	N	l	L_1	L_2	L_3	L	W
Nidelven 1922—1939	29	12.3	49.5	77.5	93.8	98.9	9.7
Arendal 1925—1931	35	9.4	49.5	78.3	98.5	100.3	11.7
Tovdalselven 1925—1932.....	21	10.9	45.5	77.8	100.1	103.2	
Flekkefjord 1927—1930	4	12.0	46.3	76.3	96.0	99.0	

Tab. VI. Number of Salmon with Spawning Marks in total (f) and in each Life Cycle Class.

Year	N	f	%	.1G+	.1G1	.2G+	.2G1	.3G1	Other groups
Nidelven									
1922 ...	113	5	4		3		2		
1923 ...	80	5	6		4	1			
1924 ...	95	9	9		9				
1925 ...	136	21	15	3	12		4	1	1 (.1G1G+)
1926 ...	299	31	10	1	27		3		
1927 ...	17	7			5		1		1 (.3G1G1)
1928 ...	80	11	14		9		2		
1929 ...	21	4	19		3				1 (.1G1G1)
1930 ...	58	5	9		3	1	1		
1931 ...	65	4	6		3	1			
1932 ...	111	16	14	3	13				1(.2G+G+)
1933 ...	131	21	16		14	1			6 1(.2G+G1)
1934 ...	65	8	12	1	3		4		4(.1G1G+)
1935 ...	109	9	8	1	6		1		1 (.2G+G1)
1936 ...	147	33	22	1	12		13		7
1937 ...	88	13	15		8	2	1		2
1938 ...	107	23	22		16		5	1	1 (.2G1G1)
1939 ...	118	19	16		12		7		
1922/39	1840	244	13	10	162	6	44	2	20
Tovdalselven									
1925 ...	22	3	14	3					
1926 ...	121	15	12	1	10	1	3		
1927 ...	30	5	17		5				
1928 ...	41	5	12		5				
1929 ...	88	8	9		6		2		
1930 ...	66	7	11	1	3		3		
1931 ...	52	1	2						1 (.3G+G1)
1932 ...	53	20	38	1	17		2		
1925/32	473	64	14	6	46	1	10		1
Arendal									1 (.1G2)
1925 ...	43	4	9		1		1		1 (.2G+)
1926 ...	71	3	4		1		2		
1927 ...	37	4	11		4				
1928 ...	117	11	9		6		5		
1929 ...	48	4	8		1		3		
1930 ...	47	0	0						
1931 ...	48	2	4	1			1		
1925/31	411	28	7	1	13		12		2
Flekkefjord									
1927 ...	16	0	0						
1928 ...	35	0	0						
1929 ...	36	2	6		1		1		
1930 ...	38	0	0						
1927/30	125	2	2		1		1		

LIST OF TERMS AND ABBREVIATIONS

During the first years' fresh water life the salmon is termed a *parr.*
Having attained the stage of emigration, it is termed a *smolt.*

Grilse	have spent	1	winter in the sea.
Small salmon	» »	2	winters in the sea.
Large salmon	» »	3	—»—
Very large salmon	» »	4	—»—

N Number of specimens examined.
L Length in cm of the fish from the snout to the tip of the tail.
l estimated length of smolt.
L_1, L_2 estimated length at the first, and second winter in the sea.
T_1, T_2 estimated increment in length during the first and second year in the sea.
T estimated increment in length during the year of capture.

M stands for the arithmetic mean

$\sigma = \sqrt{\frac{\Sigma (L-M)^2}{N}} = \sqrt{\frac{I}{N} \Sigma L^2 - M^2}$ the standard deviation (for large samples)

$\varepsilon = \frac{\sigma}{\sqrt{N}}$ standard error of the mean

$\varepsilon_D = \sqrt{\varepsilon_1^2 + \varepsilon_2^2}$ standard error of the difference (D)

W stands for the weight of the fish in kg

$\gamma = \frac{10^5 W}{L^3}$ indicates the relative weight of the fish

R stands for the average duration of river life.