Report

of

The Danish Biological Station

to

The Ministry of Fisheries



No. 54

By

Å. Vedel Tåning, Ph. D. Director

Copenhagen · C. A. Reitzel 1952

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Size and Age of the Silver Eel (Anguilla anguilla (L.)) in Esrum Lake.

By C. J. RASMUSSEN

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Introduction.

E SRUM LAKE, with an area of about 1730 ha, is the largest lake of Denmark but one. Its physiographic properties have been thoroughly described by BERG (1938); therefore only a few characteristic features of the natural conditions of the lake will be pointed out here.

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The length of the lake—taking a course nearly north-south—is about 8 km, and its breadth is 2—3 km. The maximum depth is 22 m and about half of the area has depths from 15 to 20 m, the litoral zone nearly everywhere being very narrow (fig. 1). The average depth (12.3 m) is therefore rather considerable in relation to the area of the lake.

The catchment area, which, including the lake, amounts to 78.5 sq. km, gives off insignificant affluents only. The outlet, Esrum Å, which issues from the northern end of the lake and debouches in the Kattegat, passes the water mill of Esrum, where there is an eel trap.

The lake is eutrophic and conditions of oxygen from surface to bottom show considerable variations influenced by the seasons. Thus Berg's investigations show that the saturation of oxygen at the end of the summer stagnation period in more than 15 m's depth

is less than 50 per cent. and that the water at a depth of about 20 m may be practically oxygen-free, a fact which is of a certain interest from the point of view of fishery biology as it may sometimes during part of the year prevent the fish from staying at the bottom in up to half of the area of the lake. When such conditions set in, the demersal fish are therefore compelled to making vertical, temporary feeding migrations from higher layers of water richer in oxygen. We have an interesting proof that such vertical movements take place in the case of the eel. It has long been known among the fishermen that the eels which towards the end of the summer stagnation period are hooked in deep water in Esrum Lake, are dead when collected. Investigations of the cause showed that the contents of oxygen at the depths at which the dead hooked eels were found, were so poor that they could not stay there; so the cause of death was suffocation. Consequently there can be no doubt that the demersal fish of the lake to a certain extent in late summer are compelled to lead a partly pelagic life (OTTERSTRØM 1934).

The fish population of the lake consists of the following species: eel (Anguilla anguilla (L.)), pike (Esox



Fig. 1. Chart indicating depths in Esrum Lake. (After H. W. FIEDLER'S survey of 1871, reproduced from WESENBERG-LUND, 1904).

Dybdekort over Esrum sø. (Målt og udarbejdet af H. W. FIEDLER 1887. Her gengivet efter WESENBERG-LUND, 1904).

lucius L.), perch (Perca fluviatilis L.), ruff (Acerina cernua (L.)), bream (Abramis brama (L.)), roach (Rutilus rutilus (L.)), rudd (Scardinius erythrophthalmus (L.)), tench (Tinca tinca (L.)), bleak (Alburnus alburnus (L.)), and crucian carp (Carassius carassius carassius (L.)).

The nine-spined stickleback (*Pungitius pungitius* (L.)) is found in several small affluents, but is not reported from the lake.

As for Esrum Lake and all other large Danish lakes in which rational fishing is carried on, the size and utilization of the population of eels are decisive of the profitableness of the fishery. As compared with the eel fishery the fishing for all the other species therefore is secondary and must in part be considered either as a byproduct of it or as part of the measures for its promotion.

The eel fishery is mainly carried on as trap fishing for yellow eels as well as silver eels, to which should be added a not inconsiderable hook fishing for yellow eels in spring and the early summer as long as the eels willingly take the bait and the price of eels is still fairly high.

The majority of silver eels which are not caught in the lake during the seaward migration are caught in the privately owned eel-trap at the mill of Esrum.

The population of eels is maintained partly through natural immigration of small fry and partly by rather considerable transplantation of elvers and small yellow eels (cf. Table 12).

1. Material.

Esrum Lake formerly was part of the crownland and is now the property of the Danish government, which—apart from a minor area in the south-western corner of the lake, where the right of free fishing has been conferred on the owner of the mill of Stenholt farms out the fishery for ten-year periods. Besides the economic obligations various duties concerning the management have been imposed on the lessee. He is to conform to certain directions given by the Ministry of Fisheries. Apart from these regulations he is to deliver 30 silver eels a year to the Fishery and Sea Investigations of Denmark for control of age and weight. The material for the present paper mainly originate from these compulsory deliveries and comprises the period from 1937 to 1950.

On account of the desirability of providing a material in each case which on an estimate can be considered representative of the population of silver eels in the

lake, the control eels are collected at random from the catches. Only in so far as large eels are concerned, i.e. eels from about a pound and upwards, which constitute only 5—7 per cent. of the total catch, a certain subjective estimate has proved necessary at the collection.

The male eels are of rare occurrence in the lake. Partly for this reason and partly because they mainly emigrate seawards before the female eels and therefore are extremely rare at the rather late period (from the middle of September to the end of November) when the control eels are collected, they have not been represented in the material investigated, which thus consists exclusively of female eels.

With the exception of the eels in the sample from 1938 which were killed with ether, all control eels were killed with common salt, after which measurement, weighing, determination of sex, and collection of scale samples and in some cases otoliths took place. The length is everywhere stated at the lowest whole number of centimetres and mean lengths etc. are given without correction (+0.5 cm) for this. Weighings were made with an accuracy of about 1 gramme. The killing with salt involves a certain loss in weight, which, however, within the period of the salting is so small that I have not found it necessary to correct the values found. A control experiment showed that 5 eels with a total weight of 1799 g after being kept in salt for 5 quarters of an hour had lost only 75 g (4.2 per cent.).

After removal of the slime all samples of scales were collected between the lateral line and the dorsal fin above the anal region of the fish, where the first scales develop (cf. p. 8). The samples of scales are preserved in 70 per cent. alcohol and washed in water before sorting and examination.

Whereas scales were sampled from all control eels, otoliths were taken only from the material of 1948— 50, which in all includes 110 silver eels. The otoliths are kept in alcohol with the samples of scales to which they belong.

2. Determination of Age.

(a) General Survey.

In his important work on the determination of age in the European freshwater eel GEMZØE (1907) showed that the concentric zones—more or less completely developed—in scales of eels are annual rings. His paper became the basis of a considerable number of other papers which have since then been published for the purpose of elucidating the question of the age and growth of the freshwater eel. However, as the eel does not begin developing scales until reaching a length generally of 17—18 cm, the use of the scales for the determination of age presupposes that the age of the eel at this length is known beforehand. On the basis of the measuring method GEMZØE thought it possible to establish that the first beginnings of the scales are normally started in the third year after immigrating as an elver.

EHRENBAUM and MARUKAWA (1912) found an important aid in determining the age of the freshwater eel in the otoliths, which in the case of the minor eels enable a very sure determination of their age. The advantage of using the otoliths for determination of age rather than the scales, amongst other things are due to the fact that the otoliths start developing already in the early larval stage, whereas the time for the first beginnings of the scales to no small degree—as will appear from what follows—seems to depend on the rate of growth. The elvers, which generally make their first appearance in the lower parts of the streams in the months of April-May and which according to JOHS. SCHMIDT'S investigations (1922) are about three years of age, thus already have well-developed otoliths (cf. Plate I, fig. 4).

During the stay in the freshwater the otoliths are enlarged with concentric formations of rings, which in incident light appear as alternately light and dark zones and which on the basis of growth experiments in aquaria through several years could be identified with certainty by EHRENBAUM and MARUKAWA (1913) as respectively summer and winter zones. With this means of a sure determination of age it was then rather easily shown that eels from the Lower Elbe generally do not start developing scales until the fourth year after their immigration as elvers. As a general rule it was also assumed that the age and not the size of the eel is decisive of the time when the first beginnings of scales make their appearance in free-living eels. According to these authors this means that at determinations of age on the basis of scales we should add to the number of zones of growth found, not two—as maintained by GEMZØE—but three in order to find the number of years spent in freshwater by the eel after its immigration as an elver.

Whereas according to EHRENBAUM and MARUKAWA the time for the beginning of the formation of scales in the free-living eels must be supposed to be rather closely connected with their reaching a definite age, their experiences from rearing in aquaria suggest that the formation of scales there is not connected with a definite age, but with a definite size, which in their material was 18 cm.

Later investigations have not confirmed EHREN-BAUM and MARUKAWA's observations of the formation of scales in the free-living eels being started at a definite age. These later results more nearly agree with the results of their aquarium experiments.

When examining eels from Commachio in Northern Italy HAEMPEL and NERESHEIMER (1914) found that 4 out of 5 eels of 15 cm in length and 2 of 18 cm, which were all in their second year in freshwater (I-gr.) had already beginnings of scales. In this connexion MARCUS (1919) remarks that partly because of the small number of specimens examined, partly because of the uncertainty of the age determinations caused by ignorance of the time of catch, there is also a certain uncertainty as regards the evaluation of the results of growth obtained. Regardless of the justification of this criticism it is of interest to note that HAEMPEL and NERESHEIMER's result does not agree with EHRENBAUM and MARUKAWA's experiences, but rather support the assumption that the scales in the free-living eels begin to develop when the eels reach a certain size, not a certain age. The view that the scales chiefly begin to develop in the second or-when keeping MARCUS' criticism in mind-perhaps the third year in freshwater, must be viewed in the light of the fact that the Italian eels-as shown by HAEMPEL and NERESHEIMER-at any rate during the first years grow faster than the North European eels.

MARCUS (1919) himself, who has determined the ages of nearly 9000 eels from German lakes and streams on the basis of examinations of both scales and otoliths, makes the following survey (Table 1) of the beginning of the formation of scales in eels caught in May—June in the Weser at Bremen.

Out of group II 11 (17-22 cm) were already developing scales, while 29 (13-20 cm) were scaleless (27.5 and 72.5 per cent.). Out of group III 128 (15-27 cm) had scales, while 11 (14-18 cm) were scaleless (92.1 and 7.9 per cent.). From these results MARCUS concludes that the first scales generally begin to develop when the fish has reached a length of 16-17 cm, which is in good agreement with GEMzøe's results. In the case of the eels of the Elbe as well as those of the Weser this size was mostly reached during the fourth freshwater year (group III).

NORDQVIST and ALM (1920) similarly for the Swedish eels give the fourth freshwater year as the age

TABLE 1.

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Age and length of eels from the Weser at incipient formation of scales (according to MARCUS, 1919). Weser ålenes alder og længde ved skælanlæg (efter MARCUS, 1919).

Length in cm	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Længde i cm (With scales		••	•••	• •											
Group II ¹ II-gruppen Without scales Uden skæl							2	2							
With scales														2	
Group III1 III-gruppen Without scales Uden skæl	••••	1	4	2	2	2	••	• •	•••	••	••	••	••	••	10 B

¹ Group II, respectively III, was finished in April.

II- henholdsvis III-gruppen var afsluttet i april.

at which the scales are generally formed. In older eels, however, as will appear from the calculations in Table 6 (p. 11) made on the basis of their investigations, there seems to be a tendency towards a greater deviation between the readings of scales and otoliths than in the younger age-groups. Out of the total material 62.7 per cent. should have begun developing scales in the fourth year in fresh water, 10.0 and 24.6 per cent. in the third and fifth year, respectively, and only 1.2 and 1.4 per cent. in the second and sixth year, respectively.¹

TESCH (1928), who states having examined several thousand otoliths of eels, finds identical conditions in Dutch waters, giving the length at which the first scales are formed as 16-18 cm, generally corresponding to group III (cf. Table 2).

FROST (1945) has examined more than 600 eels from the Windermere catchment area, the age of 310 of which has been determined on the basis of examinations of both scales and otoliths. She finds a difference between the readings of otoliths and scales of 1-5 years, i.e. that the formation of scales may be started in group I, II, III, IV, or V. The corresponding percentage distribution was 12, 27, 38, 16, and 6. The fact that the fourth freshwater year is not-as observed by other authors—so predominantly the year of the first formation of scales, is, according to FROST, due to the readings of otoliths in the case of the older eels being uncertain. Particularly these eels, which in her material are most strongly represented, give the great deviations. It might be added that also the uncertainty of the examinations of scales is to some

¹ Because of an error in summing up in NORDQVIST and ALM's Table 1 their statements of percentages and mine are not identical. degree increased with increasing age of the fish (cf. p. 9).

An examination by the present writer of scales as well as otoliths of eels from Ringkøbing Fjord caught during immigration into West Stadil Fjord in June 1951 supplemented by a corresponding examination in December 1951 shows so distinct a predominance for the fourth freshwater year in respect of formation of the first scales that, regardless of the numerical weakness of the material, it must be supposed to give a reliable picture of the eel population in this respect. The age and length of the fish appear from Table 3, in which the eels examined in June are included in the age-group concluded by the end of April. None of these eels showed new accretions of scales or otoliths (see p. 10). Whereas the individuals of the 0-, I-, and II-groups were all without scales, all the individuals-with the exception of a single eel (17 cm)of the III-group and the following groups had formed scales. In Table 4 the ages are stated at which the

TABLE 2.

Dutch waters. Percentage distribution of eels which have begun developing scales in the various age-groups (according to TESCH, 1928).

Hollandske vande. Procentvis fordeling af ål, der har anlagt skæl ved de forskellige alderstrin (efter TESCH, 1928).

	Localities Lokaliteter		Hollandsch Diep,
Age-gr	roup for incipient nation of scales	Zuiderzee	Haringvliet, Waal
	trin for skælanlæg	Percentage	Percentage
Group	I		0.3
	II	14.0	7.0
	III	68.3	70.0
	IV	16.5	19.9
	V	1.2	2.5
	VI	1-15-17-12-1	0.3

	1	ABLE	3	•		
West Stadil	Fjord.	Age	of	small	yellow	eels.

Alderen af små gulål.

Length in cm Længde i cm Age groups Aldersgrupper																		26							Mean length Middellængde	Number of spe Antal individer	Number of spe with scales Antal individer med skæl	Asset.
0	2	2	2	$\boldsymbol{a}_{i} \boldsymbol{a}_{i}$	• •	• •		• •	• •					• •			٠								10.0	6	0	
I			1	1	1	2									12 m										12.8	5	ŏ	
11	•			* *	÷ 2	1	2	4	4	2															16.3	13	õ	
111							• •	1	2		2	2	2.2		3.2									0.5	18.3	7	ő	
IV	• •	• •	• •	• •	Ξ.	• •						3	1		1	2	2	1		1	1	100			23.8	12	12	
V				• •						а.						100000	1000		3	5	5	3	2	4	28.9	19	19	
VI															•••	•••		•••	0	0	0	3	2	1	20.5	10	13	
									3 S	1	1.0	••	• •	1.000	• •	•••	•••			• •		0	0		30.5	0	0	

individuals belonging to the age-groups examined have formed scales, and the mean values for the difference between the number of zones in scales and otoliths (cf. Table 3 and 4).

The results mentioned, which originate from examinations of eels from streams as well as lakes and brackish water mainly situated in areas with climatic conditions similar to those in this country, compared with my examination of eels from West Stadil Fjord all point to the fourth year of life after the elver stage being the year in which the formation of scales is generally started. It must be justified to assume that this is a rule which in general also holds good of Danish conditions. It should, however, be realized that the first formation of scales does not take place, as maintained by EHRENBAUM and MARUKAWA, because the fish has reached this definite age, but because this age is usually connected with the length of 16—18 cm at which the scales begin to be formed.

(b) The Author's Investigations.

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(1) Investigations of Scales.

It is an experience already made by GEMZØE (1907) that the first scales in the eel are formed between the lateral line and the dorsal fin above the anal region, and later authors corroborate this observation, thus FROST (1945), who has made a careful examination of the age of the scales in 9 sections of the body of the eel.

The determination of age on the basis of the scales, however, besides by the uncertainty in respect of the age at which the individual formation of scales begins, is rendered difficult by the fact that the scales in the mentioned area above the anal region are by no means of the same age or at any rate do not show the same number of zones of growth. As maintained by MARcus (1919) the cause of this must be the fact that the growth of the scales in the eel more than in any other fishes is a function of the general surface growth, as

TABLE	4.

West Stadil Fjord. Age at incipient formation of scales for the inviduals belonging to the various age-groups, and corresponding mean values of the difference between zones in scales and otoliths.

Alder ved skælanlæg for de til de enkelte aldersgrupper hørende individer samt de dertil svarende middelværdier

for forskellen mellem antal af ringe i skæl og otolither.

Age groups	1	III]	[V		V		VI
Number (n) and mean length (M _l) Antal (n) og Middellængde (M _l)	n	M_1	n	$\mathbf{M}_{\mathbf{l}}$	n	M ₁	n	M_1
Scales formed in: 3. year in freshwater Skæl anlagt i: 3. år i ferskvand	3	19.0	1	29.0	1	29.0		•••
4. year in freshwater 5. — – —	3	18.0 17.0)*	10	23.6	18	28.9	3	30.3
	(1	17.0)*	1	20.0	• •	• •	3	30.7
Difference between number of otolith- and scale-zones	(2.7)		3.0		2.9		а	3.5

Forskellen mellem antallet af ringe i otolither og skæl

* Scales not yet formed in the 4th year.

the scales do not cover each other, but are situated side by side in a parquetry-like pattern. As thus the formation of scales is limited by the possibilities of extension conditioned by the surface growth, there are frequently in the scales—particularly in poorly growing eels—incomplete zone formations in the form of larger or smaller caps which generally are found at the ends of the scales, either at both ends or only at one end of the scale. More rarely they appear on the sides of the scales.

For the same reason the growth may now and then fail to appear for a year in some of the scales. The consequence is that the older the eel, the fewer scales will register the correct age, i.e. display the number of zones corresponding to the number of years of life after the formation of the first scales. The value of determinations of age made on the basis of the zones of growth of the scales therefore is conditioned by the question from where on the body the scales have been removed and on how large a number of scales the determination of age of the various individuals is based. Missing information on this point limits the value that can be attributed to a number of works on the age and growth of the freshwater eel. The determinations of age in the present work are based on the examination of generally 20 and never below 15 scales according to the number of usable scales contained in the samples. In the comparatively few cases in which it was possible to use a small number of scales only, the determinations of age have been discarded. Apart from examinations of details made at a magnification of up to about 300 times, the examinations of the scales have been made at a magnification of about 75 times. Table 5 throws light on the importance of the determination of age being based on a suitable number of scales. It shows variations in the number of zones in 20 scales from each fish in the material of 1946. I have not found HORNYOLD's (1922, etc.) general statement of the frequency of the maximum number of zones in the examined samples of scales from each individual of such a value that it should justify the inclusion of so large diagrams as would be a consequence of this procedure.

From what precedes it can be concluded that on the basis of our knowledge of the structure of the scales of the eels it must be taken for granted that at the determination of age on the basis of the scales only—regardless of the care with which the examinations are made—results will be obtained which are generally more or less at the lower limit of the actual

TABLE 5.

Esrum Lake. Variations in mumber of

scale zones illustrated by examination of 20 scales from each silver eel. (October 1946.)

Esrum Sø. Variationer i antallet af skælzoner illustreret ved undersøgelse af 20 skæl fra hver blankål. (Oktober 1946.)

Length	Weight	t	Num	ber c	of scale	e zone	es — .	Antal	skælz	oner	
cm	g	4	5	6	7	8	9	10	11	12	13
49	212			2	15	3					••
50	225			3	8	7	2			· ·	· ·
51	242			2	13	5	••	• •	• •	• •	
51	255	• •	••	5	12	2	1	• •	• •	• •	•••
52	252	• •	• •	••	16	3	1	•••			
53	232	1		4	12	3	• •	•••	• •	• •	
53	256		× *	2	7	8	3	• •			
53	274			3	12	4	1	• •	• •		••
53	282			1	9	8	2	• •		• •	••
53	285		• •	• •	4	10	4	2	• •	•••	•••
54	267		•••	8	9	3	• •	• •	• •	• •	••
54	273			••	• •	• •	12	6	2	• •	•••
54	304			1	2	4	9	4	$\mathbf{e}(\mathbf{x})$	• •	• •
55	273		3	9	6	2	••	• •		• •	• •
55	276	•••	••	• •	1	13	6	• •	••	••	• •
55	284	• •		• •		2	7	8	3	• •	
55	284			2	7	5	4	2			
55	287	• •	• •	2	6	8	4		• •	• •	• •
55	305	• •	••	3	10	4	3	••	• •	•••	• •
56	286			•••	•3.45	8	9	2	1	•	(.
56	301		• •		1	8	9	2	• •	•••	• •
57	297		••		• •	1	6	12	1	• •	• •
57	307			1	7	10	2	× ×	• •	•2.•0	1010 C
59	320	•••	•••			1	7	6	6	• •	• •
60	335		• •	• •	• •	1	•••	5	9	3	2
62	396		• •	• •	• •	4	12	3	1		•2.47
62	405	• •	•••	•••	• •	3	11	5	••	1	•6•2

numbers, but that the error is diminished the more scales underlie the individual determinations.

The question then arises whether we should not completely disregard the scales as a means of age determination and exclusively use the otoliths instead. This question cannot be answered generally. In the case of the smaller (younger) eels there can be no doubt that the best results in most cases are obtained by examination of the otoliths in preference to the scales. The determinations of age should therefore as far as possible be based on the former. In the case of larger (older) eels the otoliths, however,--regardless of grinding-mostly are of so slight value as a means of determination of age that they become more or less unusable for the purpose. This is partly due to the frequency with which false zones make their appearance (FROST (1945) "The multiple band zone type"), partly to a common blurring of the boundaries between the various annual rings, often apparently caused by a very vigorous chalk incrustation.

At the treatment of the material in hand I have in the case of the greater part been prevented from using the otoliths for the determination of age as only samples of scales were available. In order to estimate the value of the determinations made from the original material only on the basis of the scales, I have therefore also examined the otoliths in the material from 1948, 1949, and 1950, including in all 110 individuals.

(2) Investigations of Otoliths.

Because of the small size of the otoliths the grinding of these is generally stated to be a complicated and time-wasting work, which in all publications known to me is stated to have been done by rubbing the convex surface of the otoliths against a fine grinding-stone with the forefinger. This procedure, which I, too, have tried, often gives uneven ground surfaces and gives rise to frequent fractures, which only in the most favourable cases pass through the centre of the otoliths, where the greatest grinding away takes place, but which in more unfavourable cases leaves unusable fragments only. I have succeeded in eliminating these difficulties by using an improved model of an apparatus, constructed and described by JOHNSTON (1938) and intended for the grinding of small objects. By means of this apparatus I have made a considerable number of grindings of otoliths and found it both practical and guick in use.

The apparatus consists in principle of an oblong, triangular wooden plate the two hindmost and lowest corners of which rest on small metal wheels, while the foremost part of the triangle on the lower surface has a setting for the fixing of a round glass plate on which the otoliths are mounted. The apparatus thus has three points of contact, the foremost of which being constituted of the otolith(s) mounted on the glass plate. During the grinding the apparatus is moved to and fro on plane-ground lithographic slate moistened with water. In this way the grinding lasts at most a few minutes. The otolith(s) should, however, be examined now and then with a magnifying glass in order to check that not too much is ground off.

Before the otoliths are mounted on the glass plates, they are put into absolute alcohol for a few minutes in order to remove a possible content of water. For the mounting of the otoliths on the glass plates I have experimented with various adhesives and finally adopted cellulose lacquer, which besides being fastdrying, will harden much and is easily dissolved again in acetone. After grinding and later dismounting of the otoliths and washing twice in acetone, they are placed in xylol, which I have found to be most practical for clarifying as they may then be mounted direct in dammar or Canada balsam to be kept until wanted. The use of the grinder mentioned makes it possible to mount and grind both otoliths at the same time, while by the more primitive method generally only one otolith was ground. As the zones in the two otoliths may appear with unequal distinctness, it will often support the interpretation of the otoliths that both are immediately accessible for examination.

When having a suitable number of glass plates for the mounting of otoliths at one's disposal, the whole process including mounting, grinding, and the making of preparations can be carried through in 15 to 20 minutes.

With incident light, which is most suitable for the examination of the otoliths, the central field appears as a dark clear nucleus surrounded by a white ring, round which follows another narrow clear zone (cf. Plate I, fig. 4). This part of the otolith, which is found in the immigrating elvers, may be referred to the *Leptocephalus* stage and is not included in the determination of the age of the eel, which is given by the number of years of life of the fish after its immigration as an elver. After the *Leptocephalus* zones follow alternately broad, white, reflecting summer zones and narrow, dark, light-absorbing winter zones formed during the stage as a yellow eel.

At a comparison of the number of annual rings in scales and otoliths it must be considered that the zones of scales and otoliths are not formed at the same time. The summer growth of the scales is usually stated to have started at the earliest in June (GEMZØE (1907), EHRENBAUM and MARUKAWA (1913), MARCUS (1919)), but according to the last-mentioned writer it may also start as late as August. FROST (1945) for her Lake Windermere material states that the new growth of the scales starts in July. The end of the growth is referred to October—November by MARCUS (1919).

The new growth of the otoliths, however, begins considerably later than that of the scales. MARCUS (1919) thus finds the first summer zones in September —October and refers the cease of their growth to November, in which month the winter zone is gener-

TABLE 6.

Examples of the difference between the number of growth zones in scales and otoliths in different age-groups of eels. The figures in parenthesis indicate the number of individuals examined.

> Eksempler på differencen mellem antallet af tilvækstzoner i skæl og otolither hos forskellige aldersgrupper af ål. Tallene i parentes angiver antallet af undersøgte individer.

Age gro <u>Aldersgru</u> Localiti Lokalite	ies III	IV	V	VI	VII	VIII	IX	Х	XI
	Lower Elbe Nedre Elben	3.0 (2)	3.5 (20)	3.9 (77)	4.3 (50)	4.6 (12)	5.0 (3)	••	•••
MARCUS (1919)	The Rhine	••	4.0 (5)	4.1 (7)	4.6 (7)	5.1 (7)	••	1	••
	(Clare?) Ireland	1.0 (1)	3.0 (9)	3.1 (38)	3.6 (52)	4.0 (44)	4.2 (18)	4.8 (4)	5.0 (3)
NORDQVIST and ALM (1920)	Swedish eels 2.6 (2 Svenske ål	.6) 2.9 (38)	3.1 (93)	3.2 (126)	3.3 (83)	3.6 (36)	3.5 (15)	, ··	

ally considered to develop. In FROST'S material the summer zone can be observed in August and it seems to have been completed in November. In my material from Esrum Lake, which exclusively originates from the period between the middle of September and the end of November, the summer growth of the scales has always been finished. The same seems to apply to the otoliths, which all originate from eels caught in October—November. It will often, however, be difficult to establish whether the winter zone has been started, partly because there is generally a certain transparency in the outermost thin edge of the otolith, and partly because the transition between the two zones is not always sharply defined.

As mentioned above, the uncertainty of the determinations of age increases with the age of the eels. The otoliths become more difficult or impossible to interpret, and fewer and fewer scales register the correct number of zones of growth, particularly when originating from a population living under poor conditions of growth. The result is that the difference between the zones of growth of the otoliths and those of the scales show a tendency towards increasing with the age of the year-class to which the fish belongs, the more so the poorer the conditions of growth of the population. Table 6 shows examples of this borrowed from MARCUS (1919) and from NORDOVIST and ALM (1920). For reasons of space only the average difference in number of zones between scales and otoliths within the various age-groups is given.

The material mentioned, however, in respect of age only touches the lower limit of that examined by me; so a direct comparison cannot be made. FROST (1945), whose material from Lake Windermere in the case of the silver eels in many respects resembles that of mine from Esrum Lake, unfortunately has given only the previously mentioned percentage figures for the difference in the readings of scales and otoliths for the whole material of yellow eels and silver eels, so that there is not any possibility of a direct comparison here, either.

The difficulty of making a correct age determination of the older eels on the basis of the otoliths even after grinding has caused that only a small percentage of the otoliths from my Esrum Lake material could be used for a comparison with the results obtained on the basis of the examinations of the scales. A total of about two thirds of the otoliths proved unserviceable, so that the age of only 38 eels could be determined with certainty on the basis of the otoliths only. 9 of these eels were from 1948, 20 from 1949, and 9 from 1950. The difference between the readings of scales and of otoliths from these 38 eels appears from Table 7.

The tendency towards increase of the difference between the readings of scales and of otoliths with increasing age shown by MARCUS (1919) and NORD-QVIST and ALM (1920) also to a certain degree seems to apply to my material. It should, however, be noted that the difference between my readings of scales and otoliths, when the higher age of the eels is taken into consideration, is somewhat smaller than those found by the authors mentioned. However, as they have not given any detailed account of the methods used particularly at the examinations of scales, the cause of the differences ascertained escapes a closer estimate, unless, that is, these should exclusively originate from the different conditions of growth, which, however, there does not seem to be any sufficient basis for assuming. For a reasonable explanation reference

Age groups Aldersgrupper	v	VI	VII	XIII	XIV	VU	V VV
Diff. otolithzones — scalezones Diff. otolith- ÷ skælzoner	А	AI	XII	AIII	AIV	AV	X—XV
2	2	1	1		. .		4
3	6	7	4	5			22
4		3	4	1	1		9
5	••	• •	1	1		1	3
Mean difference and number of specimens	2.8 (8)	3.2 (11)	3.5 (10)	3.4 (7)	4.0 (1)	5.0 (1)	3.3 (38)

Esrum Lake. Difference between the number of growth zones of the silver eels in scales and otoliths. Esrum sø. Forskellen mellem antallet af blankålenes tilvækstzoner i skæl og otolither.

may be made to the statement on p. 9, cf. Table 5, about the number of zones of growth in the scales.

It is an obvious objection to my material that the sorted-out, unserviceable otoliths should mainly originate from the eels with the poorest growth, in which the difference between the readings of scales and otoliths is greatest, according to the authors mentioned above and that the material on the whole is too small for a correct evaluation of this question, which is extremely important for an estimate of the value of the age determinations made on the basis of the scales. This objection cannot simply be dismissed. On the other hand I have hitherto, after examining several hundreds of samples of scales and otoliths of eels from various Danish bodies of water, been unable to find any connexion between the rate of growth and the greater or smaller distinctness with which the annual rings in the otoliths appear. So I think it justifiable to maintain that the more or less distinct formation of annual rings in the otoliths can be referred to causes which on the whole are without connexion with the rate of growth of the fish.

The numerical poverty of the material does not allow any safe conclusions from the mean values for the number of zones in scales and otoliths calculated for the various age-groups. As, however, the material by its distribution according to length as well as by the mean value of this (55.1 cm) and the average age calculated on the basis of the examinations of scales (11.3 years) gives a reliable section of the whole material (cf. p. 22 and Tables 13 and 14), the mean value calculated for all age-groups (3.3) for the difference between the number of zones in scales and otoliths must also be supposed to be approximately valid for the whole material examined.

As maintained by previous authors the age determinations of eels should as far as possible be based on examinations of both scales and otoliths, although the value of the latter, as appears from the above, decreases considerably with increasing age and therefore mainly, in the case of older eels, must serve to support the determinations made on the basis of the scales. From the age of about 8 years and upwards the scales will often be the only serviceable object for determination of the age of a given material, unless one draws the consequence of the inapplicability of the otoliths increasing with age and exclusively bases the determinations of age on the minority of otoliths which allow of a sure reading of the age. The question, however, is whether so drastic a reduction of the material as would ensue, would offer greater advantages than the obvious defects that would be connected with it. On the basis of the examinations made by me I take it for granted that the analyses of scales, if made with requisite care, also in the case of the older age-groups, offer so valuable a means of determination of age that it must be considered unnecessary exclusively to make it on the basis of the relatively small number of serviceable otoliths. It is, however, inevitable that the various determinations of age involve greater or smaller errors, which in the case of the present material seem to fall within a maximum range of ± 2 years. In this connexion the ascertainment of the exact age of the individual silver eels is of less interest than the ascertainment of the average age at their seaward migration, which is obtained by adding the result of the readings of the scales to the ascertained average difference between the readings of scales and otoliths in the material examined on the basis of both. As mentioned above, this difference in the case of the Esrum Lake material amounts to 3.3 years. I have, however, instead of 3.3 years everywhere added 3 years to the readings of scales, partly because it is impractical to work with fractions, partly because in this way my results are more easily compared with the results obtained by

TABLE 7.

previous authors on the basis of examinations of scales. It cannot, however, be explained away that the use of such an average factor in the case of the youngest year-classes will involve that the age may be given somewhat too high and in the case of the older age-groups too low. In order to introduce a correction for the individual age-groups it would, however, be necessary to be in possession of a much greater material of otoliths than the one at my disposal. So my determinations of age must be considered with the consequent proviso.

Out of consideration to the comparability of the older material with the material from 1948—50 I have based all the determinations of age in what follows on the scales only, using the examinations of otoliths exclusively for control.

3. Results of Annual Examinations of the Length, Weight, and Age of Silver Eels in Esrum Lake.

Control samples of silver eels have been taken annually for the purpose of ascertaining whether the eel population of the lake is constantly in a reasonable relation to its productivity. It would seem possible to answer this question by annual examinations of the length, weight, and age of the silver eels, provided that the control samples are sufficiently large and cover a sufficiently long series of years, the latter factor depending on the question how long the eels normally stay in the lake before becoming silvery and migrating seawards.

The question how large the various samples ought to be in order that they may be considered representative, must depend partly on the normal distribution of the silver eels according to length and partly on the magnitude of the generally occurring individual differences of growth in the eel population. As appears from fig. 2, the majority of the silver eels are distributed within a range of about 20 cm, which, of course, causes the representation of the various length groups in the control samples to be slight, as they generally consist of about 30 eels only. Thus fortuity at the sampling of the silver eels may come to be expressive of the occurrence of a shifting in their average distribution according to length and weight which in reality does not exist. In this connexion it is just as unfortunate that the eel within the same biotope exhibits very considerable individual differences in growth. Thus it is not unusual within 3 cm groups in the various control samples to find age variations of the order of magnitude of 4-6 years. It is certain that individual difference in age of this magnitude can strongly influence the mean values calculated for the various control samples, the extremes of which (cf. Table 8) are respectively 10.8 and 12.3 years. In order to reduce these sources of error to some degree I have furthermore made calculations of the mean values for length, weight, and age for 3 (2) year periods (Table 9). If we first consider the mean lengths given in the

TABLE 8.

Esrum Lake. Mean values for length, weight and age of silver eels from the annual control samples. Esrum sø. Middelværdier for længde, vægt og alder af blankål fra de årlige kontrolprøver.

Year År	Meạn length Middellængde cm	Mean weight Middelvægt g	Mean age Gennemsnitsalder Years År	Standard deviation of age Standardafvigelse på alderen	Mean error of age Middelfejl på alderen	Number of specimens Antal individer
1937		352.6	11.6	+ 1.15	\pm 0.21	30
1938		348.6	11.6	\pm 1.10	\pm 0.21	27
1939		343.3	11.4	\pm 1.52	\pm 0.29	28
1940		374.2	11.4	\pm 1.32	\pm 0.23	32
1941		389.1	11.5	\pm 1.34	\pm 0.24	30
1942		338.3	11.3	± 1.58	\pm 0.29	29
1943		306.4	11,0	\pm 1.18	\pm 0.23	26
1944		312.8	11.0	\pm 1.61	\pm 0.32	25
1945		353.5	11.2	\pm 1.40	± 0.25	31
1946		285.8	11.7	\pm 1.35	\pm 0.25	29
1947		327.1	12.3	\pm 1.35	\pm 0.25	29
1948		302.7	11.6	\pm 1.16	\pm 0.22	27
1949		303.1	11.6	\pm 1.27	\pm 0.17	54
1950		306.2	10.8	+ 1.18	\pm 0.22	29

TABLE 9.														
Esrum Lake.	Mean	values	for	length,	weight,	and	age	of	silver	eels	and	length/weight	coefficient	for
				tri-(bi-)ennia	l cal	culat	tion	n perio	ds.	140	0 1 0		

Esrum sø. Middelværdier for blankålenes længde, vægt og alder samt længde/vægt koefficienten for 3-(2-)årige beregningsperioder.

Year År	Mean length Middellængde cm	Standard deviation of length Standardafvigelse på længden	Mean error of length Middelfejl på længden	Mean weight Middelvægt g	Mean age Gennnemsnitsalder -Years – år	Standard deviation of age Standardafvjgelse på alderen	Mean error of age Middelfejl på alderen	Length/weight coefficient Længde/vægt koefficient	Number of specimens Antal individer
$\begin{array}{c} 1937 39 \dots \\ 1940 - 42 \dots \\ 1943 - 45 \dots \\ 1946 - 48 \dots \\ 1949 - 50 \dots \end{array}$	57.8 58.7 56.5 55.3 55.7	$\pm 2.45 \\ \pm 3.67 \\ \pm 4.40 \\ \pm 3.33 \\ \pm 4.02$	$egin{array}{c} \pm \ 0.25 \\ \pm \ 0.38 \\ \pm \ 0.49 \\ \pm \ 0.36 \\ \pm \ 0.44 \end{array}$	$348.2 \\ 369.1 \\ 326.1 \\ 317.0 \\ 304.2$	$ 11.5 \\ 11.4 \\ 11.1 \\ 11.8 \\ 11.4 $	$egin{array}{c} \pm 1.27 \\ \pm 1.42 \\ \pm 1.98 \\ \pm 1.32 \\ \pm 1.29 \end{array}$	$egin{array}{c} \pm 0.14 \\ \pm 0.15 \\ \pm 0.22 \\ \pm 0.14 \\ \pm 0.14 \end{array}$	180 183 181 187 176	85 91 82 85 83

latter table, it will be seen that these show a tendency towards a decrease during the period of the investigations. Regardless of the fact that this decrease of the mean lengths seems statistically significant, it is not possible (cf. the remarks above) exclusively from the numerical material underlying the calculation of





Esrum sø. Blankålenes længdefordeling i det samlede undersøgelsesmateriale (1937—50) og ved en i 1948 foretaget måling af nogle af de i hyttefade i søen opbevarede blankål.



these mean values, to decide with certainty whether the population of silver eels as a whole has been subjected to such changes as regards the distribution according to length. In this connexion it would be very desirable if simultaneous more comprehensive measurements to illustrate the distribution of the silver



appears partly from the curves and partly from the average lengths calculated, which for the 647 eels from 1948 was 55.9 cm and for the whole material examined 56.9 cm, that there is no good agreement between the two curves. If, furthermore, we disregard the large eels (> 68 cm), which are represented in

Fig. 4. Esrum Lake. Mean length and average age of the silver eels \pm 3 times the mean error for 3-(2-)year calculation periods. The mean values plotted in relation to the mean values for length and age (56.9 cm and 11.4 years) calculated for the total material. (The intervals on the ordinates are chosen accidentally and have no mutual relation apart from the two mean values mentioned.)

Esrum sø. Blankålenes middellængde og gennemsnitsalder \pm 3 gange middelfejlen for 3-(2-)årige beregningsperioder. Middelværdierne indlagt i forhold til de for det samlede materiale beregnede middelværdier for længde og alder (56,9 cm og 11,4 år). (Intervallerne på ordinaterne er tilfældigt valgt og har ingen indbyrdes relation bortset fra de nævnte to middelværdier.)

eels according to length in the annual catches had been available. For want of a more exact expression of the presence of possible changes of this kind in the population of silver eels, it may be tried to approach to an answering of the question by a different road.

647 of the silver eels kept in well boxes in the lake were measured in the autumn of 1948 in order to give an impression of the general distribution according to length in the catches of silver eels. The result of these measurements is rendered graphically in fig. 2 together with the corresponding curve for the total of 426 eels which constitute the whole material examined. It larger numbers among the 647 eels from 1948 than in the material under investigation (on the reason for this see p. 5), the mean values become 54.6 and 56.7 cm, respectively. Furthermore it will be seen that there is rather a good agreement between the mean value found at the more comprehensive measurements in 1948 and the corresponding value from the control material of the same year, the latter, which exclusively consisted of eels below a total length of 68 cm, having a mean length of 55.0 cm. The disagreement between the two curves, considering the rather considerable extent of the whole material under

TABLE 10.

Esrum Lake. Average age of 3-cm length-groups for tri(bi-)ennial calculation periods 1937-50. Number of fish examined indicated in parenthesis.

Esrum sø. 3-cm længdegruppernes gennemsnitsalder for 3-(2-)årige beregningsperioder 1937-50.

Antallet af undersøgte fisk i parentes.

I. B	ength-groups 3 cn -cm længdegrupper Years – år	1 46	49	52	55	58	61	64	67	70	73	76	79
4	937—39		11.0(1)	11.3(6)	10.8(29)	11.7(24)	12.4(14)	12.2(9)	11.5(2)	•• _	• •	· · · · .	
	$340 - 42 \dots$			9.6(7)	11.3(19)	11.4(24)	12.0(30)	12.0(6)	11.0(4)	11.0(1)	• •		• •
1)43-45	9.00(1)	9.7(3)	10.3(13)	11.1(29)	11.3(22)	11.6(8)	12.7(3)	10.0(1)	10.0(1)			16.0(1)
1)46-48		11.3(3)	11.1(21)	11.8(37)	11.9(16)	13.0(7)	• •			12.0(1)		
	$940 - 40 \dots 949 - 50 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 $		10.0(3)	10.7(18)	11.3(32)	11.7(19)	12.4(8)	11.5(2)	• •		••	•••	16.0(1)

investigation, can hardly be explained except on the assumption that within the period of the investigations, there has been an actual reduction of the size of the silver eels in the lake.

An important clue to the estimate of this question is the practical experiences of the fishermen during the years. The present lessee of the fishery has stated that the usual size of silver eels, when in 1932 he came to the lake as assistant to the lessee of that time, weighed about 15-16 Danish pounds¹ a score, while the weight today is only 12-13 pounds a score. During the period from 1932 to 1939 when the present lessee took over the fishery, the fishing for yellow eels (cf. Table 11 and fig. 3) was practised extremely intensively, reaching a level which presumably to a considerable degree exceeded the normal productivity of the lake. Indeed the result was that the steep increase in yield was followed by an equally steep fall. When in 1939 the lease passed into other hands, it was therefore urgent that the population of yellow eels should be spared while at the same time regular transplantations of small fry were made. Today the lake as a consequence of these measures has a very considerable population of yellow eels of all sizes, and it will be natural to explain the actual reduction of the size of the silver eels from the lenient form in which the fishing for yellow eels has been practised during a number of years and the considerable addition to the eel population through the regular transplantations of small fry. In a later section there will be an opportunity to discuss this question in more detail. In this place it will be sufficient to state that—as indicated by the mean values calculated—an actual reduction of the size of the silver eels in the lake has taken place within the period of investigation.

As appears from Table 9 (cf. fig. 4), the reduction

¹ 1 Danish pound = $\frac{1}{2}$ kg.

of the mean length of the control samples has not been accompanied by a corresponding reduction of the average age as the smaller silver eels, constituting the material from 1946—48 and 1949—50, are not younger than the larger silver eels constituting the material from 1937—39 and 1940—42.

As a matter of fact, this is only what might be expected, as the reduction of the length of the silver eels must be interpreted as a function of deteriorating conditions of nutrition to the population as a whole and a consequent decrease in the rate of growth. The latter is not, as might be supposed, reflected in an increase in the average age of the eels within the various length groups (cf. Table 10), but exclusively in the condition characteristic of the silver eels that the length groups within rather wide limits show insignificant variations in age only (cf. further Table 13). An increase in the relative share of the smaller and more slowly growing eels in the population of silver eels therefore alone seems to condition the differences characterizing the relation between the length and age of the silver eels within the calculation periods. In other words, what has happened is this: a larger number of the eels than was the case at the beginning of the period under investigation, have been stunted in their growth.

Besides by changes in the length and age of the silver eels, changes in the conditions of nutrition might be supposed to appear in positive or negative shiftings of the length- weight coefficient (here calculated from $k = \frac{10^5 \times w}{l^3}$), unless the size of this factor is expressive of a condition necessary for the commencement of the silveriness (see p. 24). The variations to which k (cf. Table 9) is subjected, however, are rather insignificant and of an accidental character. They do not give any information of value for the elucidation of the question.

2

TABLE 11. ake Benorted catch in kg 1901_

Esrum Lake. Reported catch in kg 1901—1950. Esrum Sg. Fiskeriudbytte i kg 1901—1950.

		Eel - Ål	2						
Year År	The eel trap	The lake		Pike	Perch	Bream	Roach	Tench	Bleak
	The eel trap Ålekisten	Søen	Total	Gedde	Aborre	Brasen	Skalle	Suder	Løje
1901	4.025	750	4.775	250	50	500		• • •	
1902	• •	750		500	50			• •	
<u>1</u> 903	6.125	750	6.875	625	250	700			
1904	3.625	300	3.925	210	150	500			
<u>1905</u>	5.935	400	6.335	450	200 -	600			
1906	3.500	11 III		50					
$1907\ldots$	3.025			50					
1908	3.250	7.650	10.900	279	3.647	99	7.220	* *	••
1909	2.725	5.545	8.270	600	5.450	6.525	37.600	• •	••
1910	3.775	6.195	9.970	535	7.843	26.370	42.844		••
1911	3.025	6.272	9.297	588	3.610	14.000	8.500	•••	• •
1912	4.400	4.250	8.650	625	3.060	577	16.026		• •
1913	4.100	4.487	8.587	1.536	4.486	485	5.488	• •	2.220
1914	5.270			20				• : • :	2.220
1915	5.587			43		• •	• •	n (1939-8	1 500
1916	8.370			50	250	50	 100	• •	1.500
1917	7.529	561	8.090	272	135	55		•3.¥/	1023 1
1918	7.940						160	•20.47	• •
1919	8.934	7 X.*X.*C		1.679	1 202		5 004	• •	
1920	8.884	• •		1.079	1.323	3.234	5.231	•••	••
1921	5.639	• •	• •	• •	• •	54.64	0.000		
4022	6.554					•••			
$\begin{array}{c} 1922 \ldots \ldots \ldots \\ 1923 \ldots \ldots \ldots \end{array}$		334	6.888	1.186	167	100	3.864	14	••
	5.906							in (n	••
1924	6.570	1.120	7.690	657	• •	4.860	19.352		
1925	5.188			•••	••	••	• •		
192 <mark>6</mark>	6.916	1.600	8.516	682	260	4.610	7.210	· ·	
$1927\ldots$	5.888	4.500	10.388	146	50	••	• •	• •	• •
1928	4.880	3.615	8.495	684	45	12.225	18.310	35	
1929	4.494	1.836	6.330	925	600	12.525	12.670		
1930	7.200	2.180	9.380	980	1.025		4.130	78	
1931	3.450	5.800	9.250	740	359	4.840	· . · ·	215	
1932	4.633	15.000	19.633	1.350	1.280		7.000	125	
1933	2.489	16.000	18.489	1.850	2.600		2.500	200	
1934	6.202	14.000	20.202	2.700	5.000	600	6.000	250	• •
1935	9.358	20.700	30.058	2.800	9.200	60	2.400	50	
1936	6.189	14.200	20.389	3.100	5.000	170	280	150	
1937	4.600	11.900	16.500	1.820	4.070	109	4.830	351	
1938	4.072	11.900	15.972	1.670	5.850	170	5.700	400	
1939	4.051	9.673	13.724	1.293	3.538	10	6.456	192	••
1940	2.129	10.473	12.602	1.234	1.448	139	2.215	223	• •
1941	2.471	7.625	10.096	2.115	1.286	619	10.912	175	••
1942	2.631	7.228	9.859	1.338	485	441	3.935	241	••
1943	5.461	8.024	13.485	1.663	3.141	75	8.532	332	•::•:
1944	1.853	8.779	10.632	2.116	466	291	23.898		• •
1945	2.340	6.566	8.906	877	179			246	
1946	1.559	6.625	8.184	431		· ·	1.240		38.2°
1947		5.874			417		3.665	10	• •
1948	•••		**	1.163	1.843	377	15.930	101	
1948	3.275	6.036	44 474	678	539	303	3.320	365	···
1949		7.866	11.141	1.404	404	147	2.549	216	••
1950	3.400	7.302	10.702	1.615	3.635	53	3.038	99	••
Average catch — M	fiddeludbytte	1926—46:							Total
kg a year:	4.422	8.963	13.385	1.453	2.205	1.756	6.280	156	25.235
kg pr. år	0.50								
kg per ha:	2.56	5.18	7.74	0.84	1.27	1.02	3.63	0.09	14.59

4. Remarks on the Fishery and Population of Fishes in Esrum Lake.

Esrum Lake has always been considered a good lake for eels, both as regards the yield and the quality of the fish. The average annual yield of eels during the period 1926—46 (cf. Table 11) for which continuous and complete statements of the catches from the lake as well as the eel-trap at Esrum Mill are available, amounted to a total of 13.385 kg, i.e. 7.74 kg per ha out of a total annual yield by the fishery as a whole during the same period of 25.235 kg (14.59 kg per ha). As regards weight, the fishing for eels thus yielded 53 per cent. of the whole catch.

Both absolutely and in relation to the total yield per ha a yield of this magnitude is high according to Danish conditions, and as far as can be checked, no fishing for eels in any other large Danish lake can display a correspondingly high yield per ha.

In order, in the present case, to provide a reasonable balance between the productivity of the lake and the size of the population of eels, a regulation of the population must be made through an adaptation of the extent of the planting of fry hand in hand with an intensification or reduction of the fishing for yellow eels adapted to circumstances, and—not least through a fight against the eel's competitors for food, particularly bream and ruff.

The eel population is kept up partly through the natural immigration of eel fry (mainly elvers) from the Kattegat through the about 9 km long Esrum canal and partly through transplantations of elvers as well as small yellow eels. We have only exceptionally any knowledge of the size of the natural immigration as it is generally uncheckable. At Esrum Mill there is, however, a particular device in which the small fry of the eels is caught and the amount (weight) is checked, after which it is put into the lake. In this contrivance 250 kg was caught in 1950, which is maintained to correspond to an immigration above medium size, and in 1951 an amount of 125 kg elvers, which amounts represent about one million and half a million specimens, respectively. These figures, of course, only indicate an order of magnitude, and their value is further diminished by the fact that part—perhaps half-of the immigrating small fry is capable of passing the dam unaided. On the basis of the available information it can therefore only be estimated that the magnitude of the natural immigration presumably is between 1 and 2 million elvers a years.

Through the years the natural immigration of small fry has been supplemented with rather considerable transplantations of elvers as well as small yellow eels

TABLE 12.

Esrum Lake. Planting of elvers and small yellow eels. Esrum Sø. Udsætninger af glasål og sætteål.

	Elvers — Glasål	Small yellow	eels — Sætteå
	Number of specimens Antal stkr.	kg	Number of specimens Antal stkr.
1909		3.250	
1910			• •
1911			30.000
1912			• •
1913			
1914	700.000		
1915			• •
1916	1.500.000		
1917	1.500.000		• •
1918			• •
1919			•••
1920			
1921			
1922	30.000		
1923			
1924			
1925	30.000		
1926			
1927	160.000		
1928		• (•)	150.000
1929			
1930			
1931			
1932			
1933		450	
1934			50.000
1935			50.000
1936	725.000	344	• •
1937	375.000	644	2479
1938		235	5. C. C.
1939		484	
1940		292	
1941	160.000	189	
1942		200	
1943	145.000		
1944	85.000	1.823	
1945	145.000	2.198	
1946	260.000	390	
1947		558	••
1948	205.000	734	
1949	275.000		
1950		120	

(cf. Table 12). Since 1932 such transplantations have been made every year, but with varying amounts. Unfortunately it is not possible to obtain a fairly exact expression of the importance of these trans-

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plantations in relation to the natural immigration, in the first place because the exact magnitude of the latter is unknown, in the second place because the transplanted material is very heterogeneous.

The small yellow eels may vary considerably in size from year to year, but as a rule they fall within the order of magnitude of 150—300 specimens per kg. There is no doubt that the small yellow eels are considerably more valuable as planting material than the elvers, partly because of the greater percentage of their survival, and partly because they will reach the silver stage earlier than the elvers. Therefore it must be considered predominantly probable that plantings of the order of magnitude in question yield a very considerable addition to the natural immigration and thus may influence the size and conditions of growth of the population considerably.

Besides by the size of the annual amount of fry these factors may also be highly influenced by the amount of competitors for food of the eel. Particularly the bream and the ruff distinguish themselves in this respect, as they are both predominantly attached to the profundal zone and like the eel search for food among the larvae of chironomids on the bottom. Whereas the ruff to a certain extent serves as food for the eel and therefore often by the fishermen groundlessly is considered a useful fish in eel waters, the bream because of its size and form on the whole is not exposed to the persecutions of the eels. As furthermore it can only fetch a fraction of the price with which the eel is paid, it should always in eel waters be fought with every available means.

It does not seem to be connected with particularly great difficulties to keep the population of bream in Esrum Lake at a reasonable size. It appears from Table 11 that only during two short periods within the 50 years covered by the statistics, catches of bream of any appreciable importance have been made, and it seems that the population only slowly makes up for the losses caused by occasional intense fishing. Amongst other things this must be due to the fact that the bream does not breed until it has reached rather a considerable age and size, so that intense fishing may greatly reduce the production of small fry for a number of years. At any rate it must be considered a fact that today there is no great population of bream in the lake as, if so, the catch of bream in the eel-traps would not be so poor as it actually is. Perhaps it will be sufficient, in order to keep the population down, that no bream caught should be put out

again regardless of its size, as has been common practice during a number of years.

It has already been pointed out that the very abrupt rise of the curve of the catches of eels which started in 1931 and ended in 1935 (cf. fig. 3) is chiefly due to very intensive fishing for yellow eels; but this explanation hardly gives the whole truth. An intensified fishing for yellow eels, if other conditions do not exert any influence, to all appearance should result in a reduction in the yield of the fishing for silver eels. Whether this was the case, in so far as the fishing in the lake is concerned, can only be estimated indirectly from the catches of silver eels in the eel-trap at Esrum Mill, as the size of the catches of silvers and yellow eels has not been given separately for the lake. As might be expected, the increased fishing in the lake caused an immediate decrease in the catching of silver eels in the eel-trap, but the fall was unexpectedly interrupted by an intense increase in the catches in the years 1934 and 1935, after which the yield decreased again in time with the decrease of the catches in the lake. If the year 1935 is specially considered, when the total catch in the lake and the eel-trap amounted to about 30.000 kg, it must be considered predominantly probable that the great yield of the fishing for silver eels in the eel-trap was accompanied by a correspondingly great yield of silver eels in the lake, or in other words, that the amount of silver eels in the lake was increasing considerably at the same time as the fishing for yellow eels was practised very intensively. Conditions can hardly be explained in any way but by the presence of one or perhaps more dominant year-classes becoming silvery within a short term of years. This or these might originate from a sudden increase in the amount of fry, either due to an abnormally large natural increase, to one or more particularly comprehensive plantings, to a sudden improvement of conditions of nutrition, or to all these factors together. In this connexion there is special reason to note that in 1928 there was a rather isolated very great planting comprising about 150.000 about 25 cm long yellow eels (from the Elbe). According to EHRENBAUM and MARUKAWA (1912) eels from the Elbe of this size belong to the IV-group, and as the majority of the eels in the lake become silvery at the age of 10-13 years after the elver stage, it is not improbable that this planting has a considerable share in the increase of the seaward migration recorded in the middle of the thirties.

Both in the year when this planting took place and

in the following year a great inroad was made on the bream population, a total of about 25.000 kg bream being fished in the lake during the years 1928—29 (cf. Table 11). Therefore improved conditions of nutrition were created in part simultaneously with the considerable planting of yellow eels, conditions which must be of appreciable importance for the obtaining of an effective improvement of the population of eels through planting of small eels.

Besides bream and ruff particularly the perch must be considered a not inconsiderable inconvenience to a rational fishing for eels, especially because it severely pursues the elvers, thus influencing the amount of fry, and also because it will appear as a competitor for food to the eel, although to a less degree than ruff and bream. Perch are very numerous in the lake, and the population would profitably stand a considerably more intensive fishing than it is normally exposed to. With the prices generally obtained, particularly of small perches, a special perch fishing, however, is unprofitable. Consequently the yield mainly appears only as a byproduct of other fishing. During the last few years, however, a special perch fishing with otter trawl has been practised out of the eel season as a consequence of paying conditions in the export market, and the yield has shown a not inconsiderable increase.

As mentioned above, the decrease in size of the silver eels shown in these investigations and through the experiences of the practical fishery, should no doubt be interpreted as being connected with the very comprehensive transplantations of eels to the lake. It is a well-known fact that the silver eels at a sudden reduction of the population of eels-e.g. during particularly hard winters-during the following years are considerably larger than normally to the water in question. It does not seem possible to find any reasonable explanation of this observation but that the decimation of the population of eels has given better conditions of nutrition to the remaining eels resulting not only in an increase of the rate of growth, but also in an increased size of the eels at the end of the stage of growth. Correspondingly a decrease of the size of the silver eels should no doubt be interpreted as expressing a deterioration of conditions of nutrition. In the present case the reason seems rather a consequence of the considerable transplantations and the lenient fishing for yellow eels than a consequence of the competition for food from the other species of fish.

From an unpremeditated point of view it might seem most profitable exclusively to practise the fishing for eels in the form of fishing for silver eels, partly because the eel is most easily fished during the seaward migration and partly because the fish at this stage is full-grown and its quality best. Apart from the fact that a suitable regulation of the population of eels may make it necessary to fish for yellow eels, it is an economic question whether and to what extent fishing for yellow eels ought to be carried on. In the first place the eels will fetch a materially higher price during the fishing for yellow eels in the spring and in the early summer when there are few or no silver eels, and in the second place it must in the present case be in the interest of the government as well as the lessee that so great a part of the annual yield of the population of eels as possible falls to the share of the fishery in the lake, as long as the eeltrap at Esrum Mill is privately owned. For these reasons fishing in the lake for yellow eels to a suitable extent can hardly be dispensed with.

According to the results of the present investigations it seems advisable to intensify the fishing for yellow eels, also from the point of view that only the results of an intensified fishing will be able to show whether the form under which the fishing is now practised, secures an optimal utilization of the population of eels. At present nearly equal numbers of yellow and silver eels are fished, the greatest importance, however, being attached to the fishing for silver eels.

An intensification of the fishing for yellow eels ought of course to take place under continued due supervision, which also ought to include regularly recurrent measurements of the catches of silver eels for the purpose of ascertaining how the fishing for yellow eels influences the distribution of the silver eels with respect to size.

Usually the natural immigration of elvers does not take place until the month of June, and the maximum seaward migration of silver eels occurs from the middle of August to the middle of September, while the migration in October as well as November is slight.

In general the seaward migration in the spring is slight, but variable according to conditions of the weather. If there is early frost of a prolonged duration in the autumn, the migration of the silver eels is reduced or stops, and the spring migration in May becomes greater than normal.

The great transplantations of small yellow eels

which mainly originate from localities in which the male eels are in a majority (e.g. Ringkøbing Fjord and Roskilde Fjord) might be expected to have increased the percentage of males in the lake. This is, indeed, the case, although it is far from being so to the extent suggested by the size of the transplantations. The question has not been made the object of any particularly exact investigation, but the fishermen maintain that before the beginning of the regular plantings of small yellow eels there were practically no male silver eels in the lake. The share of the male eels in the catches of silver eels is now estimated to be about 2 per cent., the majority of which are caught in the eel-trap at Esrum Mill. In this connexion it is of interest to note that the results of the investigations made hitherto of the question of the sexual differentiation of the eel seem to corroborate that this may be influenced by external factors to a considerable extent (RASMUSSEN 1951).

5. Length, Weight, and Age of the Silver Eels in Esrum Lake and Other Bodies of Water.

Whereas for use at the annual investigations one might have wished for a considerably greater material, the aggregate material in its capacity as an average material collected during a prolonged term of years constitutes an applicable basis for an estimate of the question what properties in respect of length, weight, and age generally characterize the silver eels in Esrum Lake, and the question of the relation of the population in these respects to the results obtained by corresponding investigations from other bodies of water. These questions will be discussed in what follows. In Table 13 the whole material is divided into 3-cm groups, for which are indicated the mean age, its standard deviation and mean error, the magnitude of individual variations in age (range), and number and mean weight.

The length of the eels varied between 47 and 80 cm and their weight was within the interval 198 and 900 g with a mean value of 330.8 g. The earliest beginning of the silver stage was after a stay in freshwater for 8 years. The oldest silver eels have spent 16 years in the lake. The mean age at the seaward migration calculated for the total material is 11.4 years.

Table 14 shows the mean lengths calculated for the various age-groups, the range, the standard deviation and mean error of the average lengths, and the corresponding mean weights.

The mean age of 11.4 years at the seaward migration just mentioned is obtained by the eels at a mean length of 56.9 cm. It is conspicuous that the majority of the eels (88 per cent.) belong to the age-groups X—XIII, while relatively few individuals have become silvery after more or fewer years' stay in the lake. The wide range expressed by the difference in length between the largest and the smallest fish belonging to the same age-group (see also fig. 5) is characteristic of the eel, as mentioned above, and, as also noted by FROST (1945) in the case of her Lake Windermere material, deprives the mean values calculated of their practical applicability.

It seems natural, at any rate in part, to connect the magnitude of the range with a difference in life form between the biological types denoted as sharpnosed and broad-nosed eels.

While the smaller silver eels mainly consist of sharp-nosed eels, the food of which chiefly is the

TABLE 13.

Esrum Lake	. Age for le	ength relationship	of 3 cm groups	of silver	eels 1937—50.
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		LISTUIN	50. 0-0m	languegi	uppernes ;	gennemsn	itsaluer og	g, -vægt i	193/-30.				
Length groups 3 cm 3-cm længdegrupper	46	49	52	.55	58.	61	64	67	70	73	76	79	All fish amtlige fisk
Mean age in years. Gennemsnitsalder i år	9.0	10.4	10.7	11.3	11.6	12.2	12.2	11.0	10.5	12.0	•••	16.0	11.4
Range in years Spredning i år	•••	9—13	8—14	8—16	9—15	10—16	10—14	9—14	10—11		••		8—16
Standard deviation Standardafvigelse	••	± 1.02	± 1.17	± 1.20	± 1.34	± 1.21	± 0.91	± 1.69	• •	••	••	••	± 1.36
Mean error Middelfejl	• •	± 0.32	± 0.15	$0.10\pm$	± 0.13	± 0.15	± 0.29	± 0.64	••	••	• •	•••	± 0.07
Mean weight 2 Middelvægt		232.4	268.2	302.7	334.2	389.0	435.2	506.9	571.5	512.0	••	846.5	330.8
Number of specimens Antal individer	s 1	10	65	146	105	67	20	7	2	1	••	2	426



Fig. 5. Esrum Lake. Length and age of individual silver eels. Esrum sø. Blankålenes individuelle længde- og aldersfordeling.

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TABLE	14.

Esrum Lake. Length for age relationship of silver eels 1937-50.

Esrum sø. Aldersgruppernes middellængde og -vægt 1937-50.

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Age groups Aldersgrupper	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	All fish
Mean length in cm Middellængde i cm	53.3	55.6	54.9	56.4	57.7	58.2	58.6	59.3	69.0	Samtlige fisk 56.9
Range in cm		47—66	49—71	50—70	51—72	50—64	53—64	57—61	56—80	47—80
Standard deviation Standardafvigelse	-	\pm 4.11	\pm 3.69	\pm 3.16	\pm 3.88	\pm 3.11	\pm 3.53	\pm 1.48	± 10.24	\pm 4.00
Mean error Middelfejl		± 0.84	\pm 0.43	\pm 0.28	\pm 0.39	\pm 0.39	\pm 0.88	\pm 0.74	\pm 5.12	\pm 0.19
Mean weight in g Middelvægt i g	296.0	316.4	297.1	324.6	340.8	346.1	371.6	344.8	611.0	330.8
Number of specimens Antal individer	3	24	75	134	101	65	16	4	4	426

chironomid larvae of the profundal zone, the large eels are exclusively broad-nosed eels, which in contrast to the sharp-nosed ones to a greater extent are connected with the shallower parts in and near the litoral zone, and the food of which is chiefly small fish. These two biological types are not sharply defined, but are connected by more or less even transitions (PETERSEN 1894, EHRENBAUM 1929, and SIVERTSEN 1938). In FROST's (1945) material the large silver eels (broad-nosed), which are more numerously represented in her material than in mine, seem to show a growth deviating from that of the smaller silver eels (sharpnosed), characterized by a faster growth in the former than in the latter. It may no doubt be considered probable that corresponding, although smaller differences in growth characterize the intermediate forms. Because of the changes of the form of the head accompanying the beginning of silveriness, such a distinction between the two types, however, is not practicable in the case of the silver eels except in the case of the most characteristic extremes of the two types.

FROST (1945) from corresponding observations of the wide range of length of the silver eels within the various age groups and the slight average growth resulting from a prolonged stay in freshwater, has drawn the—as it seems—probable conclusion that the beginning of silveriness is not only a function of the age and length reached by the eel, but also must be supposed to be conditioned by a physiological condition dependent on the length-weight relationship. She bases this theory i.a. on the results obtained by BELLINI (1907, 1910) from Italian eels reared in experimental ponds. On an average they became silvery after $4\frac{1}{2}$ years when at a length of 55.1—66.3 cm, which is in good agreement with the range of length within the greater part of FROST's as well as my material.

As regards determinations of age there has been a great lack of data for comparison, not only from other Danish inland waters, but a lack also of such investigations of silver eels altogether. Thus GEMZØE's paper mentioned above has only to a very slight extent inspired Danish fishery biologists to inquire into the age and growth of the eel. The available investigations of Danish eel populations, particularly of silver eels, are partly extremely sporadic and partly without exception based on so few data that they cannot be considered population analyses proper. It is more unfortunate that these determinations of age, which have all been made exclusively on the basis of examinations of scales, have been published without statement of methods or the size of the material of scales on which the determinations of age were based in each case (cf. p. 9). At any rate the result seems to have been that in most cases, particularly in the case of older eels, the age has been estimated too low. In the section on the eel fishery in *Fiskeriet i Danmark* (1948) it is stated (vol. II p. 546) that a few female eels in Denmark become silvery already 5 years after the elver stage, and that female eels are rarely found which have stayed here for more than 10 years. These statements are not corroborated by the results of the age determinations made on silver eels from Esrum Lake. As mentioned above, the average age for the whole material from there has been calculated at 11.4 years. In this mean value, as in all other statements of age adduced here, no consideration has been given to the last, not yet concluded freshwater year, which in reality denotes a completely finished period of growth, since all silver eels examined originate from the months of September-November. A total of no

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TABLE 15.

Length for age relationship of female silver eels from various waters.

Aldersgruppernes middellængde hos hunlige blankål fra forskellige vande.

Age group Locality	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX
Esrum Lake 1937–50 ¹	• •		53.3	55.6	54.9	56.4	57.7	58.2	58.6	59.3	69.0				• •
		Ċ	(3)	(24)	(75)	(134)	(101)	(65)	(16)	(4)	(4)	* *		•	• •
Gullmarfjord 1912 ²	44.5	53.3	50.0	54.0	59.0	57.8	62.6	63.5	••	• •	•••	• •	• •	•	••
(NORDQVIST and ALM 1920)	(1)	(13)	(20)	(12)	(6)	(4)	(5)	(2)		• •	• •		•••	• •	÷ 8
Trollhättan 1918 ¹	• •			73.7	74.0	86.0		• •	•••		•••	* *	•••	• (• •
(NORDQVIST and ALM 1920)	а ж	• •		(3)	(4)	(3)	• •	••	• •	• •	• •	• •		•	· • =
Börringesjön 1919 ¹	••	• •	58.0	65.9	70.0	72.3	78.0			<i>.</i> .			• •	• •	••
(NORDQVIST and ALM 1920)	••	••	(1)	(6)	(12)	(10)	(2)	•••	••	• •	••		• •	•	•••
Cumberland, Newby Bridge,														~~~~	
Windermere 1920 ¹			••		47.8	50.5	53.7		61.9	64.0	85.0	73.0	• •	88.0	83.0
(JESPERSEN 1926)			•••		(17)	(39)	(29)	(17)	(7)	(5)	(2)	(1)	••	(1)	(1)
Lake Windermere ³		••	• •	52.9	and the second second	57.7	57.4	60.5	61.3	70.8	85.8	87.4		90.0	
(Frost 1945)	•	•••	• •	(9)	(29)	(59)	(54)	(40)	(13)	(19)	(5)	(9)	•••	(3)	••

¹ Age determination from scales (Aldersbestemmelse efter skæl). ² Mainly silvery or half-silvery. Age determination from otoliths; in some cases from scales (Overvejende blanke eller halvblanke. Aldersbestemmelse efter øresten; i nogle tilfælde efter skæl). ³ Age determination from scales and otoliths (Aldersbestemmelse efter skæl og øresten).

less than 399 of the eels examined, or 93.7 per cent., belonged to the X-group or older groups, and no individuals younger than the VIII-group were found.

Among the neighbouring countries Germany, Sweden, and England are somewhat better off as regards such investigations, although there, too, age determinations have mainly been made on yellow eels.

The most comprehensive investigations of the age and growth of the eel have been made by MARCUS (1919), who has determined the age of nearly 9000 eels from various German waters, but apparently this work in the case of the female eels deals with yellow eels only, and no German investigations seem to have been published later which may serve to throw light on the question under discussion.

NORDQVIST and ALM's investigations (1920) of Swedish eels i.a. include a small number of silver eels from the Gullmar Fjord on the coast of the Skagerak and from freshwater, caught at Trollhättan and Börringesjön. Apart from the eels from the Gullmar Fjord, the age of which is mainly determined on the basis of the otoliths, the determinations of age are exclusively made on the basis of analyses of scales.

From England there are partly a study on silver eels from Cumberland (Newby Bridge, Windermere) made by JESPERSEN (1926) and a later study by FROST (1945) on the age of silver eels from the Windermere catchment area. Whereas JESPERSEN's investigations are exclusively based on the scales, FROST for her determinations of age used both scales and otoliths. The results from the waters mentioned above are listed in Table 15 together with the results of the age determinations of silver eels in Esrum Lake made by me. In the cases where the determinations of age are not based on otoliths, the age is indicated as the number of scale-rings +3.

Among the Swedish eels those from the Gullmar Fjord seems to correspond quite well to the eels from Esrum Lake, both as regards size and age, whereas the eels from Trollhättan and Börringesjön show greatly deviating conditions. This is probably connected with the fact mentioned above, that the large broad-nosed eels of which these samples mainly consist have a relatively faster growth than the smaller, sharp-nosed eels. On the whole these large eels are characteristics of many Swedish inland waters and their size and fast growth should presumably be considered expressive of the good conditions of growth which these waters must be assumed to offer the eel, being remote from the breeding places of the eel or accessible with difficulty and hence poorly stocked.

In rate of growth the eels from Newby Bridge are somewhat inferior to the eels of Esrum Lake and in general they seem to be smaller than these at the beginning of the silveriness. Presumably this fact must be considered expressive of the validity of the rule indicated above, that slow growth gives small silver eels and fast growth gives large silver eels.

In this connexion FROST'S (1945) investigations from Lake Windermere, however, are most interesting, because the eels from there on several points seem to display properties nearly identical to those

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Age for length relationship of 3 cm groups of female silver eels from Esrum Lake and Lake Windermere. 3 cm længdegrupperses gennemsnitsalder i Esrum sø og Lake Windermere.

	o om mengaegrappenges gennems	intsaluer	i instanti se	og Lake	windermei	е.			
Length groups 3 cm 3 cm længdegrupper		46	49	52	55	58	61	64	
Esrum Lake	Mean age in years	9.0	10.4	10.7	11.3	11.6	12.2	12.2	1
	Number of specimens	1	10	65	146	105	67	20	
Lake Windermere (Frost 1945)	(Mean age in years Gennemsnitsalder i år	11.0	10.2	11.3	11.3	11.7	12.1	12.6	
	Number of specimens	1	13	32	38	61	31	27	

of the eels from Esrum Lake. FROST on the basis of examinations of scales as well as otoliths determined the age of a total of 240 female silver eels, which in length range from 47 to 97 cm and in weight from 210 to 2040 g. FROST's material is distinct from mine by a more numerous representation of the large eels, a fact which ought not to be considered as expressive of a commoner occurrence of these in Lake Windermere than in Esrum Lake, but which is mainly to be ascribed to a certain subjectivity in the selection of my material of large eels (cf. p. 5). Whereas eels above 65 cm in length only constitute 2.8 per cent. of my material, they represent 15.4 per cent. of the Lake Windermere eels. This cannot, of course, help influencing the calculated mean values to a certain extent. While the average length of the eels from Lake Windermere examined is 60.8 cm, the corresponding value for the eels of Esrum Lake is only 56.9 cm. If we make a corresponding calculation for both lakes, leaving out all eels above 65 cm, the average lengths calculated become 57.1 and 56.5 cm, respectively. As FROST states her measurements of the large eels, which in this connexion presumably

means all silver eels, at the nearest half centimetre, whereas my measurements always refer to the lowest whole centimetre, a positive correction of my values of half a centimetre is necessary to obtain a direct comparability. From this it appears that the average lengths of the eels constituting the majority of the silver eels in the two populations are actually identical. A comparison between the average lengths of the age groups in the two lakes shows the presence of a corresponding agreement. The high mean values in FROST'S material from the XIV-group and upwards can again be referred to the effect of the relatively more numerous representation of the large, faster growing eels in her material than in mine. The identity in conditions of growth appear with still greater distinctness from Table 16, in which the average ages of the 3-cm groups, including eels to a total length of 65 cm inclusive, are given for the populations mentioned.

The results of these few investigations show the presence of considerable differences, both as regards the age of the eels and their size at the end of the period of growth and the beginning of the silvery stage.

Conclusion.

It is a general impression of the investigations of the age of the silver eels in Esrum Lake reported here as well as corresponding investigations reported from other waters that the eel in a temperate climate is a slowly growing fish, but that the rate of growth is rather variable from place to place, dependent on the conditions of nutrition prevalent in the various localities. The primary reason for the slow growth is no doubt to be sought in the fact that the eel is the most

heat-loving of our useful fish, probably of all our freshwater fish. The consequence is that the period of growth becomes of short duration and the growth much poorer than e.g. in the Mediterranean area, where the period of growth at any rate is interrupted only by short intervals caused by cold in the consumption of food.

The continued investigations of silver eels from various Danish inland waters suggest the presence of

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eel populations with better as well as poorer conditions of growth than those in Esrum Lake. It will not, however, be possible to establish whether the growth of the eels and the size of the silver eels in Esrum Lake can be considered characteristic of the Danish inland waters until the treatment of material collected has been finished.

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Dansk Resumé.

Blankålenes størrelse og alder i Esrum sø.

Indledning.

Esrum sø med et areal på c. 1730 ha er Danmarks næststørste sø. Dens fysiografiske egenskaber er indgående beskrevet af BERG (1938), hvorfor der her kun skal fremhæves enkelte karakteristiske træk i dens naturforhold.

Søen er i længderetningen, der forløber omtrent nord-syd, c. 8 km og bredden 2—3 km. Maksimaldybden er 22 m, og c. halvdelen af arealet udgøres af dybder fra 15 til 20 m, idet litoralzonen næsten overalt er meget smal (fig. 1). Gennemsnitsdybden (12.3 m) er derfor ret betydelig i forhold til søens areal.

Nedbørsområdet, der indbefattet søen udgør 78,5 km², afgiver kun ubetydelige tilløb. Afløbet, Esrum å, der udgår fra søens nordlige ende og udmunder i Kattegat, passerer Esrum mølle, til hvis drift vandkraften anvendes, og ved hvilken der findes ålekiste.

Søen er eutrof, og iltforholdene fra overflade til bund udviser betydelige, af årstiden prægede, variationer. BERGS undersøgelser viser således, at iltmætningen i slutningen af sommerstagnationsperioden under 15 meters dybde er mindre end 50 $^{0}/_{0}$, og at vandet i c. 20 meters dybde kan blive så godt som iltfrit, et forhold som er af en vis fiskeribiologisk interesse, idet det undertiden udelukker, at fiskene i en periode af året stationært kan opholde sig ved bunden på op til halvdelen af det af søen omfattede areal. Bundfiskene er derfor i eftersommeren ofte henvist til at føre en delvis pelagisk tilværelse (OTTERSTRØM 1934).

Søens fiskebestand udgøres af følgende arter: ål, gedde, aborre, hork, brasen, skalle, rudskalle, suder, løje og søkaruds.

For Esrum sø som for samtlige andre større danske indsøer, i hvilke der drives rationelt fiskeri, er ålebestandens størrelse og udnyttelse afgørende for fiskeriets rentabilitet. I forhold til ålefiskeriet er fiskeriet efter samtlige andre fiskearter derfor sekundært og må til dels betragtes enten som biprodukter ved dette eller som led i foranstaltninger til dets fremme.

Ålebestanden vedligeholdes dels gennem naturlig indvandring af yngel og dels ved ret betydelige indplantninger af yngel og sætteål (jvfr. tabel 11).

1. Materiale.

Esrum sø ejes af staten, og fiskeriforpagteren er foruden økonomiske og driftsmæssige forpligtelser pålagt årlig at levere 30 blankål til Danmarks Fiskeriog Havundersøgelser til alders- og vægtkontrol. Materialet til denne afhandling hidrører overvejende fra disse pligtleveringer og omfatter tidsrummet fra 1937 til 1950.

Kontrolålene er af hensyn til ønskeligheden af i hvert enkelt tilfælde at tilvejebringe et materiale, som skønsmæssigt kan betragtes som repræsentativt for søens blankålsbestand, udtaget tilfældigt af fangsterne, og kun for så vidt angår de store ål, d.v.s. ål fra ca. 1/2 kg og opefter, der kun udgør 5—7 0/0 af fangsten, har et vist subjektivt skøn ved udtagelsen været nødvendigt.

Foruden skælprøver, der er udtaget på samtlige 426 kontrolål, er der desuden taget øresten på materialet fra 1948 til 1950, der ialt omfatter 110 blankål.

Samtlige kontrolål er hunner, idet hanålene er yderst fåtallige i søen.

2. Aldersbestemmelse.

a. Almindelig oversigt.

Den første, der påviste, at de koncentriske ringe, der i mere eller mindre fuldstændig udvikling kan påvises i åleskællet, er årringe, var danskeren GEMZØE (1907). Han mente desuden på grundlag af målemetoden at kunne fastslå, at de første skælanlæg sædvanligvis dannes i det tredie år efter indvandringen som glasål, når ålen almindeligvis er 17—18 cm lang.

Et vigtigt hjælpemiddel ved bestemmelsen af ferskvandsålens alder fandt Ehrenbaum og Marukawa (1913) i ørestenene, der i modsætning til skællene anlægges allerede i det tidlige larvestadium. Glasålene, der indvandrer om foråret, og som ifølge Johs. Schmidts undersøgelser (1922) er c. 3 år gamle, har således allerede veludviklede øresten (jvfr. Tavle I, fig. 4).

Under gulålsstadiet udbygges ørestenene med koncentriske ringdannelser, der i påfaldende lys fremtræder som skiftevis lyse og mørke ringe, og som af EHRENBAUM og MARUKAWA på grundlag af flerårige opvækstforsøg i akvarier med sikkerhed kunne identificeres som henholdsvis sommer- og vinterringe. Med dette middel til en sikker aldersbestemmelse i hænde lod det sig derefter påvise, at ålene ikke, som af GEMZØE antaget, sædvanligvis anlægger skæl i det tredie, men først i det fjerde år efter indvandringen som glasål. D.v.s., at man skal addere det fundne antal vækstzoner i skællene med 3 for at finde det antal år, ålene har tilbragt i ferskvand efter indvandringen som glasål.

En række senere undersøgelser (MARCUS 1918, NORDQVIST OG ALM 1920, TESCH 1928 samt FROST 1945) bekræfter, at skællene hos nordeuropæiske ål i almindelighed anlægges i det fjerde år efter glasålsstadiet, men at ikke alderen som sådan, men derimod længden, er bestemmende for, hvornår de første skælanlæg opstår. Denne længde på 16—18 cm opnår ålene imidlertid sædvanligvis i det fjerde år efter glasålsstadiet (jvfr. tabel 1, 2, 3 og 4).

b. Egne undersøgelser.

1. Skælundersøgelser.

Aldersbestemmelsen på grundlag af skællene vanskeliggøres foruden ved usikkerheden med hensyn til det alderstrin, ved hvilket den individuelle skældannelse indtræder, ved den kendsgerning, at skællene selv i det område over gatregionen, hvor de første skælanlæg opstår, ingenlunde alle fremviser det samme antal tilvækstzoner. Årsagen hertil må som fremhævet af MARCUS (1919) tilskrives, at skællenes vækst hos ålen mere end hos andre fisk er en funktion af den almindelige overfladevækst, idet skællene ikke dækker hinanden, men ligger side om side i et parketagtigt mønster. Da skældannelsen således er begrænset af de udvidelsesmuligheder, overfladevæksten betinger, optræder der hyppigt i skællene — navnlig hos dårligt voksende ål — ufuldstændige ringdannelser, ligesom tilvæksten hos nogle af skællene af samme grund nu og da helt kan udeblive et år. Konsekvensen heraf bliver, at jo ældre ålen er, desto færre skæl vil registrere den rette alder, d.v.s. fremvise et antal ringe svarende til det antal år, som ålen har levet efter anlægget af de første skæl. Værdien af aldersbestemmelser foretaget alene på grundlag af skællenes tilvækstzoner er derfor i meget høj grad betinget af, hvor skællene er udtaget, samt hvor stort et antal skæl, der ligger til grund for aldersbestemmelsen af de enkelte individer. Manglende oplysninger herom begrænser den værdi, der kan tillægges en række arbejder over ferskvandsålens alder og vækst. Til grund for aldersbestemmelserne i nærværende arbejde ligger undersøgelsen af sædvanligvis 20 og aldrig under 15 skæl alt efter, hvor mange anvendelige skæl prøverne har indeholdt. Til belysning af den rolle, aldersbestemmelsens basering på et passende stort antal skæl spiller, bringes tabel 5, der viser variationer i antal af ringe i 20 skæl fra hver fisk i materialet fra 1946.

Man kan af ovenstående udlede, at det ud fra det kendskab, man har til åleskællenes opbygning, må anses for givet, at man ved aldersbestemmelse på grundlag af skællene alene — uanset den omhu, hvormed undersøgelserne iøvrigt er foretaget — vil opnå resultater, der almindeligvis ligger mere eller mindre i underkanten af de virkelige tal, men at fejlen formindskes jo flere skæl, der ligger til grund for de individuelle aldersbestemmelser.

Spørgsmålet bliver derfor, om man ikke helt burde se bort fra skællene som et middel til aldersbestemmelse, og i stedet udelukkende anvende ørestenene. Dette spørgsmål kan ikke besvares generelt. For de mindre (yngre) åls vedkommende kan der ikke være tvivl om, at man i de fleste tilfælde opnår de sikreste resultater ved undersøgelse af ørestenene frem for skællene, og at man derfor så vidt muligt bør basere aldersbestemmelserne på førstnævnte. For de større (ældre) åls vedkommende er ørestenene imidlertid uanset slibning — som oftest af så ringe værdi som middel til aldersbestemmelse, dels på grund af den hyppighed, hvormed falske ringe optræder, dels på grund af en almindeligt forekommende udviskning af grænserne mellem de enkelte årringe, ofte tilsyneladende forårsaget af en meget kraftig kalkinkrustering, at de bliver mere eller mindre uanvendelige til formålet.

Ved behandlingen af det foreliggende materiale har jeg for størstedelens vedkommende på forhånd været afskåret fra at benytte ørestenene til aldersbestemmelse, idet kun skælprøverne forefandtes. For at bedømme værdien af de på det oprindelige materiale alene på grundlag af skællene foretagne aldersbestemmelser har jeg derfor desuden undersøgt ørestenene i materialet fra 1948, 49 og 50 omfattende ialt 110 individer.

2. Ørestensundersøgelser.

Efter slibning af ørestenene fremtræder centralfeltet i påfaldende lys som en mørk, klar kærne omgivet af en hvid ring, uden om hvilken der atter følger en smal, klar zone (jvfr. tavle I, fig. 4). Denne del af ørestenen, der forefindes hos de indvandrende glasål, kan henføres til larvestadiet og medregnes ikke ved bestemmelsen af ålens alder, der angives ved det antal år, fisken har levet efter indvandringen som glasål. Efter larvezonerne følger skiftevis bredere, hvide, lysreflekterende sommerzoner og smallere, mørke, lysabsorberende vinterzoner dannet under gulålsstadiet.

Som nævnt bliver usikkerheden ved aldersbestemmelserne større, jo ældre fiskene er. Ørestenene bliver efterhånden vanskeligere eller umulige at tyde, og færre og færre skæl registrerer det rigtige antal tilvækstzoner, især hvor de hidrører fra en bestand med dårlige vækstforhold. Resultatet bliver, at differensen mellem ørestenenes og skællenes tilvækstzoner viser tilbøjelighed til at øges, jo ældre aldersgruppe fisken tilhører, og des mere jo ringere bestandens vækstforhold er. I tabel 6 er angivet eksempler herpå hentet fra MARCUS (1919) samt fra NORDQVIST og ALM (1920).

Vanskeligheden ved selv efter slibning at gennemføre en sikker aldersbestemmelse af de ældre ål på grundlag af ørestenene har medført, at kun en mindre procentdel af ørestenene fra mit materiale fra Esrum sø har ladet sig anvende til sammenligning med de på grundlag af skælundersøgelserne opnåede resultater. Ialt har således omtrent 2/3 af ørestenene vist sig uanvendelige, hvorved kun 38 ål har kunnet aldersbestemmes sikkert på ørestenene alene. Forskellen mellem skæl- og ørestensaflæsningerne hos disse 38 ål fremgår af tabel 7.

Den af MARCUS (1919) og NORDQVIST Og ALM (1920)

påviste tendens til øgning af differensen mellem skælog ørestensaflæsningerne med tiltagende alder synes således også til en vis grad at gøre sig gældende for mit materiale, omend forskellen mellem mine skælog ørestensaflæsninger, når man tager ålenes højere alder i betragtning, er en del mindre end de af de nævnte forfattere fundne differenser.

Materialets talmæssige svaghed tillader ingen sikre slutninger ud fra de for de enkelte aldersgrupper beregnede middelværdier for forskellen mellem antallet af ringe i skæl og øresten. Da materialet imidlertid såvel ved dets længdefordeling som ved dennes middelværdi (55.1 cm) og den på grundlag af skælundersøgelserne beregnede gennemsnitsalder (11.3 år) giver et tilforladeligt udsnit af det samlede materiale (jvfr. pag. 34 samt tabel 13 og 14), må den for samtlige aldersgrupper beregnede middelværdi (3.3) for forskellen mellem antallet af ringe i skæl og otolither også antages at være tilnærmet gyldig for det samlede undersøgelsesmateriale. Det kan imidlertid ikke undgås, at de enkelte aldersbestemmelser bliver behæftede med større eller mindre fejl, der for det foreliggende materiale synes at ligge inden for et maksimalt udsving på ca. ± 2 år. Større interesse end at fastslå de enkelte blankåls nøjagtige alder har det imidlertid i denne forbindelse at konstatere den gennemsnitlige udvandringsalder, som fremkommer ved til resultatet af skælaflæsningerne at addere den konstaterede gennemsnitsforskel mellem skæl- og ørestensaflæsningerne på det på grundlag af begge undersøgte materiale. Denne differens udgør som nævnt på Esrum sø materialet 3.3 år. Jeg har imidlertid til skælaflæsningerne i stedet for 3.3 overalt adderet 3 år, dels fordi det er upraktisk at manøvrere med brudte tal, dels fordi mine resultater derved lettere lader sig sammenligne med de af tidligere forfattere på grundlag af skælundersøgelser opnåede resultater. Det lader sig imidlertid ikke bortforklare, at anvendelsen af en sådan gennemsnitsfaktor for de yngste årganges vedkommende vil medføre, at alderen muligvis angives noget for højt og for de ældre aldersgruppers vedkommende for lavt. For at kunne indføre en korrektion for de enkelte aldersgrupper, måtte man imidlertid være i besiddelse af et langt større ørestensmateriale end det, der har stået til min disposition, og mine aldersbestemmelser må derfor betragtes med det deraf følgende forbehold.

Af hensyn til sammenligneligheden mellem det ældre materiale og materialet fra 1948—50 har jeg baseret samtlige i det følgende anførte aldersbestemmelser på skællene alene, således at jeg udelukkende har anvendt ørestensundersøgelserne til kontrol af de på grundlag af skællene foretagne aldersbestemmelser.

2. Resultaterne af de årlige undersøgelser over blankålenes længde, vægt og alder i Esrum sø.

Hensigten med de årligt udtagne kontrolprøver af blankål har været at søge konstateret, hvorvidt søens ålebestand til stadighed står i et rimeligt forhold til dens produktionsevne. Dette spørgsmål skulle det være muligt at besvare ud fra årligt tilbagevendende undersøgelser over blankålenes længde, vægt og alder.

Som fig. 2 viser, fordeler hovedparten af blankålene sig inden for et spredningsfelt på ca. 20 cm, hvilket nødvendigvis må medføre, at de enkelte længdegruppers repræsentation i kontrolprøverne, der sædvanligvis kun består af ca. 30 ål, må blive svag, hvorved tilfældigheder ved blankålenes udtagelse vil kunne give udtryk for forekomsten af forskydninger i deres gennemsnitlige længde- og vægtfordeling, som måske ikke reelt er til stede. Lige så uheldigt er det i denne forbindelse, at ålen inden for samme biotop udviser meget betydelige individuelle vækstforskelle. Det er således ikke ualmindeligt inden for 3 cm-grupper i de enkelte kontrolprøver at finde aldersvariationer af størrelsesordenen 4-6 år. Det er givet, at individuelle aldersforskelle af denne størrelse kan influere stærkt på de for de enkelte kontrolprøver beregnede middelværdier, hvis yderpunkter (jvfr. tabel 8) er henholdsvis 10, 8 og 12,3 år. For i nogen grad at reducere disse fejlkilder har jeg yderligere foretaget beregninger af middelværdierne for længde, vægt og alder for 3-(2-) årige perioder (tabel 9).

Betragter vi først de i sidstnævnte tabel anførte middellængder, vil man se, at disse viser en tendens til aftagen inden for det af undersøgelsen omfattede tidsrum. Uanset at denne aftagen af middellængderne synes statistisk veldefineret kan man (jvfr. de ovenfor anførte bemærkninger) ikke alene ud fra det talmateriale, der ligger til grund for beregningen af disse middelværdier, med sikkerhed afgøre, hvorvidt blankålsbestanden som helhed har været underkastet sådanne ændringer, hvad længdefordelingen angår. Det ville i denne forbindelse have været meget ønskeligt, om man til sammenligning havde været i besiddelse af samtidige mere omfattende målinger til belysning af blankålenes længdefordeling i de årlige fangster. I mangel af et mere eksakt udtryk for tilstedeværelsen af eventuelle sådanne ændringer i blankålsbestanden må man forsøge at nærme sig spørgsmålets besvarelse ad anden vej.

For at få et indtryk af den almindelige længdefordeling i blankålsfangsterne måltes i efteråret 1948 647 af de i hyttefade i søen opbevarede blankål. Resultatet af disse målinger er i kurveform gengivet på fig. 3 sammen med den tilsvarende kurve for det samlede undersøgelsesmateriale. Det fremgår dels af kurverne og dels af de beregnede gennemsnitslængder, der for de 647 ål fra 1948 udgjorde 55.9 cm og for det samlede undersøgelsesmateriale 56.9 cm, at en god overensstemmelse mellem de to kurver ikke er til stede. Ser man yderligere bort fra de store ål (68 cm), der er stærkere repræsenteret i de 647 ål fra 1948 end i undersøgelsesmaterialet (om årsagen hertil se pag. 28), bliver middelværdierne henholdsvis 54.6 og 56.7 cm. Det vil endvidere ses, at der er ret god overensstemmelse mellem den ved de mere omfattende målinger i 1948 fundne middelværdi og den tilsvarende fra samme års kontrolmateriale, idet sidstnævnte, der udelukkende bestod af ål under 68 cm totallængde, havde en middellængde på 55.0 cm. Alt i alt kan uoverenstemmelsen mellem de to kurver, når man tager det samlede undersøgelsesmateriales ret betydelige omfang i betragtning, næppe forklares på anden måde end, at der inden for den periode, undersøgelsen omfatter, er sket en reel formindskelse af blankålenes størrelse i søen.

Et vigtigt holdepunkt for bedømmelsen af dette spørgsmål afgiver også de af fiskeriets udøvere gennem årene gjorte rent praktiske erfaringer. Den nuværende fiskeriforpagter har således oplyst, at den almindelige størrelse blankål, da han i 1932 kom til søen som medhjælper for den daværende forpagter, vejede ca. 15—16 pund snesen, medens vægten i dag kun er 12-13 pund snesen. I tidsrummet fra 1932 og indtil 1939, da den nuværende forpagter overtog fiskeriet, blev gulålsfiskeriet (jvfr. tabel 11 og fig. 3) drevet overordentlig intensivt og nåede op på et niveau, der formentlig i væsentlig grad har oversteget søens normale afkastningsevne. Resultatet udeblev da heller ikke, idet der efter den bratte stigning i udbyttet fulgte et næsten lige så brat fald. Da forpagtningen i 1939 gik over på andre hænder, var det derfor en bydende nødvendighed at skåne bestanden af gulål samtidig med, at der foretoges regelmæssige vngelindplantninger. I dag har søen som følge af disse foranstaltninger en meget betydelig bestand af

gulål i alle størrelser, og det vil være naturligt at stille den faktiske nedgang i blankålenes størrelse i relation til den skånsomme form, hvorunder gulålsfiskeriet gennem en årrække har været drevet, og det betydelige tilskud, som fornyelsen af ålebestanden har fået gennem de regelmæssige yngelindplantninger. Der vil i det følgende afsnit blive lejlighed til at komme nærmere ind på dette spørgsmål, hvorfor det foreløbig må være tilstrækkeligt at konstatere, at der, som også de beregnede middelværdier antyder, er sket en reel formindskelse af blankålenes størrelse i søen inden for det af undersøgelsen omfattede tidsrum.

Den konstaterede formindskelse af kontrolprøvernes middellængde er, som det vil ses af tabel 9, jvfr. fig. 4, ikke ledsaget af en tilsvarende formindskelse af gennemsnitsalderen, idet de mindre blankål, som udgør materialet fra 1946—48 og 1949—50, ikke er yngre end de større blankål, der udgør materialet fra 1937—39 og 1940—42.

Dette er for så vidt kun, hvad man på forhånd måtte forvente, idet formindskelsen af blankålenes længde må være at opfatte som en funktion af forringede ernæringsbetingelser for bestanden som helhed og deraf følgende formindskelse af tilvæksthastigheden. Denne giver sig imidlertid ikke, som man kunne formode, udtryk i form af en forøgelse af ålenes gennemsnitsalder inden for de enkelte længdegrupper (jvfr. tabel 10), men udelukkende gennem det for blankålene karakteristiske forhold, at længdegrupperne inden for ret vide grænser kun viser ubetydelige aldersvariationer (jvfr. også tabel 13). En forøgelse af de mindre og langsommere voksende åls relative andel i blankålsbestanden synes derfor alene at betinge de forskelle, som karakteriserer forholdet mellem blankålenes længde og alder inden for beregningsperioderne. Der er med andre ord sket det, at en større del af ålene, end tilfældet var ved undersøgelsesperiodens begyndelse, er blevet forsat i vækst.

Foruden ved forandringer i blankålenes længde og alder kunne ændringer i ernæringsbetingelserne tænkes at give sig udslag i positive eller negative forskyd-

ninger af længde-vægt koefficienten (her beregnet efter $k = \frac{10^5 \times v}{l^3}$), medmindre størrelsen af denne faktor er udtryk for en for blankhedens indtræden nødvendig kondition (se pag. 35). De variationer, som k (jvfr. tabel 9) er underkastet, er imidlertid ret ubetydelige og tilfældigt prægede og giver ikke oplysninger af værdi for spørgsmålets belysning.

4. Bemærkninger vedrørende fiskeriet og fiskebestanden.

Esrum sø har altid været betragtet som en god ålesø, både hvad angår afkastningens størrelse og ålenes kvalitet. Den gennemsnitlige, årlige afkastning af ål har i perioden 1926—46 (jvfr. tabel 11), for hvilken der foreligger kontinuerlige og fuldstændige opgørelser over fangstudbyttet fra såvel søen som ålekisten, udgjort ialt 13.385 kg eller 7.73 kg pr. ha af en samlet årlig afkastning af fiskeriet som helhed i samme tidsrum på 25.235 kg (14.59 kg pr. ha). I henseende til vægt har ålefiskeriet således udgjort 53 %/0 af den samlede fangst.

Både absolut og i forhold til det samlede hektarudbytte er en afkastning af denne størrelse efter danske forhold høj, og så vidt det lader sig kontrollere, kan ålefiskeriet i ingen anden større dansk sø fremvise et tilsvarende højt hektarudbytte.

For i det foreliggende tilfælde at skabe en rimelig balance mellem søens produktionsevne og ålebestandens størrelse må en regulering af ålebestanden ske gennem en tilpasning af yngelindplantningernes omfang hånd i hånd med en efter forholdene afpasset intensivering eller reduktion af gulålsfiskeriet, og ikke mindst gennem en bekæmpelse af ålens næringskonkurrenter, især brasen og hork.

Ålebestanden vedligeholdes dels gennem den naturlige indvandring af åleyngel (hovedsagelig glasål) dels gennem indplantninger af såvel glasål som sætteål af forskellig størrelse. Ved Esrum mølle findes en særlig fangstindretning, hvor den opvandrende åleyngel optages og mængden (vægten) kontrolleres, hvorefter yngelen udsættes i søen. I denne fangstindretning fangedes i 1950 250 kg, der hævdes at svare til en opgang over middelstørrelse, og i 1951 125 kg glasål, hvilket repræsenterer henholdsvis c. 1 og 1/2 million stkr. Disse tal angiver naturligvis kun en størrelsesorden, og deres værdi forringes ved det faktum, at en del - måske c. halvdelen - af den indvandrende yngel er i stand til ved egen hjælp at passere stemmeværket. Ud fra de foreliggende oplysninger kan man derfor kun skønne, at størrelsen af den naturlige indvandring antagelig ligger mellem 1 og 2 millioner stkr. glasål årlig.

Den naturlige indvandring af yngel suppleres med ret betydelige indplantninger af såvel glasål som sætteål (jvfr. tabel 12). Siden 1932 er sådanne indplantninger foretaget årlig, men i varierende mængde. Desværre er det ikke muligt at få et nogenlunde eksakt udtryk for, hvad disse udsætninger betyder i forhold til den naturlige indvandring, for det første fordi dennes nøjagtige størrelse ikke er kendt, og for det andet fordi indplantningsmaterialet er meget heterogent.

Sætteålene kan variere betydeligt i størrelsessammensætning fra år til år, men ligger sædvanligvis inden for størrelsesordenen 150—300 stkr. pr. kg. Der er ingen tvivl om, at sætteålene er væsentlig mere værdifulde som indplantningsmateriale end glasålene dels på grund af deres større overlevelsesprocent, og dels fordi de hurtigere vil nå blankålsstadiet. Det må derfor anses for overvejende sandsynligt, at indplantninger af den størrelsesorden, som der her er tale om, yder et meget betydeligt tilskud til den naturlige indvandring, og derigennem kan influere væsentligt på bestandens størrelse og vækstforhold.

Disse faktorer kan foruden af yngeltilgangens størrelse også i høj grad påvirkes af mængden af næringskonkurrenter til ålen. Som sådanne udmærker sig specielt brasen og hork, der begge aldeles overvejende er knyttet til barbunden og ligesom ålen hovedsagelig lever af larver af dansemyg. Medens horken i en vis udstrækning tjener til føde for ålen, og derfor ofte uberettiget af fiskerne anses for en gavnlig fisk i ålevande, er brasenen på grund af sin størrelse og kropsform i det store og hele ikke udsat for ålenes efterstræbelser. Da den yderligere kun kan indbringe en brøkdel af den pris, hvormed ålen betales, bør den altid i ålevande bekæmpes med alle til rådighed stående midler.

Det synes ikke at være forbundet med særlige vanskeligheder at holde brasenbestanden i Esrum sø nede på en rimelig størrelse. Som det vil fremgå af tabel 11. har der kun i to kortvarige perioder inden for de 50 år, som statistikken omfatter, været gjort brasenfangster af nogen større betydning, og det synes, som om bestanden kun langsomt overvinder de tab, som et lejlighedsvis stærkt fiskeri forvolder. Årsagen hertil må bl.a. være at finde i det forhold, at brasenen først yngler, når den har nået en ret betydelig alder og størrelse, hvorved et kraftigt fiskeri for en årrække vil kunne reducere yngeltillæget stærkt. Det må i hvert fald betragtes som en kendsgerning, at der i dag ikke findes nogen stor brasenbestand i søen, idet der i så fald næppe ville fanges så få brasen i åleruserne, som tilfældet er. Muligvis er det tilstrækkeligt til at holde bestanden nede, at ingen fanget brasen, som det gennem en årrække har været praktiseret, genudsættes uanset størrelsen.

Det er allerede påpeget, at den meget bratte stigning i fangstkurven for ål, der begyndte i 1931 og afsluttedes i 1935 (jvfr. fig. 3), hovedsagelig skyldes et meget intensivt fiskeri efter gulål; men denne forklaring rummer næppe hele sandheden. Et intensiveret gulålsfiskeri, skulle, såfremt ikke andre forhold øver deres indflydelse, efter alt at dømme resultere i en nedgang i udbyttet af blankålsfiskeriet. Hvorvidt dette har været tilfældet, for så vidt angår fiskeriet i søen, kan man kun indirekte skønne over ud fra blankålsfangsterne i ålekisten, idet størrelsen af blank- og gulålsfangsterne ikke er opgivet særskilt for søen. Som det kunne forventes, medfører det forøgede fiskeri i søen en øjeblikkelig nedgang i fangsten af blankål i ålekisten, men faldet afbrydes uventet af en kraftig stigning i fangsten i årene 1934 og 1935, hvorefter udbyttet igen aftager i takt med fangsternes aftagen i søen. Betragter man specielt året 1935, hvor den samlede fangst i søen og ålekisten beløb sig til ca. 30.000 kg, må det skønnes overvejende sandsynligt, at det store udbytte af blankålsfiskeriet i ålekisten har været ledsaget af et tilsvarende stort blankålsfiskeri i søen eller med andre ord, at mængden af blankål i søen har været i betydelig stigning samtidig med, at gulålsfiskeriet er drevet meget intensivt. Forholdet kan næppe forklares på anden måde end ved tilstedeværelsen af en eller måske flere dominerende årgange, der er blevet blanke inden for et kort åremål. Denne eller disse kan hidrøre fra en pludselig forøgelse af yngeltilgangen enten hidrørende fra en unormalt stor naturlig opgang eller fra en eller flere særlig omfattende udsætninger, eller den kan skyldes en pludselig forbedring af ernæringsforholdene eller samtlige disse faktorer i forening. Der er i denne forbindelse speciel grund til at bemærke, at der i 1928 ret isoleret foretoges en meget stor indplantning omfattende 150.000 stkr. ca. 25 cm lange sætteål (fra Elben). Elb-ål i denne størrelse tilhører ifølge EHRENBAUM OG MARUKAWA (1913) IV-gruppen, og da hovedparten af ålene i søen bliver blanke i en alder af 10-13 år efter glasålsstadiet, er det ikke usandsynligt, at denne udsætning har en væsentlig andel i den i midten af trediverne konstaterede forøgelse af blankålsudtrækket.

Såvel samme år, som denne udsætning skete, som det efterfølgende blev der gjort et kraftigt indhug på brasenbestanden, idet der i årene 1928—29 tilsammen fiskedes omtrent 25.000 kg brasen i søen (jvfr. tabel 11). Der er derfor til dels samtidig med den betydelige udsætning af sætteål også skabt forbedrede ernæringsbetingelser, som må være af væsentlig betydning for at opnå en effektiv forbedring af ålebestanden gennem udsætning.

Foruden brasen og hork må i særdeleshed også aborren betragtes som værende til ikke uvæsentlig ulempe for et rationelt ålefiskeri, navnlig fordi den i følelig grad efterstræber glasålene, og derved influerer på yngeltilgangens størrelse, men også fordi den, omend i mindre grad end hork og brasen, kan optræde som ålens næringskonkurrent. Aborren er meget talrig i søen, og bestanden kunne utvivlsomt med fordel tåle en væsentlig kraftigere befiskning, end den normalt er udsat for. Med de priser, som sædvanligvis kan opnåes navnlig på små aborrer, er et specielt aborrefiskeri imidlertid urentabelt, hvorfor afkastningen hovedsagelig kun fremkommer som biprodukt ved andet fiskeri. I det sidste par år har der dog som følge af rentable afsætningsforhold på eksportmarkedet været drevet specielt aborrefiskeri med skovlvod uden for ålesæsonen, og udbyttet har som følge heraf vist en ikke uvæsentlig stigning.

Den ved undersøgelsen og gennem det praktiske fiskeris erfaringer påviste aftagen i blankålens størrelse må, som tidligere berørt, utvivlsomt være at opfatte som stående i forbindelse med de meget omfattende indplantninger af ål i søen. Det er en kendt sag, at blankålene ved en pludselig formindskelse af ålebestanden - f.eks. i særlig strenge isvintre - i de følgende år er betydeligt større end normalt for det pågældende vand. Det synes ikke muligt at finde anden rimelig forklaring på denne iagttagelse, end at decimeringen af ålebestanden har givet de resterende ål bedre ernæringsforhold resulterende ikke blot i en forøgelse af væksthastigheden, men også i en forøget størrelse af ålene ved vækststadiets afslutning. På tilsvarende måde må en formindskelse af blankålene uden tvivl være at opfatte som udtryk for en forringelse af ernæringsforholdene. I det foreliggende tilfælde synes årsagen hertil nærmere at være en følge af de betydelige indplantninger og det skånsomme gulålsfiskeri end af den af de øvrige fiskearter påførte næringskonkurrence.

Det kunne umiddelbart synes mest fordelagtigt udelukkende at drive ålefiskeriet i form af blankålsfiskeri, dels fordi ålen er lettest at fiske under udtrækket, og dels fordi fisken på dette stadium er udvokset og kvaliteten bedst. Bortset fra, at en passende regulering af ålebestanden kan nødvendiggøre fiskeri efter gulål, er det et økonomisk spørgsmål, hvorvidt og i hvilken udstrækning fiskeri efter gulål bør drives. For

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det første opnår ålene en væsentlig bedre pris under gulålsfiskeriet om foråret og forsommeren, hvor der er få eller ingen blankål, og for det andet må det i det foreliggende tilfælde, så længe ålekisten er i privat besiddelse, være i såvel statens som forpagterens interesse, at så stor en del af ålebestandens årlige afkastning som muligt tilfalder søfiskeriet. Af disse grunde vil et gulålsfiskeri af passende omfang i søen næppe kunne undværes.

Det synes efter de foreliggende undersøgelsesresultater tilrådeligt at intensivere gulålsfiskeriet ud fra det synspunkt, at kun resultaterne af et intensiveret fiskeri vil kunne vise, hvorvidt den form, hvorunder fiskeriet nu drives, sikrer en optimal udnyttelse af ålebestanden. For øjeblikket fiskes omtrent lige mange gulål og blankål, idet dog hovedvægten ligger på blankålsfiskeriet.

En intensivering af gulålsfiskeriet bør naturligvis ske under fortsat behørig kontrol, der også bør omfatte regelmæssigt tilbagevendende målinger af blankålsfangsterne, med det formål at konstatere, hvorledes gulålsfiskeriet indvirker på blankålenes størrelsesfordeling.

Den naturlige indvandring af glasål finder sædvanligvis først sted i juni måned, og det maksimale udtræk af blankål sker fra medio august til medio september, medens såvel oktober- som novemberudtrækket kun er ringe.

Forårsudtrækket er i almindelighed ringe, men variabelt efter vejrforholdene. Hvis der kommer tidlig frost af længere varighed om efteråret, reduceres eller standser blankålsudtrækket, og forårsudtrækket i maj bliver da større end normalt.

De store indplantninger af sætteål, der hovedsagelig hidrører fra lokaliteter, hvor hanålene er i flertal (f.eks. Ringkøbing fjord og Roskilde fjord) kunne forventes at have forøget hankønsprocenten i søen. Dette er også tilfældet, omend ikke på langt nær i den udstrækning, som udsætningernes størrelse lader formode. Spørgsmålet har ikke været gjort til genstand for mere eksakt undersøgelse, men det praktiske fiskeris udøvere hævder, at der, før de regelmæssige indplantninger af sætteål begyndte, i realiteten ikke fandtes hanlige blankål i søen. Hanålenes andel i blankålsfangsterne anslås nu at være c. 2 %, hvoraf størsteparten fanges i ålekisten. Det er i denne forbindelse af interesse at bemærke, at resultaterne af de hidtil foretagne undersøgelser over spørgsmålet om ålens kønsdifferentiering synes at bekræfte, at denne i betydelig udstrækning er påvirkelig af ydre faktorer (RASMUSSEN 1951).

5. Blankålenes længde, vægt og alder i Esrum sø og andre vandområder.

Medens man til brug for de årlige undersøgelser kunne have ønsket et væsentlig større materiale, udgør det samlede materiale i dets egenskab af et gennemsnitsmateriale over en længere årrække et anvendeligt grundlag til bedømmelse af, hvilke egenskaber med hensyn til længde, vægt og alder, der i almindelighed karakteriserer blankålene i Esrum sø, og hvorledes bestanden i disse henseender forholder sig til de ved tilsvarende undersøgelser fra andre vandområder opnåede resultater. Disse spørgsmål vil i det følgende blive gjort til genstand for behandling.

I tabel 13 er det samlede materiale opdelt i 3-cm grupper, for hvilke er angivet gennemsnitsalder, dennes standardafvigelse og middelfejl, størrelsen af individuelle aldersvariationer (spredningen) samt antal og middelvægt.

Ålenes længde har varieret mellem 47 og 80 cm og deres vægt har ligget inden for intervallet 198 og 900 g med en middelværdi på 330,8 g. Blankålsstadiet er tidligst indtrådt efter et ferskvandsophold på 8 år, medens de ældste blankål har tilbragt 16 år i søen. Den for det samlede materiale beregnede gennemsnitlige udvandringsalder er 11.4 år.

I tabel 14 er angivet de for de enkelte aldersgrupper beregnede middellængder, spredningen, standardafvigelsen og middelfejlen på middellængderne samt de tilsvarende middelvægte.

Den foran nævnte gennemsnitlige udvandringsalder på 11.4 år opnår ålene ved en middellængde på 56.9 cm. Det er iøjnefaldende, at størstedelen af ålene (88 $^{0}/_{0}$) tilhører aldersgrupperne X—XIII, medens kun relativt få individer er blevet blanke efter flere eller færre års ophold i søen. Den store spredning udtrykt ved forskellen i længde mellem største og mindste fisk tilhørende samme aldersgruppe (se også fig. 5) er som tidligere nævnt karakteristisk for ålen og berøver de beregnede middelværdier deres praktiske anvendelighed.

Det synes rimeligt i hvert fald delvis at sætte spredningens størrelse i relation til forskelle i livsform mellem de som spidshovede og bredhovede ål betegnede biologiske typer.

Medens de mindre blankål hovedsagelig udgøres af spidshovede ål, hvis føde overvejende er barbundens dansemyglarver, er de store ål udelukkende bredhovede, som i modsætning til de spidshovede ål i højere grad er knyttet til de mere lavvandede partier i

og i nærheden af bredzonen, og hvis overvejende føde er småfisk. Disse to biologiske typer er ikke skarpt adskilte, men forbundet med mere eller mindre jæyne overgange (PETERSEN, 1894, EHRENBAUM 1929 og SIVERTSEN 1938). FROST (1945) har påpeget, at de store blankål (bredhovede), der er stærkere repræsenteret i hendes materiale end i mit, synes at udvise et fra de mindre blankål (spidshovede) afvigende vækstbillede, karakteriseret ved en hurtigere tilvækst hos de førstnævnte end hos de sidstnævnte, og det tør vel anses for sandsynligt, at tilsvarende omend mindre vækstforskelle karakteriserer mellemformerne. På grund af de ændringer af hovedformen, som ledsager blankhedens indtræden, er en sådan adskillelse af de to typer imidlertid ikke praktisk gennemførlig på blankål, når lige bortses fra typernes mest karakteristiske yderpunkter.

FROST (1945) har ud fra tilsvarende iagttagelser over størrelsen af blankålenes længdespredning inden for de enkelte aldersgrupper og den ringe gennemsnitlige tilvækst, som er resultatet af et forlænget ferskvandsophold, draget den - forekommer det - sandsynlige slutning, at blankhedens indtræden ikke alene er en funktion af den alder og længde, ålen har opnået, men tillige må antages at være betinget af en af forholdet mellem længde og vægt, d.v.s. af konditionen afhængig fysiologisk tilstand. Denne teori støtter hun bl.a. på resultaterne af opvækstforsøg med italienske ål, der allerede blev blanke efter 4¹/₂ års forløb og ved en længde på 55.1-66.3 cm, hvilket svarer ganske godt til længdespredningen inden for hovedparten af såvel FROSTS som mit materiale.

For så vidt angår aldersbestemmelserne, har det i høj grad skortet på sammenligningsmateriale ikke blot fra andre danske indvande, men på sådanne undersøgelser af blankål i det hele taget. De undersøgelser, der foreligger over danske ålebestande og specielt over blankål, er dels yderst sporadiske og bygger dels uden undtagelse på et alt for ringe materiale til, at de kan betragtes som egentlige bestandsanalyser. Uheldigere er det, at resultaterne af disse aldersbestemmelser, der alle er foretaget udelukkende på grundlag af skælundersøgelser, er anført uden opgivelse af metodik eller omfanget af det skælmateriale, der i hvert enkelt tilfælde har ligget til grund for aldersbestemmelserne (jvfr. pag. 29). Resultatet synes i hvert fald at være blevet, at man i de fleste tilfælde, navnlig hvor det drejer sig om ældre ål, har bedømt alderen for lavt. I afsnittet om ålefiskeriet i

»Fiskeriet i Danmark« (1948) angives (bd. II, pag. 546), at enkelte hunål hos os bliver blanke allerede 5 år efter glasålsstadiet, og at det er sjældent at finde hunål, der har været her mere end 10 år. Disse angivelser finder ikke bekræftelse gennem resultaterne af de foretagne aldersbestemmelser på blankål fra Esrum sø. Gennemsnitsalderen for det samlede materiale herfra er som allerede tidligere nævnt beregnet til 11.4 år, idet der i denne middelværdi ligesom ved alle andre her anførte aldersangivelser ikke er taget hensyn til det sidste endnu ikke afsluttede ferskvandsår, der i realiteten betegner en fuldt afsluttet tilvækstperiode, eftersom samtlige undersøgte blankål hidrører fra månederne september-november. Ialt har ikke mindre end 399 af de undersøgte ål eller 93.7 % tilhørt X-gruppen eller ældre aldersgrupper, og der er ikke fundet individer yngre end VIII-gruppen.

Vender man sig mod nabolandene, viser det sig, at Tyskland, Sverige og England er noget bedre stillet med hensyn til sådanne undersøgelser, omend man også her hovedsagelig har beskæftiget sig med aldersbestemmelser af gulål.

Den mest omfattende undersøgelse over ålens alder og vækst er foretaget af MARCUS (1919), der har aldersbestemt næsten 9000 ål fra forskellige tyske vandområder; men dette arbejde omhandler for hunålenes vedkommende, så vidt det kan ses, udelukkende gulål, og der synes ejheller siden fra tysk side at være publiceret resultater af undersøgelser, der kan tjene til belysning af det foreliggende spørgsmål.

NORDQVIST og ALM'S undersøgelser (1920) over svenske ål omfatter bl.a. et mindre antal blankål fra Gullmarfjorden på Skagerak-kysten samt fra ferskvand fanget ved Trolhättan og i Börringesjön.

Fra England foreligger dels en undersøgelse af blankål fra Cumberland (Newby Bridge, Windermere) foretaget af JESPERSEN (1926) samt en senere af FROST (1945) udført undersøgelse over alderen hos blankål fra Lake Windermere og tilstødende vandområder.

Resultaterne af undersøgelserne fra de her omhandlede vande er opført i tabel 15 sammen med resultaterne af de af mig foretagne aldersbestemmelser af blankål fra Esrum sø.

Af de svenske ål synes ålene fra Gullmarfjorden, både hvad angår størrelse og alder, at svare ganske godt til ålene fra Esrum sø, medens ålene fra Trollhättan og Börringesjön viser et stærkt afvigende vækstbillede. Dette hænger sandsynligvis sammen med det allerede tidligere berørte forhold, at de store

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bredhovede ål, hvoraf disse prøver hovedsagelig udgøres, har en relativt hurtigere tilvækst end de mindre. spidshovede ål. Disse store ål er i det hele taget karakteristiske for mange svenske indvande, og deres størrelse og hurtige tilvækst må formentlig ses som udtryk for de gode vækstvilkår, som disse fra ålens ynglepladser fjerntliggende eller vanskeligt tilgængelige og derfor tyndt besatte vande må formodes at byde ålen.

Ålene fra Newby Bridge står i væksthastighed en del tilbage for Esrum søs ål, ligesom de i almindelighed ved blankhedens indtræden synes at være mindre end disse. Formentlig må forholdet tages som udtryk for gyldigheden af den tidligere antydede regel, at dårlig vækst giver små blankål og hurtig vækst store blankål.

Mest interessant i denne forbindelse er imidlertid FROST's (1945) undersøgelser fra Lake Windermere, fordi ålene herfra på flere punkter synes at fremvise næsten identiske egenskaber med Esrum søs ål. FROST har på grundlag af såvel skæl- som ørestensundersøgelser aldersbestemt ialt 240 blanke hunål, der i længde spænder fra 47 til 97 cm og i vægt fra 210 til 2040 g. FROST's materiale adskiller sig fra mit ved en stærkere repræsentation af de store ål, et forhold som ikke bør tages som udtryk for en almindeligere forekomst af disse i Lake Windermere end i Esrum sø, men som hovedsagelig kan tilskrives en vis subjektivitet ved valget af mit materiale af store ål (jvfr. pag. 28). Ser vi bort fra samtlige ål over 65 cm's længde i såvel FROST's som mit materiale og foretager en korrektion for forskelle i længdeangivelse, bliver de beregnede middellængder, henholdsvis 57.1 og 57.0 cm. Det vil heraf fremgå, at gennemsnitslængderne på de ål, som udgør hovedparten af blankålene i de to bestande, i realiteten er identiske. En sammenligning af aldersgruppernes gennemsnitslængde for de to søer godtgør tilstedeværelsen af en tilsvarende overensstemmelse. De høje middelvær-

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dier i FROST's materiale fra XIV-gruppen og opefter kan igen henføres til virkningen af de store, hurtigere voksende åls relativt stærkere repræsentation i hendes materiale end i mit. Identiteten i vækstforhold fremgår med endnu større tydelighed af tabel 16, hvor 3-cm-gruppernes gennemsnitsalder, omfattende ål til og med 65 cm's totallængde, er anført for de nævnte bestande.

Resultaterne af disse fåtallige undersøgelser viser således tilstedeværelsen af ret betydelige forskelle, både for så vidt angår ålenes alder som deres størrelse ved vækstperiodens afslutning og blankhedens indtræden.

Slutning.

Det almindelige indtryk af såvel de her refererede undersøgelser over blankålenes alder i Esrum sø som af tilsvarende undersøgelser fra andre vandområder er, at ålen i tempereret klima er en langsomt voksende fisk, men at tilvæksthastigheden er ret variabel fra sted til sted afhængig af de på de forskellige lokaliteter rådende ernæringsforhold. Den primære årsag til den langsomme tilvækst må utvivlsomt være at søge i den kendsgerning, at ålen er den mest varmeelskende af vore nyttefisk og sandsynligvis af samtlige vore naturligt forekommende ferskvandsfisk. Heraf følger, at vækstperioden bliver kortvarig og tilvæksten langt ringere end f. eks. i Middelhavsområdet, hvor vækstperioden i hvert fald kun er afbrudt af kortere af kulde forårsagede pauser i fødeoptagelsen.

De fortsatte undersøgelser over blankål fra forskellige danske indvande antyder tilstedeværelsen af ålebestande med såvel bedre som ringere vækstforhold end i Esrum sø; men først når det indsamlede materiale er færdigbehandlet, vil det være muligt at fastslå, hvorvidt ålenes vækst og blankålenes størrelse i Esrum sø kan betragtes som karakteristisk for danske indvande.

Plate I. Otoliths of female silver eels from Esrum Lake. Øresten af blanke hunål fra Esrum sø.

Fig. 1. 53 cm, 264 g. Group X. Fig. 2. 53 cm, 260 g. Group XI. Fig. 3. 55 cm, 260 g. Group XII. Fig. 4. 55 cm, 320 g. Group XIII.

L indicates the larval stage of the otolith. L angiver ørestenens larvestadium.



Transplantation of Plaice from the Coast of Jutland to the Doggerbank in the Years 1932-1938.

By ERIK URSIN

By experimental transplantations carried out in the years 1903—1912 and 1920—1924 GARSTANG, BOR-LEY and others showed that the conditions of growth are more favourable on Doggerbank than elsewhere in the North Sea. The International Council for the Exploration of the Sea therefore appointed a subcommittee to find out whether it would be remunerative to transplant Plaice from the Horns Reef area to the Doggerbank. At a meeting in Lowestoft in 1930 the committee came to the result that a large-scale transplantation would be remunerative. The delegates from the countries interested in North Sea fishery were requested therefore to inquire whether their respective governments would give financial support to large-scale experimental transplantations.

Since necessary support from the different governments was not obtained the matter was dropped. Denmark continued however the experiments, and in the years 1932-38 marked Plaice were transplanted by the "Dana" from the Horns Reef area to the Doggerbank. The purpose was, among other things, to study the growth of the Plaice on the Doggerbank and the migrations in the area. The outbreak of the second world war however stopped these experiments, but the work was resumed after the war when the decline of the fishery for Plaice began to show. In 1949 and 1950 about 125.000 kg and about 70.000 kg small Plaice resp. were transported to the Doggerbank. The results of the commercial transplantations will be published later on. These grand-scale experiments differ so much from the preliminary experiments in 1932-38 that it seems' reasonable to give an account of the results obtained from the 1932-38 experiments in a separate publication.

The experiments were started by Professor Dr. JOHANNES SCHMIDT. After Prof. SCHMIDT'S death in 1933 Dr. Å. VEDEL TÅNING continued these researches. Preliminary surveys of the results obtained were published by Dr. TÅNING (1934, 1935).

Material. The Plaice used in the transplantation experiments were caught by well-cutters off the Jutland coast between Sylt and Horns Reef. They were transported to Esbjerg where after storage in 1-8 days in well-boxes in the harbour they were taken onboard the Danish research vessel "Dana". The positions of liberation on the Doggerbank are shown in fig. 1. The following number of Plaice was transported on deck in basins with running water: 394 in May 1932, 500 in July 1933, 341 in April 1934, and 300 in April 1938. In April 1934 286 Plaice in addition were transported in wooden boxes on the deck of the "Dana". The boxes were placed in two piles with seven boxes in each. On top of each pile was a box with ice. The boxes were covered with moistened stramin and a tarpaulin, protecting the fish against draughts. 154 of the Plaice transported



Fig. 1. Positions of liberation of marked Plaice 1932—38.
The figures are the last figure of the year of liberation.
Transplantation experiments. × Local marking experiments.
Udsættelsesteder for mærkede Rødspætter 1932—38.
Transplantationsforsøg. × Lokale Mærkningsforsøg.

		5			Tran	splantat	ion e	xp.					cal Dogger ank exp.
Year of exp No. released		32 94		933 00		934 73		938 ⁻ 100	1	932—3 1667			932—33 303
Recapture	no.	⁰ / ₀	no.	°/0	no.	º/o	no.	º/o	no.	°/0	⁰ / ₀ of no. rec.	no.	$^{0}/_{0}$ of $^{0}/_{0}$ no. rec.
1st 3 months	17	4.3	18	3.6	64	13.5	14	4.7	113	6.7	38.2	113	37.3 66.5
1st 6 months	18	4.6	30	6.0	101	21.4	37	12.3	186	11.2	62.8	120	39.6 70.6
1st year ¹)	19	4.8	64	12.8	107	22.6	47	15.7	237	14.2	80.0	147	48.5 86.5
2nd year	1	0.3^{2})	16	3.7^{2})	21	5.7^{2})	10	4.0^{2})	48	3.4^{2}) 16.2	19	12.2^{2}) 11.2
3rd year			3	0.7	3	0.7			6	0.4	2.0	2	1.5 1.2
4th year	æ .	•	-4	1.0	1	0.3	• •		5	0.4	1.7	1	0.7 0.6
Year of rec. unknown			•••		(1979)		• •	• •		<mark>.</mark> .		1	0.3 0.6
Total recapture	20	5.1	87	17.4	132	27.9	57	19.0	296	17.8	100.0	170	56.1 100.0

1) 1 year = 360 days. . *) Calculated after subtraction of the number recaptured during the previous year.

in boxes were purchased separately from a cutter and gave no recaptures, though they were transported together with the rest of the Plaice. These Plaice were possibly debilitated before embarkation. Apart from the Plaice in this unsuccessful experiment which is not included in the tabulations altogether 1667 specimens were transplanted in 1932—38. When liberated they had a length of 22—31 cm (average 26 cm). In the experiments of 1933 the VI-group plaice predominated, in the 1934-experiments the V-group, and in the 1938-experiments the III- and IV-groups.

In 1932, 1933, and 1934 moreover 491 Plaice were marked which were captured and released off the coast between Sylt and Horns Reef (23—30 cm, average 26 cm). In 1932 and 1933 altogether 303 specimens were marked (24—50 cm, average 34 cm), which were captured and liberated on the Doggerbank. The purpose of these experiments was to make it possible to compare the recovery percentage, growth etc. in transplanted and non-transplanted Plaice.

The Danish black ebonite buttons fastened with

a silver wire between the radials of the dorsal fin were used in all the experiments.

Recapture percentage. Table 1 shows the recapture percentage in the transplantation experiments and in the local Doggerbank experiments. It is about 3 times as large in the local marking experiments as in the transplantation experiments.

It might have been expected that a long transport in rainy and windy weather was one of the causes why the recapture percentage was so low in the transplantation experiments. Table 2, however, shows that there is no indication in this respect.

Nor is there any clear correlation between the recapture percentage and the mode of transportation (conveyance in wooden boxes or in tanks of running water): In the experiments of 1934 33 $^{0}/_{0}$ of the Plaice transported in tanks were recovered. The recapture percentage varied from 25 to 43. In the two experiments in which the Plaice were transported in wooden boxes 10 $^{0}/_{0}$ and 38 $^{0}/_{0}$ resp. were recaptured, 17 $^{0}/_{0}$ on an average. This percentage is considerably smaller than the recovery percentage in the other experiments of 1934, but the recovery is not noticeably

Conditions	No. released	Percentage recaptured
Transplanted in April—May	1167	18
Transplanted in July	500	17
Wind at time of liberation Beaufort Force 2 or less	1194	15
Wind at time of liberation Beaufort Force 3 or more	473	24
Wind during transport Beaufort Force 2 or less	878	13
Wind during transport Beaufort Force 3 or more	789	23
Duration of transport below 24 hours	1034	16
Duration of transport above 24 hours	633	. 21

TABLE 2.

Rate of recapture of Plaice transplanted under different conditions 1932-38.

TABLE 1. Number and percentage of fish recaptured. below the average recovery percentage in the transplantation experiments of 1932—38, which was $18 \, {}^{0}/_{0}$; it varied from $6 \, {}^{0}/_{0}$ to $43 \, {}^{0}/_{0}$ in the individual experiments.

The Plaice could stay for a short time in a tank without suffering any injury. In one of the local Doggerbank experiments the Plaice were stored for about ten hours in a tank before they were marked. 130 marked Plaice were liberated and of these 105 were recovered (81 $^{0}/_{0}$).

The Plaice from the local marking experiments were recovered more quickly than the transplanted specimens. This is obvious from table 1 in which the number of fish recovered in the course of the first three months, six months, etc., is calculated in percentage of the total number of *recovered* Plaice. It will be seen that in the local Doggerbank experiments about two thirds of the recoveries were received during the first three months after release, while in the transplantation experiments only about one third of the recaptures was received in this period. This is probably due to the fact that a great proportion of the recovered Plaice was taken with the commonly used large-meshed Danish seine which is not suitable for fishing Plaice which are much smaller than 30 cm. The comparatively small Plaice transplanted have had little chance of being recaptured immediately after release. This is an advantage since it is important that the transplanted Plaice are allowed to grow before they are recaptured. The small possibility of



Fig. 2. Growth in length. A & B: Transplantations from the Jutland coast in 1904—23 and 1932—38 respectively. C: Transplantations from the coasts of England, Holland, and Jutland in 1904—09. Length at release 25—29 cm. D: Local marking experiments off the Jutland coast in 1929—32. See text pp. 40—42.

Længdetilvækst. A & B: Transplantationer fra Horns Rev i henholdsvis 1904-23 og 1932-38. C: Transplantationer fra Kysterne af England, Holland og Jylland i 1904-09_(25-29 cm ved Udsættelsen). D: Lokale Mærkninger i Horns Rev Omraadet 1929-32. recovery of the smallest length groups just after the release results in a smaller total recovery percentage in the transplantation experiments than in the local marking experiments on the Doggerbank, since there is a certain mortality among the Plaice which is not due to fishery. This mortality results in a decrease of their number before the transplanted Plaice have grown so large that they do not pass through the meshes.

In the transplantation experiments in 1938 no Plaice were recovered later than in the second year after release. The cause is probably that the fishery in the Doggerbank area became less intensive after the outbreak of the second world war.

The English experiments carried out in 1904-09 with transplantation of Plaice from the English, Dutch and Danish coasts to the Doggerbank gave an average recovery percentage of 17 in the first year of liberty (BORLEY 1916, appendix 2, p. 116). In the individual experiments the recovery percentage varied from 3 to 38 in the first year of liberty. The Danish experiments in 1932-38 gave a recovery percentage of 14 in the first year varying from 4 to 33 °/o (experiments with less than 50 Plaice liberated are not included in the calculation). The Danish experiments in this respect therefore do not differ in any essential degree from the English experiments at the beginning of the century.

Growth. Fig. 2 shows the increase in length of the Plaice from the transplantation experiments in 1932 -38 recovered in the first two years of liberty. The curve (B) is rather uneven, but it looks as if the growth in the first year was about 11 cm and in the 2nd year about 4 cm. The rate of growth in the first year of liberty of Plaice which in the English experiments were transplanted from the Jutland coast to the Doggerbank is also shown in fig. 2 (A). In the Danish experiments the rate of growth is calculated per month of 30 days. In the English experiments calculations were made per calender month. Therefore the points of the two curves are displaced half a month. It is obvious that the growth is larger in the English experiments than in the Danish ones, especially in the autumn months in the year of liberation.



Fig. 3. Percentage length distribution of Plaice. Experiments in 1932—38. See text p. 41. Længdefordeling ved Mærkning og Genfangst. Transplantationer og (øverst til højre) lokale Mærkninger i Horns Rev Omraadet.

BORLEY (1916 p. 122) gives a survey of the growth from month to month in Plaice from the transplantation expriments in 1904—09. It appears that Plaice transplanted in May had a more rapid growth than those transplanted in April. In addition, Plaice whose length was 25—29 cm when released, showed a smaller growth rate than those which were only 15— 24 cm long when liberated.

The majority of the recaptured Plaice from the Danish marking experiments were liberated in April, some in July and a few in May. The Danish experiments therefore can best be compared with the English April experiments. The length of the recovered Plaice when released was 26.3 cm on an average in the Danish marking experiments. This figure is very near the average length for the 25—29 cm group in the English experiments. (Since this group represents the upper end of a length distribution curve, the average is supposed to be nearer to 25 cm than to 29 cm.)

Fig. 2 C shows the increase in length in Plaice which were 25-29 cm long when released, and which were transplanted from the English, Dutch and Danish coasts to the Doggerbank in April 1904-09. There is good agreement between the growth in these Plaice and in those from the Danish experiments (fig. 2 B). It has been shown (Borley and Thursby-Pel-HAM 1924 p. 57) that Plaice transplanted from the Danish coast to the Doggerbank had a somewhat quicker growth than Plaice transplanted from the Dutch coast. The growth rate shown in fig. 2 C therefore is a little less than would have been the case if marking experiments from the Danish coast only had been included. On the other hand, the number of Plaice released on Tail End was comparatively greater in the Danish experiments than in the English ones. In this part of the Doggerbank the amount of growth seems to be a little smaller than elsewhere on the Bank. This was found to be the case in the English experiments (BORLEY 1912 p. 4), and seems to be confirmed by the results obtained in the Danish experiments.

It looks as if the growth rate in transplanted Plaice released on the Doggerbank is almost the same in the two series of experiments carried out in 1904-09 and 1932-38 respectively.

HICKLING (1938 p. 51) gives a table of the average growth by quarters after release of Plaice marked in 1929—32 near the coast of Jutland (fig. 2 D). It will be seen that the amount of growth in the Plaice within this area is much smaller than in the transplanted fish. The amount of growth off the coast of Jutland was about 4 cm in the first year of liberty and about 3 cm in the second year. In the second year after liberation the growth rate in the English experiments at the coast of Jutland highly approximates the growth in the second year in the Danish transplantation experiments (4 cm). This must be due to the fact that the transplanted Plaice in the course of one year attained a size at which the increase in length is considerably reduced.

In the Danish transplantation experiments in 1932 —38 the length of the recaptured Plaice when liberated was 26.3 cm on an average. The average length of the same fish when recaptured was 32.4 cm. The increment was thus 6.1 cm. The corresponding figures in the Danish local marking experiments off the Jutland coast were 26.8, 27.1 and 0.3 cm. The extremely small amount of growth in the Jutland coast experiments is due to the the slow growth in the coastal area indicated in fig. 2 D and to a very rapid recapture of the marked fish. The average number of days in sea between marking and recapture was 47 in the Danish Jutland coast experiments as against 199 in the transplantation experiments.

The combined effect of the two factors, growth and rate of recapture, is shown in fig. 3 for the marking experiments off Jutland in 1932—34 and for the transplantation experiments in 1932—38. The figure shows the percentage frequency of the different length groups (1 cm groups) at the time of liberation and recapture. The curves of length at release comprise only the fish which were recovered. In the coastal experiments there was hardly any difference in the length distribution at the time of marking and recapture, while the difference was significant in the transplantation experiments.

TABLE 3.												
Recaptures	according	to	nationality	of	fishing	vessels.						

	Total	Percentage recaptured by vessels from					
	no. rec.	Denmark	Gr. Britain	Holland			
Transplantation exp. 1932—8	296	74	23	3			
Local Doggerbank exp. 1932—3	170	84	11	5			

TABLE 4.

Recapture and growth in relation to length at release. Transplantation experiments 1932-38.

				0				0			- -					
Length at		No.	Recaptures during first						Total		Growth	Weight at		Increment		Av. no.
	release	released	3 m	onths	6 n	nonths	3	ear	2	rec.	in length	release	recapture	in w	eight	of days
	cm	roroused	no.	º/o	no.	°/o	no.	º/o	no.	º/o	\mathbf{cm}	g	ĝ	g	°/o	in sea
	31.5	1	••	• •	• •				• •	• •	• •	• •	• • •	• •		
	30.5	1				• •		• •	• •			• •		• •	••	
	29.5	26	2	(7.7)	3	(11.5)	4	(15.4)	5	(19.2)	(4.4)	(240)	(430)	(190)	(79)	(184)
	28.5	129	20	15.5	26	20.1	29	22.5	35	27.1	4.4	210	390	180	86	134
	27.5	248	29	11.6	48	19.4	57	23.0	68	27.4	5.4	185	390	205	111	183
	26.5	293	23	7.8	37	12.6	46	15.7	58	19.8	6.3	165	380	215	130	222
	25.5	395	24	6.1	35	8.9	48	12.2	56	14.2	5.8	150	320	170	113	177
	24.5	465	15	3.1	33	7.1	50	10.8	66	14.2	7.6	135	355	220	163	267
	23.5	102			3	2.9	6	5.9	8	7.8	(9.9)	120	(405)	(285)	(238)	(283)
	22.5	7		• •	• •	• •	× .	••	• •	••	••		••	• •	••	••

Recaptures according to nationality of fishing vessels. By far the majority of recaptures of Plaice from the Danish Doggerbank experiments were made by Danish fishermen (table 3).

The share of the recaptures of the British vessels was twice as large in the transplantation experiments as in the local Doggerbank experiments. The cause of this is not known. The share of the trawlers in the recapture of small Plaice was not larger than that of the cutters using the Danish seine.

BORLEY and THURSBY-PELHAM (1925 p. 60) gave a survey of the share of the different nations in the recoveries from the English transplantation experiments to the Doggerbank in 1903-24. In all these years the share of the British vessels was about 90 $^{\circ}/_{0}$. Before World War I no transplanted Plaice were recaptured by Danish fishermen, although there are 898 recoveries from the experiments in 1903-12. Of 385 recovered Plaice from the experiments in 1920-24 9 % were taken by Danish vessels. In the Danish experiments in 1932-38 about three fourths were recaptured by Danish and one fourth only by British vessels. This is a consequence of the increasing Danish share of the Doggerbank fishery. According to the international fishery statistics the Danish share of the Plaice fishery in the North Sea has risen from $4 \, {}^{0}/_{0}$ in 1903 to 33 % in 1938. This rise is not as considerable as the rise in the Danish share of the recaptures of marked Plaice from the Doggerbank experiments. This is especially due to the fact that the Danish seine cutters from Esbjerg in the last decades have fished intensively on the Doggerbank. It should also be borne in mind that the Danish marking experiments are scattered over the Dogger, while the English experiments were made almost exclusively in that part of the Doggerbank which is situated farthest from Denmark.

Dispersion. The Plaice from the transplantation experiments in 1932—38 distributed themselves 40 nautical miles on an average in the period between liberation and recapture. The local Doggerbank fish migrated 33 nautical miles on an average. The transplanted Plaice were, however, 60 days on an average longer in sea than the local ones (199 days as against 139). This presumably counterbalances the small difference in the dispersion. 47 °/₀ of the recaptures of marked transplanted Plaice were made less than 30 nautical miles from the place of liberation. This was the case of 57 °/₀ of the recoveries which were made in the course of the first six months after release, and of 32 °/₀ of those which were made later on.

Recapture, growth etc. in correlation to the length of the Plaice when released. Table 4 and fig. 4 show that the recapture percentage in the transplantation experiments in 1932—38 depended on the length of the fish when released, so that the largest fish gave the highest recapture percentage. This is a common phenomenon when marking small Plaice in the North Sea, both at the coasts and in the open sea (see HICK-LING 1938 p. 36). The phenomenon has been explained in different ways by the different authors, according to the conditions under which the experiments were made. In the Danish transplantation experiments the most important cause probably was that it was difficult to catch the smallest Plaice by the large-meshed Danish seine in the first time after liberation. In accordance herewith fig. 4 shows that the initially small fish were caught later on an average than the large ones.

BORLEY (1916 p. 17) gives the percentage of Plaice transplanted in April—June 1904—09 which was recaptured in the first year after liberation. Of the length groups 15—19 cm, 20—24 cm and 25—29 cm 11, 18 and 27 $^{0}/_{0}$ respectively were recaptured in the course of this period. In the Danish transplantation experiments $10 \, {}^{0}/_{0}$ of the fish measuring $20-24 \, \mathrm{cm}$ when released and $17 \, {}^{0}/_{0}$ of those which were $25-29 \, \mathrm{cm}$ long were recaptured in the first year of liberation. These figures are considerably lower than the corresponding English figures. As mentioned above the average percentage of recaptured fish was almost the same in the Danish and the English transplantation experiments. This is due to the fact that somewhat larger Plaice were used in the Danish experiments than in the English ones. None of the fish in the Danish transplantation experiments were smaller

than 22 cm when released. In the Plaice from the transplantation experiments in 1932–38 the amount of growth in length declines with increasing length when released (fig. 4). As said above, the English experiments showed a slightly smaller amount of growth in the largest fish than in the rest (BORLEY 1916) and it is supposed that a similar difference in the rate of growth in large and small Plaice has manifested itself in the Danish experiments, but the material is too small to show this difference. The difference in growth in the period between marking and recapture in fish of different size groups shown in fig. 4 is, however, far greater than would be expected if it was due to a difference in the rate of growth in large and small fish. It must therefore be due to the fact that the larger fish have been in the sea for a shorter period of time than the small ones. This agrees with the fact that the average number of days in the sea between marking and recapture and the average amount of growth in length varies in the same way with the length of the fish when released (see fig. 4).

The weight of the Plaice when recaptured is calculated on the basis of curves of the ratio between length and weight in Plaice from the Horns Reef area (small fish) and from the Doggerbank (large fish). The weight of the fish when recaptured is calculated on the basis of the *average* length at recapture of each group of length at release. As the weight is, however, no linear function of the length (weight increases more rapidly than length), the average weight is calculated a little too low. If the weight is calculated on the basis of the length distribution curve for all the recovered fish so that the weight of each cm-group is calculated separately, the average weight of the fish when recaptured will be about 400 g.

The increment in weight in grammes (table 4) in the period between marking and recapture varies only slightly from one length group to the other, and not so much as to show any correlation between this increment and the length of the fish at liberation. The increment in weight expressed in percentage of the weight at liberation is greatest therefore in the fish which were smallest when released. This is of importance to transplantations made on a commercial basis, since here the increment in weight per kg fish released is more important than the increment in weight per specimen.





Fig. 4. Transplantation experiments in 1932—38. Genfangstprocent (nederst), Længdetilvækst (næstøverst) o.a. i Forhold til Længden ved Udsættelsen.

Percentage weight recapture. Calculated on basis of an average weight of 400 g per specimen when recaptured.

-	Release	÷	Recapture						
Length cm	Weight	No. per 1000 kg	4/0 of no.released	Per 1000 k no.	g released kg	% of weight of fish released			
28.0 - 29.9	215	4700	26	1200	480	48			
26.0 - 27.9	175	5700	23	1300	520	52			
24.0 - 25.9	140	7100	14	1000	400	40			
22.0 - 23.9	120	8300	7	600	240	24			

Since the result of the transplantation is determined by the ratio between the recapture percentage and the percentage increment in weight it is of interest to watch this ratio for Plaice of different length at liberation. Since the weight at liberation is known the number per 1000 kg can be calculated for each group of length at liberation. When recovered the Plaice are estimated to weigh 400 g per specimen on an average, irrespective of their length at liberation, if this varies from 22 cm to 30 cm. As the percentage recovery for each length group is known it can be calculated how many of the released Plaice are recaptured, and how much they weigh in all when recovered. The recovered weight percentage can then be calculated. Table 5 gives such a calculation for 2-cm-groups on the basis of the material from the transplantation experiments in 1932-38. It will be seen that the length group 26.0-27.9 cm gave the highest weight percentage recapture.

The difficulties and costs involved by procuring Plaice of a certain length are, however, of great importance to transplantations on a commercial basis. Therefore, Plaice of 26—27 cm length are not always preferable for transplantation from the Jutland coast to the Doggerbank, though the experiments in 1932 —38 seem to show that Plaice of just this length are most suitable for transplantation.

Some marked Plaice may lose their buttons, and some buttons from recovered Plaice were probably not returned. Again, the mortality among the marked Plaice may have been higher than that of the untreated fish. This involves that the recovery percentages mentioned in this survey are smaller than they would have been if all the recovered marked Plaice had got into the hands of the laboratory.

The paper was translated by Mrs. Agnete Volsøe.

Summary.

During the years of 1932—38 about 1700 marked Plaice were transplanted from the Horns Reef area to the Doggerbank on board the "Dana". Some were transported in basins with running water and some in wooden boxes on the deck.

When Plaice af equal length etc. are compared, the growth rate was found to be almost the same as in the English transplantation experiments carried out in the years 1904—09, the results of which have been published by BORLEY a.o. The percentage recaptured was, however, lower in the Danish experiments than in the English ones.

As in the English experiments the growth rate of transplanted Plaice was considerably higher than that of the untransplanted Horns Reef stock. The difference in yield produced in this way is strongly increased by the more intensive fishing in the Horns Reef area leaving the Plaice a very short time to grow up before being recaptured. The two factors, rate of growth and rate of recapture, cooperate so that in the coastal experiments there is hardly any difference in the length distribution at the time of release and recapture, while the difference is considerable in the transplantation experiments (fig. 3).

The highest percentage recaptured $(27 \ ^{0})$ is obtained when large Plaice (27-28 cm) are transplanted, but the highest percentage weight increment (ab. 200 0) when small Plaice (23-24 cm) are used. Therefore, a calculation has been made (table 5) showing that transplantation of fish of the length group 26.0-27.9 cm gave the highest percentage weight recapture $(52 \ ^{0})$.

The share of the Danish fishing vessels in the recapture of the transplanted Plaice was $74 \, {}^{0}/_{0}$ while that of the British vessels amounted to $23 \, {}^{0}/_{0}$ and that of the Dutch to $3 \, {}^{0}/_{0}$.

The transplanted fish did not show any tendency to return to the Jutland coast or other coastal areas. After all, they did not disperse more than did the local Doggerbank Plaice.

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Dansk Oversigt.

I Aarene 1932—38 omplantedes der af "Dana" ca. 1700 mærkede Rødspætter fra Horns Rev Omraadet til Doggerbank. Nogle transporteredes i Bassiner med rindende Vand og andre i Fiskekasser paa Dækket.

Væksten viste sig at være omtrent som i de engelske Omplantningsforsøg, der udførtes i Begyndelsen af Aarhundredet, og hvis Resultater er offentliggjort af BORLEY o.a., forudsat at man sammenligner Rødspætter af samme Længde. Genfangstprocenten var derimod lavere end i de engelske Forsøg.

Ligesom i de engelske Forsøg viste det sig, at de omplantede Rødspætter voksede betydelig hurtigere end Fiskene i Horns Rev Omraadet. Det viste sig ogsaa, at Rødspætterne ved Horns Rev opfiskedes betydelig hurtigere end de omplantede. Sammen med Forskellen i Væksthastighed bevirker dette, at medens der i Omplantningsforsøgene er meget stor Forskel paa Fiskenes Længdefordeling ved Udsættelsen og ved Genfangsten, er der næsten ingen Forskel paa Udsættelses- og Genfangstlængderne i Horns Rev Omraadet (Fig. 3).

Den højeste Genfangstprocent (27 °/₀) opnaaedes ved Omplantning af temmelig store Rødspætter (27— 28 cm), medens den største procentvise Vægtforøgelse (c. 200 °/₀) opnaaedes ved Anvendelse af smaa Fisk (23—24 cm). En Beregning har vist, at Længdegruppen 26,0—27,9 cm frembragte den største Genfangst-Vægtprocent (52 °/₀).

74 0 af de genfangne omplantede Rødspætter blev taget af danske Fiskere. Engelske Fartøjer tog 23 0 og hollandske 3 0 .

De omplantede Fisk viste ikke nogen Tendens til at vende tilbage til den jydske Kyst eller til andre Kystomraader. De vandrede i det hele taget ikke mere end de lokale Doggerbank-Rødspætter. Index to the Reports of the Danish Biological Station

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